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THE ECOLOGICAL NICHES OF CERTAIN SPECIES OF HORSE-FLIES (*DIPTERA, TABANIDAE*) IN THE KAMPINOS FOREST NEAR WARSAW

Z Zakładu Ekologii PAN w Warszawie

I. INTRODUCTION

Tabanidae belong to the well-known groups of flies and have been mentioned in almost all textbooks on medical entomology for a considerable period. In certain areas they form a far more serious sanitary problem than *Culicidae* or *Melusinidae*. Many scientific institutions are carrying out research on the ecology of *Tabanidae*. Although there are numerous works on this subject there has so far been no complete study of the ecology of Central European species, and the data given in textbooks are often out-of-date. The following work has two aims — the first, to supply data on the ecology of common European species, and the second, to review the opinions hitherto held on the ecology of this group on the basis of general ecological and physiological conceptions.

Research was finacial and carried out under the leadership of Professors K. Petrusewicz and K. Tarwid. I obtained subsidies for this work first from the Zoological Institute of the Central School of Rural Economy in Warsaw, and later from the Department of Ecology and the Zoological Institute of the Polish Academy of Sciences in Warsaw. The following took part in collecting material from the area investigated: E. Dauksza, A. Gajewski, S. Leszczyński, W. Mikołajczyk, A. Mońko, W. Sujkowska, K. Trojan, R. Trojanowa, H. Bańkowska and K. Trojan helped me to compile the statistical material. I should like to express my gratitude to all the above, and to the institutions concerned. My thanks are also due to the forest administration authorities of Kampinos, in particular to Mr. T. Więckowski, the forest intendant, for his hospitality and help to all the research workers throughout the entire period over which material was collected. I would also like to offer my sincere thanks to Professor T. Jaczewski for checking the manuscript of this work, and for his many valuable comments. Research work, which forms the basis of this work, was carried out in the Kampinos Forest near Warsaw from 1951—1955. This Forest forms one of the most interesting natural districts of Central Poland, and was described from the geographical standpoint by Kaczorowska in 1926. The flora and phyto-sociological relations there were examined by Kobendza in 1930. An exact description of the area and the vegetation groups of the Forest were given in these two works.

The most vital factor influencing the formation of the fauna of this area is the genesis and history of the Forest. The origin of the Forest is connected with the post-glacial period, at this time the European lowlands were covered with great patches of forest. The tajga of the East European lowlands and the forests of Poland were formed more or less in the same period, and their flora originates from similar centres (Soczawa, 1953). The forests of the tajga are even today, at least in places, entirely primaeval in character, and are to a very small extent disturbed by human activity, but the forests of Central Europe have been altered by human economy. The Kampinos Forest is no exception in this respect. About 80% of its area is covered by pine woods, and for a long time now the forest stand of these parts of the Forest has been regulated by forest economy, and it is therefore impossible to speak here of the primaeval Forest. The situation is different, however, in the marshy sections covered by alder groves. Felling is carried out here on a lesser scale, and renewal of the forest and its further development are not controlled. No afforestation by additional species of tree is introduced, and for this reason it is possible to speak of the more primaeval character of the alder groves.

The Kampinos Forest once formed a large forest area, bounded by the Vistula and Utrata rivers. Colonisation of this area brought about gradual clearing of the forest and cultivation of the arable portions of the area. In former times the area was protected as royal hunting grounds, but during the 19th and 20th centuries it has been subjected to intense exploitation, which will lead to serious damage to the forests.

For the purposes of the research carried out, it is essential to understand what the Forest represents as an environment for the *Tabanidae*. The most important point here is the age of the Forest, and its connection with the tajga, in particular the tajga of the Russian plateau. This applies both to the flora and the fauna which colonised these areas ofter the recession of the glacier. It is probable that the breaking up of the dense forest belt in Europe took place in relatively recent times, and therefore the fauna of the Forest and the tajga may be expected to be related. The great areas of marsh encountered today in the Forest may form a reserve of tajga fauna. Tarwid (1952) drew attention to the tajga characteristics of mosquitoes (*Culicidae*) occurring in this area. I discovered many species forming a tajga element when I was collecting *Diptera* in the Forest, amongst which the most interesting were the *Thereva nigripes* Loew., *Psilocephala nigripennis* Ruthe., *Solva marginata* (Walk.).

As the *Tabanidae* of the Kampinos Forest were thoroughly examined during the course of our research work, they may serve as material for a more detailed analysis.

One of the ways of carrying out a zoo-geographical analysis is to link up a certain systematic group with a definite environment, in the broadest sense of this word, that is, understood as a landscape. In the case of research on specialised phytophagytes, their parasites, predaceous species etc. (Nowikow, 1953), the matter of course admits of no discussion, but in a great number of cases the connection of the group examined with the areas in question is not too clear. This applies to research on *Tabanidae*. The fact of the connection of certain systematic groups, especially of the *Tabanus* L. genus, with definite areas is well known, for example species belonging to the sub-genus *Therioplectes* Zell. occur in the mountains of South Europe and the Caucasus Mountains. The majority of species of the sub-genus *Ochrops* Szil. is connected with steppe or semi-desert areas. In the same way the *Tylostypia* End. embraces several groups of tajga species. The knowledge obtained up to the present of the ecology of adult forms is not sufficient to establish the causes of the occurrence of particular groups in these or other territories. It is possible that the causes of this connection may lie in the special characteristics of the biology of *Tabanidae* larvae. The lack of data on the ecology of the *Tabanidae* larvae, makes it difficult, however, to prove this opinion.

Preliminary research on the *Tabanidae* of the area round Warsaw was carried out comparatively recently (Trojan, 1955). The list published contained a relatively large number of species occurring in the Kampinos Forest. At present the list of species inhabiting the Forest area is as follows:

Chrysops caecutiens (L.)
Chrysops pictus Meig.
Chrysops relictus Meig.
Chrysops sepulchralis (Fabr.)
Chrysops rufipes Meig.
Tabanus (Ochrops) fulvus Meig.
Tabanus (*Ochrops*) *rusticus* L.
Tabanus (*Tabanus*) *maculicornis* Zett.
Tabanus (*Tabanus*) *bromius* L.
Tabanus (*Tabanus*) *miki* Brau.
Tabanus (*Tabanus*) *autumnalis* L.
Tabanus (*Tabanus*) *sudeticus* Zell.
Tabanus (Tabanus) bovinus Loew
Tabanus (*Tabanus*) *spodopterus* Meig.
Tabanus (*Tylostypia*) *confinis* Zett.
Tabanus (*Tylostypia*) *luridus* Fall.
Tabanus (*Tylostypia*) *solstitialis* Schin.
Tabanus (*Tylostypia*) *tropicus* Panz.
Tabanus (*Tylostypia*) *fulvicornis* Meig.
Tabanus (*Tylostypia*) *montanus* Meig.
Tabanus (*Tylostypia*) *distinguendus* Verr.
Chrysozona hispanica (Szil.)
Chrysozona pluvialis (L.)
Chrysozona crassicornis (Wahlb.)
Chrysozona italica (Meig.)

The occurrence in the Kampinos Forest of 25 species of the *Tabanidae* has thus been confirmed up to the present, among which are four species not so far listed in Poland, i.e.: *Tabanus miki* Brau., *T. confinis* Zett., *T. montanus* Meig. and *Chrysozona* *hispanica* (S z i l.). Of the remaining species, the following had not so far been known in Central Poland: *Tabanus spodopterus* M e i g., *T. distinguendus* V e r r. and *Chrysozona crassicornis* (W a h l b.)

Eleven species, that is, 44% of the species occurring in this area, are tajga or forest species. The *Chrysops sepulchralis* (F a b r.) belongs to these, being represented in the Kampinos Forest by melanic forms characteristic of marshy areas. Amongst the species belonging to the *Tabanus* L. genus, the most interesting are the *T. confinis* Z e t t., a typical representative of the tajga (its habitat in the Kampinos Forest is the most westerly in Europe), together with that of the *T. montanus* M e i g., which is a typical relic of the tajga. Faunistic data on its occurrence in other parts of Poland are based on erroneous observations.

Only two species connected with the steppe occur in the Kampinos Forest. i.e. less than 10%. These are the *Tabanus fulvus* M e i g. and *Chrysozona hispanica* (S z i l.).

Species of European origin form about 50% of the total number of species, the most common being the *Tabanus bromius* L. and *Chrysozona pluvialis* (L.)

The Kampinos Forest is therefore inhabited by three elements heterogenous in origin. The tajga element, the oldest, occurs mainly in the spring, then after the disappearance of the spring species, the summer species, the European element, appear. The steppe element, very poorly quantitatively represented, forms only a small addition to the general composition of the species. The lack of other tajga species in the Forest, such as are found in other parts of Poland, e.g. the *Tabanus borealis* L o e w., *T. plebeius* F a l l. and *T. tarandinus* L., which are defined as post-glacial relics, bears witness to the transformation which took place in this area. These undoubtedly formerly occurred throughout Poland. In spite of this the Kampinos Forest may be treated as a tajga-type environment in which numerous tajga species, usually occurring in great numbers, have been preserved.

The aim of this research work was to obtain a knowledge of the ecology of the *Tabanidae*, connected with the forest areas. The Kampinos Forest forms in this respect a typical object suited to research of this kind.

Work on the ecology of the *Tabanidae* has been undertaken in three main areas in the world — North America, the Sowiet Union and South Africa. In other areas research has been carried out intermittently, and as a rule takes the form of minor ecological contributions. J. S. Hine began publishing his first ecological works in 1901, and gave a series of observations on the ecology of the *Tabanidae* based chiefly on collections made during entomological expeditions. They deal with the place, period of occurrence and activity of attack of the respective species. This author also pointed out that the males most often escape the notice of collectors during the collections made on such expeditions. He also gave the circumstances in which it is possible to find the males in the area concerned.

C. A. Mosier and T. E. Snyder carried out ecological research work in Florida from 1915—1920. They drew attention to the way in which the *Tabanidae* recognise the host by sight, having been attracted by the moving vehicles. They also discussed the causes of mass occurrence of the *Tabanidae* in certain areas completely devoid of large mammals, and presumed that not all species of the *Tabanidae* must, in fact, draw blood in order to develop the ovaries. T. H. Jones and W. S. Bradley also carried out ecological observations of *Tabanidae* in Louisiana. The work of North American authors during the period 1913—1930 on the ecology of *Tabanidae* (Osburn, 1913; Cameron, 1926; Stone, 1930) does not contribute any new ideas or data to the views held up to that time on the ecology of *Tabanidae*. In recent times three authors in the U.S.A. have been working on the ecology of *Tabanidae*. The idea of the numerical seasonal dynamics of the *Tabanidae* in Panama occurs for the first time in the work of C. B. Fairchild (1942). This author accepts a collection made over a period of two days as a basic test for the purpose of defining the numerical occurrence of the respective species. The work of N. S. Bailey and S. W. Frost is of a compilative character and does not introduce any new ideas to the problems described.

The greatest achievement of the North American school of entomologists working on the ecology of the *Tabanidae* is the number of works published. The authors were mainly specialists in faunistics or systematics, and the material they published, although dealing with ecological problems, is treated not so much from the point of view of ecology as from faunistics. In no case were thorough quantitative investigations made, with the exception of the later work of C. B. Fairchild (1942). This only permitted the authors to confirm the fact of occurrence or non-occurrence of certain species in the area examined, or the mass character of the occurrence. The methods of collection used in such investigations was to catch the insects flying towards the collector, or attacking horses or cattle.

Investigation of the ecology of *Tabanidae* in Europe was carried out almost entirely in East European area. Research work was begun by J. Porczyński, who published a short ecological and biological monograph on *Tabanidae*. Some of the data contained in this publication is even today of great value from the ecological point of view. He also worked on the methods of collecting *Tabanidae*, and of these the "pool of death" method has preserved its usefulness up to the present. In more recent times the ecology of *Tabanidae* has been the object of intensive research work in the Soviet Union, on account of the possibility of these insects being carriers of various infectious diseases. The works of N. G. Ołsufiew and A. W. Gucewicz should be given priority of mention here. Recently parasitological problems connected with *Tabanidae* have become less important on account of the various prophylactic measures perfected during research work, nevertheless the ecology of *Tabanidae* still continues to be the object of fairly intensive research. Z. M. Denisowa (1952) has dealt with it from the physiological standpoint. K. W. Skufin (1949, 1951, 1952a, 1952b) has published a series of interesting works on the ecology of *Tabanidae*. He has examined the problems of collection methods, seasonal dynamics, and the regularity of the insects' distribution per area. His latest research on the ecology of *Chrysops relictus* Meig. he attempts to define the connection of this species with its environment. W. W. Szewczenko (1953) examined the ecology of the *Tabanidae* of Ala-Tau and Kara-Tau mountains. The works of Russian, and later Soviet investigators exhibit a much closer linking of parasitological and ecological problems than the work of the American school. The first period, up to the end of the last World War, is characterised by works of a clearly parasitological aspect. The sanitary importance of the research work undertaken caused the quantitative treatment of this subject to far more precise, and a far greater amount of material was collected for each individual work than is the case with American authors.

The post-war period is characterised by research on the *Tabanidae* in connection with certain ecological theories, mainly concerned with questions of area distribution of these insects.

Interesting results were obtained by a group of mainly English entomologists working in South Africa, the reason for their studying the ecology of these insects being the parasitological importance of the *Tabanidae*. This research work was carried out with a great deal of ingenuity, using the quantitative methods of collection, especially in the case of the group led by A. J. Haddow, and a large amount of data was contributed to the ecology of *Tabanidae*, particularly as regards their vertical distribution and activity over a period of 24 hours.

Research on *Tabanidae* was carried out only spasmodically in other countries. Data published by P. V. Isaacs on the ecology of *Tabanidae* in India correspond more or less to similar material given by faunists in the first years of the twentieth century, and the subject is treated in a similar manner in the work of H. Wentges (1952) on the mating flights of the *Tabanus sudeticus* Zell. in Bavaria.

The development of quantitative research on the ecology of *Tabanidae* which took place in the Soviet Union and in South Africa, together with a great precision in results obtained, brought about an impoverishment of the methods employed. Only the females searching for hosts were examined. All the conclusions contained in these works were based on material obtained from females only, collected by means of food bait. Attempts at increasing the number of methods of ecological collections of *Tabanidae* undertaken by the Soviet research workers N. G. Olsufiew and K. W. Skufin have not so far been successful, and for this reason the problems dealt with are very limited in scope, or refer to section problems only. In none of the works has any attempt been made to define the living environment of the *Tabanidae*. The influence of certain generally accepted micro-climatic factors on the phenomena of the flight activity, or the influence of the vegetation mantle on distribution in the respective environments is assumed.

The author of this work, in beginning investigation of the ecology of these insects, made it his aim to combine the various connections and ecological dependences so far revealed into one whole. In reviewing the numerous works on the ecology of *Tabanidae*, or other animal groups, it is necessary to consider what exactly is understood by the term "ecology" of a certain systematic group. The range of problems taken into consideration in such a case is very wide, and it is out of the question to deal with them in one work, however broad in scope, the more so as not all problems can be examined using the same material. It is therefore always necessary to make a choice of ecological problems, but as such a choice should not be governed by chance as regards investigation of the elementary ecological properties of *Tabanidae,* I have endeavoured to refer to the general conceptions of the connection of the organism with the environment, one of them being the theory of the ecological niche.

The idea of the ecological niche is not constantly synonymous (Trojan, 1956). It was introduced by Ch. Elton (1927) "the niche defines the place of the animal in the biotic environment, its relation to its food and enemies". In addition to the idea of the ecological niche, we encounter different definitions of the connection of the organism with its environment, e. g. habitat, to define the place in which the given species lives. E. P. Odum (1954) defines the causes of the connection of the species with the group, or biocenosis. They result, in his opinion, from specific structural, physiological and psychological adaptations. Both the "living place" and the place of the given species in the biocenosis are defined by the adaptation of the species. The expression "living place" (habitat) is used in the sense of the environment in which a given species may be encountered, in connection with faunistic research, rather than in the sense of an exact ecological term.

In research on the ecology of *Tabanidae,* in order to define the connections of the respective species with the environments in which they live, it will be more convenient to use the idea of an ecological niche, but in a slightly different form. By an ecological niche, I imply a group of conditions occurring in a given environment, with which the species is actually connected, which play an important part in its life, and to which it must in the first place adapt itself. Thus both the connection of the given species with the biocenosis, its dependence on the micro-climate etc. enter into the picture.

Comparatively important conclusions as to the method of investigating the environment in which the given species occurs can be drawn from such a definition. The ecological niche, or the environment of the species, does not consist of everything which the investigator may observe in the surroundings of the given species, but only that which plays a decisive part in the life of this species. A description of the environment should only include those elements which are essential for the life and continuation of the species. This involves the investigator at the beginning in methodological difficulties, forces him to select certain factors, to form a theory as to the character of the connection of the species under investigation with the chosen features of the environment, but also to a great degree eliminates freedom of choice of factors for investigation, and makes it possible to obtain an exact knowledge of the environment of the species.

In practical ecological research work, a different method of treating these connections is in general applied. The investigations concern the environment as a whole, and its division into small units. The treatment of this subject by W. Tischler (1949) may be cited as an example. He divides the environment into biotopes, biotopes into biochoria, biochoria into strata, strata and supplementary biochoria into structural sections (Strukturteile) etc. The corresponding species encountered in these units are then classified as those proper to the given biotope (Biotopeigene), those temporarily staying there (Besucher) entering from neighbouring biotopes (Nachbarn) and occurring accidentally (Irrgäste). There are many such classifications and treatments, but they are in general very similar. First the environment is examined and suitably classified, then the species occurring there are forced into the framework of such classification. The result of such research work is the classification of the species according to where they are caught in the environment under investigation. Such classification expresses very little of the real connection of the various species with their environment. Classification is not a method of investigating ecological connections in natural conditions. Such classification is fundamentally artificial, since part of the species examined in this way always appear not to possess an environment of their own, and treating them as accidental visitors if not of great help. In beginning our investigations from the environment, we must make a great effort to examine it from all possible angles. This work, however, is as a rule beyond the possibilities of ecologists, and when treated, for instance, from the standpoint of climatology, does not always supply a sufficient basis for the ecology of animals, even when the "most scrupulous examination" has been made. It is far more economical to begin such research with the species. The problem of classification is thereby avoided, but in practice it will be found that each species has its own environment, which it chooses from a group of the most heterogenous factors occuring in a given biotope. The methodological correctness of such treatment is indicated by statements made by F. P e u s (1954) and N. P. N a u m o w (1955).

Such treatment of the connection between the species and its environment has further prospects, especially for the systematics. The generally accepted views of specialists in this science with regard to a species assume the existence of differences in ecology between various species. Examination of the ecological niche of closely-related species makes it possible to check our views on the distinctness of species, the boundaries between which are often established only on the basis of a morphological analysis.

The material I have gathered over a period of five years' work in the Kampinos Forest near Warsaw has made it possible to establish wath is, in my opinion, the basic connection of the *Tabanidae* with the forest environment. A series of suggestions regarding the causes governing ecological phenomena are put forward, and methods of investigating the problems in question have been worked out.

II. METHODS

One of the fundamental difficulties arising during research on the ecology of the *Tabanidae* is undoubtedly choice of method. This applies both to the collection technique used for the *Tabanidae*, to means of differentiating between tests, and to drawing conclusions from the material collected (T r o j a n, 1956).

In literature on this subject three variants of collection methods are encountered; i.e. collection using a human being as bait, the Skufin trap, and the pool of death method. In the majority of ecological works all material is collected by means of sweeps using a human being as bait. The Skufin trap, which has been known for a few years only, has not so far been used in ecological collections, and the pool of death, although known for many years, is not an instrument of research in constant use, chiefly on acco unt of the difficulty in determining the material cought by this means, and the wide variations in the number of insects in a test pool, which makes it difficult to interpret the material and draw conclusions from it. A second difficulty is encountered in choosing a suitable size of test. In making collections using the collector himself as bait, the size, or duration of the test, is defined by the time during which the material was collected. This time varies in different works. The following times were used as tests: a 4-hour trip (Skufin, 1949), 2 whole days (Fairchild, 1942), 20 minutes (Gucewicz, 1947), (Skufin, 1952), a day, an hour (Haddow and others, 1950). In many cases the collection time of the test, which is of fundamental importance in comparing numerical results, is completely fluid, and on this account makes comparison impossible.

Many new methods of quantitative collection were used during the research work carried out in the Kampinos Forest. This made it possible to define certain ecological problems and in some cases at least, to solve them. Collections using a human as the bait is the method most of ten used to collect *Tabanidae*. The results obtained are mainly influenced by the attractiveness of the bait. It would appear that the smell of the bait is of minor importance in such cases, since the *Tabanidae* recognise their host by sight. The most important factor is the clothing worn by the human bait. During collections the collector should always form a more or less uniform mass, which can be effected by wearing clothing uniform in colour. The colours attracting the *Tabanidae* most are black and navy-blue. Light colours, as would appear from the results of J. Porczyński's observations (1915) attract *Tabanidae* to a lesser degree. The physiological state of the *Tabanidae* population also exerts an influence on quantitative results. Material obtained by this method only refers to the females searching for a host. Results also depend on the activity of flight of the females, which is connected with definite micro-climatic conditions. The area in which collection takes place also influences the value of the quantitative tests. Open areas with good visibility permit the *Tabanidae* to find their hosts more easily than in densely overgrown areas. All these objections with regard to collection using a human as bait make it difficult to arrive at a true estimate of the connection between the test obtained and the actual number of insects present in the given area, and the results can be seriously distorted by the above mentioned circumstance.

A modification of the above method is the use of a horse or cow instead of a human being as bait. A description of a new method of quantitative collection of these insects (Skufin, 1951) has recently been published, that is, the Skufin trap. This consists of a wooden frame covered with black material, the whole slightly resembling a cow in appearance. It is a most convenient bait and attracts *Tabanidae* in large numbers. Material can be collected automatically by means of a fly-paper secured to the upper part of the Skufin trap. Individuals which in attempting to attack the trap from below penetrate to the inside of the tent-like construction formed by the material stretched over the wooden frame, adhere to this paper. In addition the *Tabanidae* flying to the trap can be collected straight from its walls. In using the Skufin trap, one of the disadvantages of using a human as bait is removed, since the attraction of the bait is constant. In addition, the trap can be attended to by several people, since collection depends only to a small extent on the individual ability of the collector. Almost all the *Tabanidae* flying to the bait were caught on the sides of the trap. Individuals beaten off by strokes of a net almost always returned immediately to the trap.

Conclusions can be drawn as to the numerical occurrence of *Tabanidae* using the above-mentioned methods of collection, only when taking into consideration the factors, mentioned above, which alter the value of the tests, or by carrying out collection in comparable conditions.

"Pools of death" were introduced by J. Porczyński (1915) as a method of destroying *Tabanidae* in steppe regions, where there is only a small number of stretches of water. Later attempts at using this method for ecological research did not yield good results, as specimens coated with petroleum are difficult to determination. Results obtained during collection from a pool of death depend on the way in which the insect takes up water. Of the Polish species, only representatives of the *Tabanus* L. and *Chrysops* Meig. genera hit the surface of the water with their bodies in their downwards flight. The number of individuals caught depends on the insects' need for water, so that the largest numbers are caught during the greatest flight activity. In addition, the distance of the water from areas attractive to the *Tabanidae*, and the amount of water in the area accessible to the *Tabanidae*, influence the quantitative results obtained. Material obtained by this method applies both to males and females, and therefore gives a fuller picture of the life of the population than methods based on the use of food as a bait.

"Panes of glass" also give good quantitative results during the months in which mass flight of the *Tabanidae* takes place. This method has been used for the first time for the collection of *Tabanidae*. Collection is carried out by means of square of glass 1 sq.m. in area, four of which were hung on a pole. The surface of the panes was covered with the sticky substance used in orchards. Insects adhering to the panes were collected twice daily, at dawn and at dusk. Insects with small body-measurements adhered to the panes, chiefly species belonging to the *Chrysozona* Meig. and *Tabanus* L. genera, similar to the *T. bromius* L. in size. Material obtained by this method is very convenient for statistical work, and permits of investigation being made of phenomena connected with the areas and activity of flight, divorced from bait of any description.

The quantitative scoop as a means of ecological collection of the *Tabanidae* has not so far been used, as this method is not successful in catching these insects at all, or only in such small quantities that it is impossible to draw any conclusions from the material collected. The quantitative scoop gives good results only when collection is carried out in the nocturnal resting-places of the *Tabanidae*. In the Kampinos Forest, these are the clumps of trees and bushes surrounding the meadows. The insects generally settle on tree-tops and this is where the sweeps with the scoop should be directed. Practically speaking, this is only possible in the case of young trees which can be bent down to the ground by means of a long-handled hook.

Other methods were tried out in addition to the foregoing, for instance, pieces of coloured cardboard covered with adhesive, and fly-papers attracting by smell, were hung up in appropriate places, and collection using a bright light, but none of these gave any results.

Material for quantitative collection was obtained by mass methods, and in the case of each particular method the size of the test was defined. Methods involving the use of bait (collection using a human as bait, the Skufin trap, and pool of death) were made with the size of the test being defined by the time taken for collection. No typical test was established as is the case with certain other authors. The only criterion used in establishing the size of the test was its effectiveness for the purposes of the problem being worked upon, and the principle of making the most economical use of the time. When working on the seasonal dynamics of *Tabanidae* a longer 2-hour test was used, which permitted the elimination of quantitative fluctuations resulting from the insects approaching the bait in aggregations, and yet supplied ample enough material to establish the numerical relation between the various species.

A test of 10-minutes duration was used to discover the dependence of the various species of *Tabanidae* on micro-climatic factors.

When carrying out ecological research on the *Tabanidae*, the periods during which it is possible to gather material are sometimes exceedingly short. The flight of certain species sometimes lasts only a few days, and collections can only be made on the hot and fine days of this period, in order to make comparison of the result possible. Collection of material by quantitative methods permits statistical methods to be applied, which enables the data obtained to be assessed. The use of small tests wherever possible facilitated the execution of a comparatively large number of repeat tests using small numbers of individuals. Material of this kind is far easier to work on than large tests, containing tens or hundreds of insects, and at the same time the results are more accurate on account of the numerous repeat tests.

The possibility of comparison of data is of great importance especially in calculating numerical relations and occurrence indicators. In this work they correspond to arithmetical averages.

The flight activity varies with individual species depending on the microclimatic conditions of the environment. Comparison of numerical data is only possible in cases where flight conditions are similar and, preferably, optimal, for the species.

When analizing existing works dealing with the ecology of *Tabanidae*, one of the most striking features is that the material obtained as proof is of very little value. This is to a great extent the result of the limited number of methods used to obtain material.

The results obtained do not give synonymous answers, and can often be interpreted from the standpoint of varying hypotheses. Conclusions can only be checked by using other methods, or by examination of the processes governing ecological phenomena, sections of which we can observe in the quantitative material collected. In this work, analysis was based on the physiological properties of *Tabanidae* and their way of life formed by physiological phenomena. Where possible the results obtained were checked by the use of other methods.

During research work in the Kampinos Forest from 1951—1955, the following sweeps were carried out, using various methods:

Method	Number of tests	Number of individuals
Quantitative scoop	336	57
Panes	448	225
Pools of death	52	239
Human as bait	141	475
Skufin trap		
1-minute test	533	493
5- „ „	483	1182
10- „ „	513	4392
Roads	661	428

A total of 2997 tests, containing 7491 individuals, were collected using all methods of quantitative collection. The material obtained refers mainly to 8 species: *Tabanus bromius* L., *T. miki* Brau., *T. maculicornis* Zett., *T. fulvicornis* Meig., *T. tropicus* Panz., *T. bovinus*, Loew., *Chrysozona pluvialis* (L.) and *Ch. hispanica* (Szil.). All the ecological conclusions contained in this work are based on an analysis of material concerning these species.

III. COMPOSITION AND STRUCTURE OF THE *TABANIDAE* POPULATION

The methods used up to the present to collect *Tabanidae* and the knowledge of the physiological variation in adult forms force one to consider if the results obtained refer to the entire population of the given species, or merely to a section of these populations. Material obtained from collections using humans as bait undoubtedly gives a picture of one section only. Only the females in the food penetration period are caught — we know nothing, practically speaking, of the rest of the population, and yet the conclusions drawn usually refer to the population as a whole.

The physiological state of individuals undergoes regular changes during their life-time. After leaving the chrysalis, they gather in mating groups, which are, in the case of many of the species, often encountered in the area. In the Kampinos Forest, especially in the spring, the mating flight of the *Tabanus fulvicornis* Meig., *T. confinis* Zett. and *T. luridus* Fall. takes place in the clearings. After the mating flight the situation changes, the females begin their flight in search of a host, from which they can obtain the blood necessary for the development of the ovaries. Later on the research worker encounters only females, the males never being caught at all. Quantitative examination of *Tabanidae* there refers to females during their search for a host.

It is known, however, that some of the females, having obtained blood, do not react to the host, and, therefore, like males, are never caught during quantitative sweeps. On this account it might be presumed that the *Tabanidae* population is at first uniform, then after the mating flight is split into sub-populations, so to speak, males and females. These two groups again split up into two groups — satiated and non-satiated, i.e. searching for a host. It may be presumed that these three groups lead separate lives.

During the dry summer of 1954, in July, pools of death were prepared in small ponds, near the village of Nart. The collection made here yielded a fairly large amount of quantitative material of some species of the *Tabanus* L. genus. The *Tabanus bromius* L., *T. bovinus* Loew., and *T. fulvicornis* Meig. were present in specially large numbers. Among the individuals collected from the pools were both males and females — males representing about 80% of the individuals in the material collected (Tab. I). Data obtained from the pool of death permit conclusions to be drawn as to the way of life of individuals flying to the pool. The *Tabanidae* need water urgently only during an intensive penetration flight — this will be dealt with more exhaustively later on in this work. The fact that males are collected as well as females, and in far great numbers, is evidence of the greater selectivity of this method as compared with the Skufin trap, or the method using a human as bait. The high percentage of males collected indicates that their flight is far more active than that of the females. While the reason for the penetration flight of the females are clear to us from the point of view of their biology, the causes of the more intensive flight of the males are more difficult to discover. It is possible that they accompany the females on their flight, or fly more actively in their search for females. One fact is indisputable, that the males fly with the females in the area.

Numerical ratios between males and females caught in June 1954 using the pool of death method

Stosunki ilościowe między samcami i samicami złowionymi w czerwcu 1954 r. na kałużę śmierci

Tab. I

Species Gatunek	♂♂ Occurence indicator Wskaźnik występowania	♂♂ %	♀♀ Occurence indicator Wskaźnik występowania	♀♀ %
Tabanus bovinus Loew.	5,92	78,3	1,64	21,7
Tabanus bromius L.	2,42	75,0	0,81	25,0
Tabanus fulvicornis Meig.	4,57	83,0	0,93	17,0

A second method, which does not divide the males from the females, is the collection of the insects from panes. The results refer to species *Tabanus bromius* L. and *Chrysozona pluvialis* (L.) (Tab. II). Collections of the *Ch. pluvialis* (L.) indicate a considerably greater number of females (over 80%), while in the case of the *T. bromius* the females only form about 30%. Data on collection from panes refer to individuals flying freely in the alder-trees area, not attracted by any bait factor such as food or water, and also to their way of life and flight activity independent of the action of bait, which tends to produce a gathering of insects and could alter the correct picture of the flight. From the figures obtained it may be concluded that the *Chrysozona pluvialis* (L) is a species, the males of which fly far less than the females. Of course, assuming that we have a more or less even number of males and females under natural conditions, and other data indicate that this is so, (Tab. III). Data obtained regarding *T. bromius* L. indicate that the flight activity of the males is greater than that of the females. Comparison of the percentage of males and females obtained during collection from panes and from the pool of death is given in Tables I and II. Quantitative results depend mainly on the flight activity of the species investigated. The very small difference in the percentage of occurrence of females by both collecting methods indicates the correctness of the results obtained. As the *Tabanus bromius* L. is not represented in numbers sufficient to make it possible to draw certain statistical conclusions, there are no indicators as to the actual numerical relations of males and females in a natural state, and for this reason any conclusions drawn on the more intensive penetration flight of the males as compared with the females might be inaccurate. The difference in quantitative occurrence may only be the result of the greater number of males than females.

Numerical ratios between males and females according to data obtained by use of „pane" method, from material collected in June and July 1954
Stosunki ilościowe między samcami i samicami według danych z szyb, na podstawie materiałów zebranych w czerwcu i lipcu 1954 r.

Tab. II

Species Gatunek	♂♂		♀♀	
	Number of individuals Liczba osobników	%	Number of individuals Liczba osobników	%
Chrysozona pluvialis (L.)	25	15,6	135	84,4
Tabanus bromius L.	30	71,4	12	28,6

A third method, by means of which material on both males and females can be obtained, is the quantitative scoop. Collections carried out in July 1955 in a clump of birch and aspen trees in the southern part of Kampinos Forest refer to *Chrysozona pluvialis* (L.). Other species were only very sparsely represented in this period and in this part of the Forest. The results obtained (Tab. III) show that the nocturnal resting-places are the same both for males and females. This species does not exhibit ecological variation in this respect.

Numerical ratios between males and females of *Chrysozona pluvialis* (L.) according to material collected by scoop in July 1956
Stosunki ilościowe między samcami i samicami u *Chrysozona pluvialis* (L.) według materiałów czerpakowych z lipca 1956 r.

Tab. III

Sex Płeć	Occurence indicator Wskaźnik występowania	%
♂	0,4	59,7
♀	0,27	40,3

In addition to these data, the observations carried out during research work in the Forest may be cited. The *Tabanidae* in the area are usually noticed at the moment when they begin to attack a human or animal. Large species are also visible during flight. During walks across the Forest, it is possible to encounter *Tabanidae* which have not yet noticed humans, and have not yet attacked them — this usually occurs in forests. In the middle of a very shady forest *Tabanidae* do not occur in large numbers, but on warm open clearings they gather at certain times in relatively large numbers. Coming out from the dense forest, I have several times observed groups of individuals gliding near the earth. Both males and females were encountered when collecting groups of this kind. Later, during the mass flight period, particularly of the *Tabanus fulvicornis* Meig., when the collector is literally besieged by the horse-flies, I was able to collect males as well as females from the masses surrounding me. They never attack a human, but fly towards him together with the females. Naturally males are far more difficult to catch, and remain a certain distance away from humans, and in this way usually escape the notice of the collector.

Investigation of the physiological state of the females was carried out on material obtained by the pane collection method.

Amongst the individuals collected there were, in addition to females not satiated with blood, numerous others, in the alimentary canals of which the presence of blood was established. This indicates that the behaviour of the females is similar whether satiated or not.

Division of the populations of the various species into a series of ecologically separate groups does not occur. In practically all situations in their life the males and females occur together and lead the same type of life. The occurrence during collections made by means of the Skufin trap, or by a human as bait, of only one category of individuals is the result of the selective action of these methods of collection, which attract only certain categories of individuals during the flight period of the whole population.

The population structures of the *Tabanidae* were investigated during the penetration flight. During collection by means of the Skufin trap, over a suitable shorter period of time, the numbers of individuals in the respective tests show great variations, exceeding the normal order for arithmetical averages. This phenomenon is expressed by the irregular flight of the insects to the trap. Most often a certain number of individuals flies to the trap, and after they have been caught, for a certain time no insects appear near the trap at all. The intervals between the approach flights of the various gorups may, of course, vary a great deal. In July 1952 systematic control of a section of the area on the right fringe of the Kampinos Forest was carried out. The area in which the observations took place was about 1 km. long by 0,5 km. wide. Part of the area was covered by pine wood, the rest by fallow or cultivated fields, with a road running more or less through the centre. Observations were carried out three times daily during the period of flight activity of these insects. The whole area was patrolled three times during the course of the day and the places in which the observer was attacked by the insects was marked on a succession of maps. Comparison of these maps made it possible to establish the patchy nature of occurrence and re-distribution of the patches of occurrence in time. The data referred to *Chrysozona pluvialis* (L.). The results of these observations led me to form my theories on the aggregational structure of the *Tabanidae* population.

In order to confirm whether the facts observed are of an accidental character, or whether we are in fact dealing with aggregations, quantitative collections by means of the Skufin trap and the puddle of death were carried out. On account of the speed of the penetration flight of *Tabanidae*, it was decided to make short tests of 1-minute duration, which in practice makes a larger number of repeat tests possible. With such short tests, there are greater chances of catching individual groups than with longer ones, since in the latter case, e.g., over a period of 20 minutes, most often several groups of insects are caught as they approach, which blurs the picture formed, and in addition it is impossible to register the short intervals between the approach of the various groups. Diagrams were made of the frequency of each of the numerical variants, and the quantitative results worked out statistically. Poisson's scheme was calculated for each average, and inchlud ed on the diagram. Both curves, actual and theoretical corresponding to the accidental scheme for animals under natural conditions, were compared using the X^2 criterion. The data (Figs. 1 and 2) refer to the *Tabanus bromius* L., represented in the greatest numbers during this period. Schemes actually obtained from collections by means of the Skufin trap do not appear to differ from Poisson's schemes, which show the accidental way in which the population penetrates the area, without the occurrrence of quantitative structures. On both diagrams, however, a note is made that in the scheme obtained, a larger number of negative tests, and tests of te highest value for the given scheme occurred, than is anticipated by Poisson's scheme. In the case of the smaller serie collected on the forest intendancy station, (Fig. 1) the probability that the scheme observed in the natural state is accidental, and that *Tabanidae* population does not possess any set structure, is $p = 0{,}0029$, the difference between the two schemes is therefore of real importance. The difference between the actual scheme and Poisson's is even more clearly defined in the case of the series collected from the alder-groves (363 repeats) (Fig. 2). The results obtained by comparison are:

$$\frac{(X^2 - k)}{\sqrt{2k}} = 22$$

showing that the divergences in the numerical scheme on the diagrams are regular in character. A similar series of sweeps was made, using the pool of death method, in June 1954. The material obtained refers to three species of the *Tabanus* L. genus, *Tabanus*

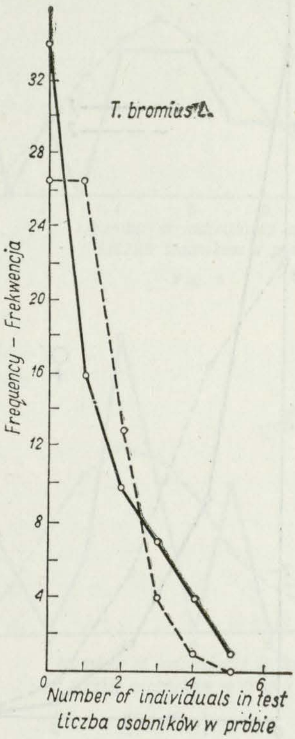


Fig. 1

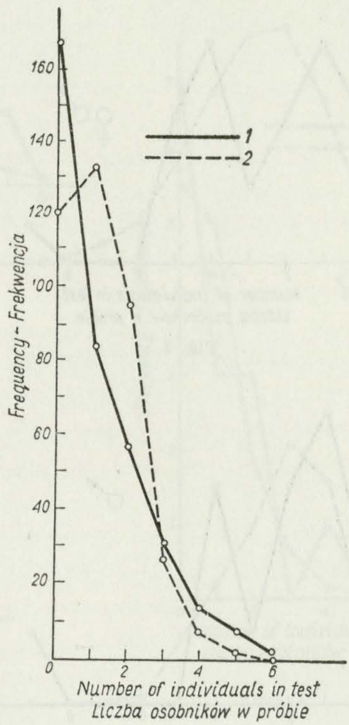


Fig. 2

Fig. 1—2. *Tabanus bromius* L. Frequency of respective quantitative variants obtained during collections lasting one minute, using Skufin trap: 1 — scheme obtained, 2 — Poisson's scheme

Tabanus bromius L. Frekwencja poszczególnych wariantów ilościowych uzyskanych podczas jednominutowych połowów na pułapkę Skufina: 1 — rozkład uzyskany, 2 — rozkład Poissona

bromius L., *T. fulvicornis* Meig. and *T. bovinus* Loew, both males and females being obtained during these sweeps. The results were calculated both in relation to the sexes separately, and to the two sexes combined, and here we do not find the regularity found in collections using the Skufin trap (Figs. 3—11). The difference between the number of individuals in the various tests is much greater. This is to a great extent the result of the small number of repeat tests made in this series. Despite the considerable numerical fluctuations, the material illustrating the actual scheme shows di-

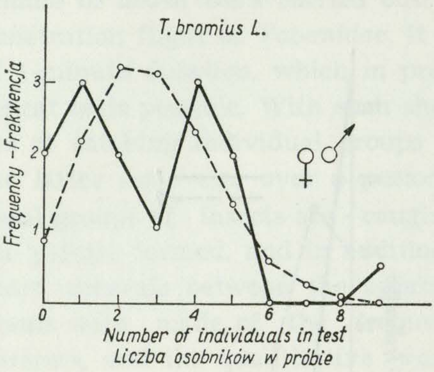


Fig. 3

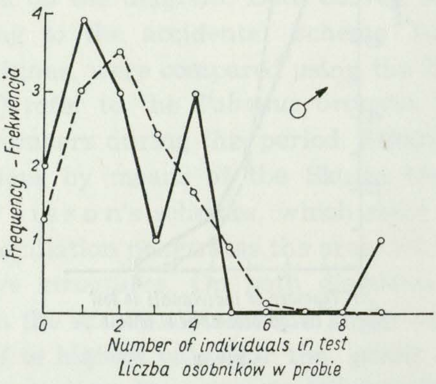


Fig. 4

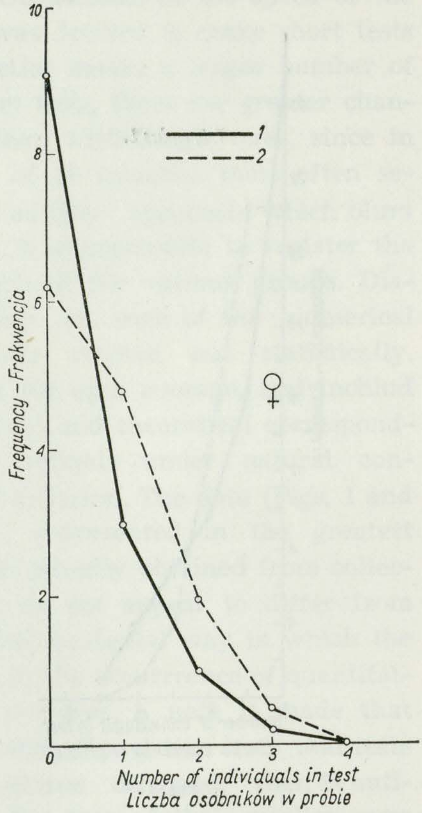


Fig. 5

Fig. 3—5. *Tabanus bromius* L. Frequency of respective quantitative variants obtained during collections lasting one minute, using the pool of death method: — schemes obtained for the whole population and for each sex, 2 — corresponding Poisson's schemes

Tabanus bromius L. Frekwencja poszczególnych wariantów ilościowych, uzyskanych podczas jednominutowych połowów na kałużę śmierci: 1 — rozkłady uzyskane dla całości populacji oraz poszczególnych płci, 2 — odpowiadające im rozkłady Poissona

vergences from P o i s s o n's scheme in every case similar to those observed in the material collected by the Skufin trap method. The number of tests containing negative, and maximum, results within the given variability limits is greater than that envisaged in the Poisson scheme. On account of the small number of tests made, the differences calculated by means ot the X^2 criterion are not

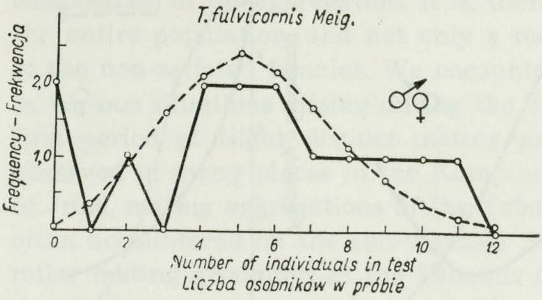


Fig. 6

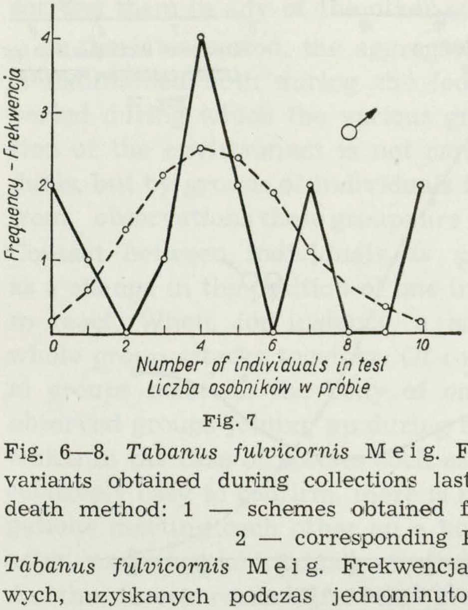


Fig. 7

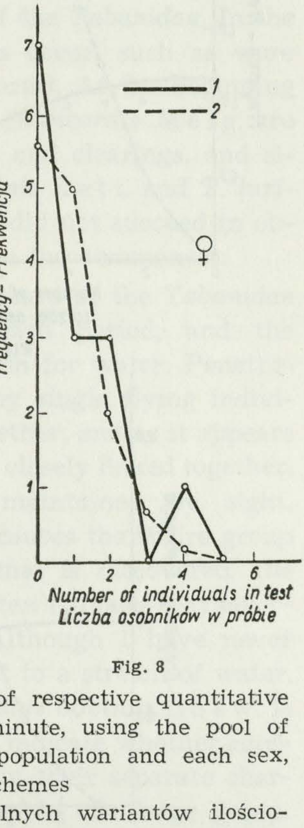


Fig. 8

Fig. 6—8. *Tabanus fulvicornis* Meig. Frequency of respective quantitative variants obtained during collections lasting one minute, using the pool of death method: 1 — schemes obtained for whole population and each sex, 2 — corresponding Poisson's schemes

Tabanus fulvicornis Meig. Frekwencja poszczególnych wariantów ilościowych, uzyskanych podczas jednominutowych połowów na kałużę śmierci: 1 — rozkłady uzyskane dla poszczególnych płci, 2 — odpowiadające im rozkłady Poissona

always of basic importance. The most distinct divergence from the accidental theoretical scheme is shown by *Tabanus bovinus* Loew., where the number of tests of a a value approximate to an arithmetical average is the smallest in the series examined.

From the material obtained it is possible to confirm the preliminary assumptions as to the existence of a population structure

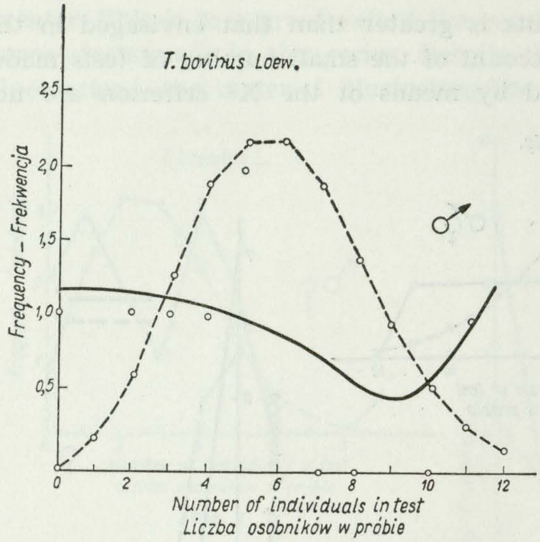


Fig. 9

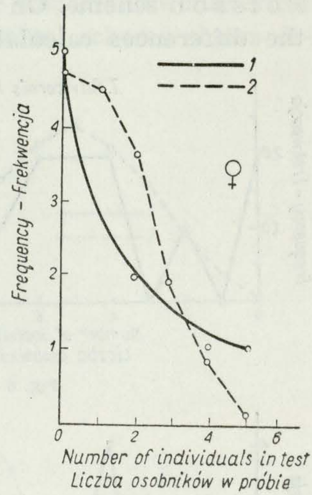


Fig. 10

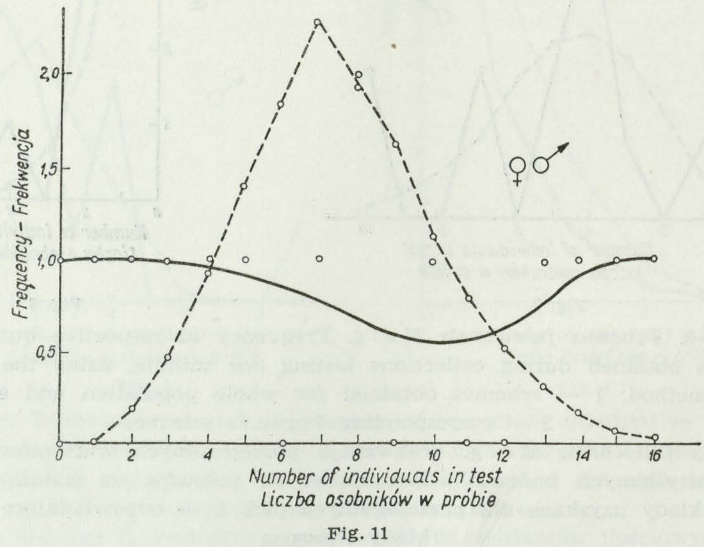


Fig. 11

Fig. 9—11. *Tabanus bovinus* Loew. Frequency of respective quantitative variants obtained during collections lasting one minute, using the pool of death method: 1 — schemes obtained for the whole population and for each sex, 2 — Poisson's schemes

Tabanus bovinus Loew. Frekwencja poszczególnych wariantów ilościowych, uzyskanych podczas połowów jednominutowych na kałużę śmierci: 1 — rozkłady uzyskane dla całości populacji oraz poszczególnych płci, 2 — rozkłady Poissona amongst the *Tabanidae*. Statistics calculated from the results indicate the occurrence of aggregational structures in the populations of the various species. Both males and females are included in the composition of the aggregation. It is, therefore, a general property of the entire population, and not only a means of penetration peculiar to the non-satiated females. We encounter this population structure in various situations arising during the life of the *Tabanidae*. In the first period of flight distinct mating groups occur, such as were observed in many places in the Kampinos Forest. At the beginning of June, mating aggregations of the *Tabanus fulvicornis* Meig. are often encountered on the sun-warmed dunes and clearings, and similar mating groupings of the *Tabanus confinis* Zett. and *T. luridus* Fall. were observed in May, although I did not succeed in observing them in any of the other species, even the commonest.

In the later period, the aggregational structure of the *Tabanidae* is maintained both during the food penetration period, and the period during which the various groups search for water. Penetration of the environment is not carried out by single flying individuals, but by groups of individuals flying together, and as it appears from observations these groups are relatively closely linked together. Contact between individuals is probably maintained by sight, as a change in the position of one individual causes the entire group to react. When, for instance, a large mammal is discovered, the whole group attacks together. Of course it often happens that several groups meet on the body of one host. Although I have never observed groups joining up during mass flight to a stretch of water, which in the case of species such as the *Tabanus bovinus* Loew. is relatively easy to confirm, there is nothing to indicate whether agregations meeting each other on a host maintain their separate character, exchange individuals or simply join up in one large group. As the forest roads offer the greatest opportunities of meeting a host, and as the host always resists the female's attempt to draw a portion of blood, the time of contact is often of fairly long duration. In such cases the aggregation is transferred from one environment to another, this being especially true along roads frequented by humans and animals. This will be discussed in detail in the final section of this work.

The size of the aggregation is difficult to establish, it being never certain if an entire group is caught during quantitative collection, or only part of it. Numerical data obtained during collections and observation of groups of *Tabanidae* indicate that they consist several individuals — only rarely are larger aggregations encountered. The largest group of *Chrysozona pluvialis* (L.) observed consisted of more than 80 individuals, but as a rule we are concerned with smaller numbers.

When investigating the aggregational structure, a series of interesting problems arises, important both from the standpoint of ecology and from that of other biology problems. First and foremost among these is the question of there being one or more species in the *Tabanidae* aggregation, the conditions of their formation and their duration. Investigation of these problems has been started, but methods have so far not been worked out capable of solving them. Investigation of the history of aggregations is bound up with effecting repeat captures of the same groups of individuals. Marking by means of oil paint has no adverse effect on the individuals' chance of survival. A considerable amount of return information was obtained which indicates that the flight activity and ability to attack a host did not undergo any change.

IV. THE ECOLOGICAL NICHE OF THE *TABANIDAE*

A. DEPENDENCE OF THE HORSE-FLIES ON ENVIRONMENT FACTORS

As a starting point in the search for factors having a basic influence on the ecology of the *Tabanidae*, I took the mode of life of these insects, and the physiological phenomena connected with it.

The most striking point as regards the *Tabanidae* is their peculiar flight. Flight, especially rapid flight, has left its mark on the build and physiology peculiar to these insects. As in the case of birds, we find here the handicap of chemical recognition of environment, the chief organ of analysis being the eyes. This insects search for food while flying, when settling on grass or the leaves of trees have great difficulty in finding food of any sort. Species occurring in the Kampinos Forest, bred in jars, could only with difficulty find the honey provided as food, although when placed on cotton wool spread with honey they ate readily and quickly, thus bearing out the opinion of many authors that sweet substances are readily eaten by the *Tabanidae*. It would, however, appear that on account of the visual recognition of surroundings, in the natural state the female at any rate, rarely makes use of other sources of nutriment than large mammals and water. Flight takes place during the day, night-flying species being rare exceptions. In Europe only one species is known whose flight takes place at dusk, the *Tabanus paradoxus* Jaenn. The most intensive flight of the *Tabanidae* takes place at noon and in the afternoon, when the temperature is highest, and the radiation of the sun strongest. These insects are amongst those which fly in open spaces under the direct action of the sun's rays. On cool days flight is less intensive, or ceases altogether. This biological peculiarity of the *Tabanidae* must be reflected in their physiology. The influence of the thermal properties of the environment on their flight is very apparent.

The action of their muscles during flight, and the direct radiation of the sun, cause heating of the organism and rapid evaporation of water. As a result, in addition to thermal phenomena, the water balance — loss and replacement of water by the organism — is important from the ecological point of view. These phenomena take place differently depending on certain properties of the environment.

Reaction of *Tabanidae* to thermal changes in the environment

The basis for investigation of the thermal reaction of *Tabanidae* to changes in temperature is formed by material collected by the Skufin trap method. Specimens were collected during the period of greatest numerical occurrence of the various species. Data from the beginning and end of the flight period cannot be compared with data obtained from the middle of that period, on account of the great difference in the numbers of *Tabanidae* occurring. The time taken to collect the specimens was 10 minutes. The temperature of the air was measured as each test was made. The numerical data obtained were tabulated according to temperature value. Arithmetical averages were calculated from data obtained in successive divisions of temperature showing the average flight activity of the species in question at a given temperature. These averages were then shown in the form of diagrams. Of the 25 species occurring in the Kampinos Forest we succeeded in collecting material statistically credible for 8 species, which enabled us to analyse the influence of temperature on flight activity. A suitable air temperature is necessary for the insects to begin their flight, the temperature required being characteristic of the species in question, e.g. for *Tabanus fulvicornis* M e i g., *T. tropicus* P a n z. and *Chrysozona hispanica* (S z i l.) the air temperature threshold at which flight begins is 14°C. All these species in the Kampinos Forest are among the typical representatives of spring fauna, the remaining species of those examined, *Tabanus maculicornis* Z e t t., forming an exception in this respect, since its flight begins at an air temperature above 18°C. This boundary line is also characteristic of the *Tabanus bromius* L. and *T. bovinus* L o e w., which are species occurring in the summer.

The species related to *T. bromius* L., the *T. miki* B r a u., begins its flight at air temperatures above 22°C. The lower limit at which the flight of the *Chrysozona pluvialis* (L.) begins flight — 16°C, corresponds with the data given in literature on this species.

In the natural state, and especially in experiments carried out under laboratory conditions, a striking feature is the difference in behaviour of the insects during direct action of the sun's rays, and during cloudy periods. On a hot sunny afternoon, the temporary hiding of the sun by clouds has a very slight effect on the air temperature, yet cuts off the direct access of the sun's rays to the insects and lowers their flight activity. This phenomena was clearly visible during observations of artificially bred species. Under natural conditions the following species react most strongly to the direct action of the sun's rays: species belonging to the sub-genus *Tylostypia* E n d., especially *Tabanus (Tylostypia) fulvicornis* M e i g. and *Tabanus (Tylostypia) tropicus* P a n z. The decrease in the flight activity observed among these species in the afternoon usually precedes the more or less constant fall in temperatures during this period. The radiation of the setting sun is far weaker at this time than during the afternoon. In the Kampinos Forest, the maximum temperature in the alder groves, i.e. areas of the greatest quantitative occurrence of horse-flies, during the summer, reaches 30°C. The active flight of *Tabanidae* takes place within the thermal limits — 14—30°C. The individual species react to temperature in different ways. Three types of adaptation to this 16° scale of the insects' — flight can be defined.

Species belonging to the *Chrysozona* M e i g. genus, *Ch. pluvialis* (L.) and *Ch. hispanica* (S z i l.) fly at any of the temperatures included in this scale. In the case of the *Ch. pluvialis* (L.) only a slight increase in flight activity can be observed at temperatures from 16°—25°C. At temperatures over 25°C (Fig. 13) flight activity increases many times over. In the case of the *Ch. hispanica*

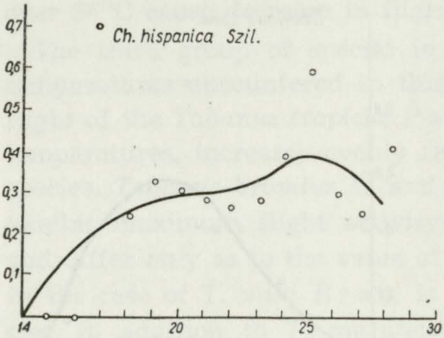


Fig. 12

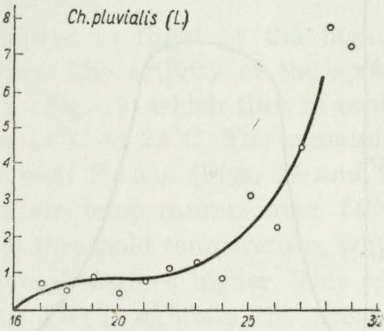


Fig. 13

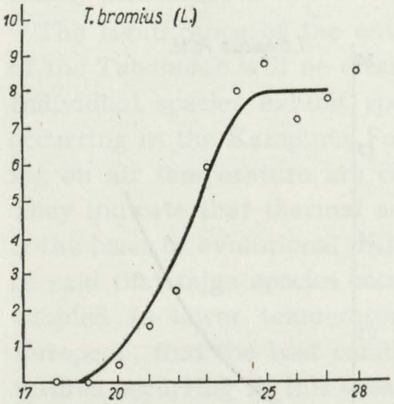


Fig. 14

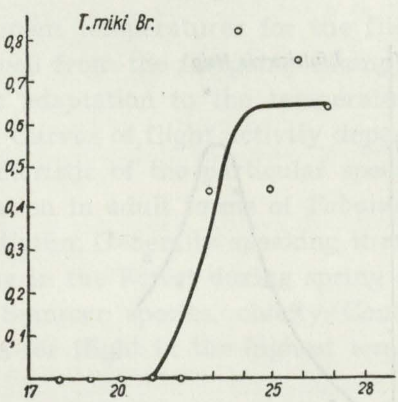


Fig. 15

Fig. 12—15. Dependence of flight of *Tabanidae* on air temperature: horizontal axis — temperature scale, vertical — flight activity indicator

Zależność lotu *Tabanidae* od temperatury powietrza: oś pozioma — skala temperatur, pionowa — wskaźnik aktywności lotu

(S z i l.) a species which flies at any of the temperatures in the scale, the greatest jump in flight activity takes place between 14—17°C. (Fig. 12). Over 17°C flight is more even, and no further increases in activity are noticeable with further rises in temperature.

The remaining species display greater selectivity as regards temperature. The *Tabanus fulvicornis* M e i g., *T. maculicornis* Z e t t. and *T. bovinus* L o e w. select only a narrow range of a few de-

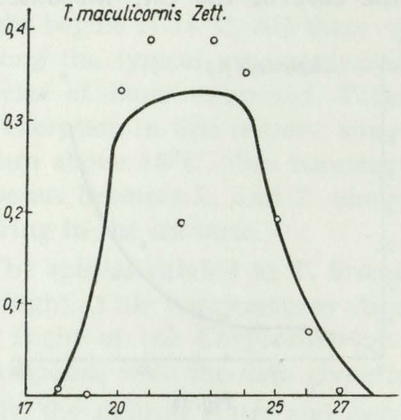


Fig. 16

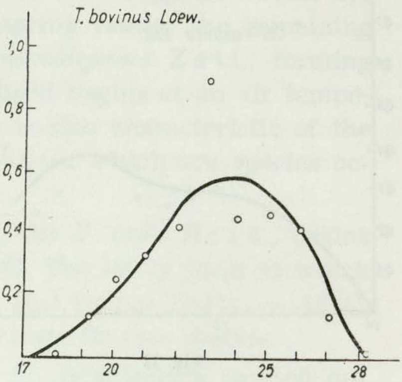


Fig. 17

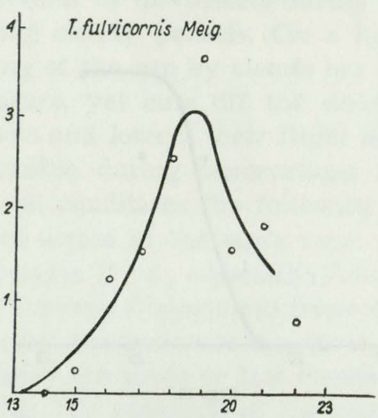


Fig. 18

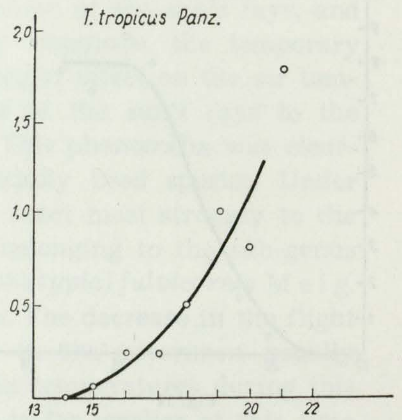


Fig. 19

Fig. 16—19. Dependence of flight of *Tabanidae* on air temperature: horizontal axis — temperature scale, vertical — flight activity indicator

Zależność lotu *Tabanidae* od temperatury powietrza: oś pozioma — skala temperatur, pionowa — wskaźnik aktywności lotu

grees only from the above temperature scale, the selectivity being most distinct in the case of *T. maculicornis* Z e t t. (Fig. 16), whose flight only takes place within the limits 18—27°C, with optimum at 20—25°C. Flight activity outside these limits is practically nonexistent. The range of temperature of the *Tabanus fulvicornis* M e i g. (Fig. 18) is 14—23°C, with maximum activity occurring at 18—19°C, and of the *Tabanus bovinus* L o e w. (Fig. 17) the temperature range is 18—27°C, with flight activity increasing at temperatures between 18—27°C., optimum 22—26°C. Temperatures over 26°C cause decrease in flight activity.

The third group of species is adapted to flight at the highest temperatures encountered in this area. The activity of the spring flight of the *Tabanus tropicus* P a n z. (Fig. 19) which flies in cooler temperatures, increases evenly from 14°C to 22°C. The remaining species, *Tabanus bromius* L. and *T. miki* B r a u. (Figs. 14 and 15) exhibit maximum flight activity at air temperatures over 24°C., and differ only as to the value of the threshold temperature, which in the case of *T. miki* B r a u. is several degrees higher. This species, in addition to *T. maculicornis* Z e t t. exhibits the greatest thermal selectivity amongst all the representatives of the *Tabanidae* family examined in this area.

The significance of the environment temperatures for the flight of the *Tabanidae* will be clearly seen from the foregoing examples. Individual species exhibit specific adaptation to the temperatures occurring in the Kampinos Forest. Curves of flight activity depending on air temperature are characteristic of the particular species. They indicate that thermal adaptation in adult forms of *Tabanidae* is the basis of evolutional differentiatiin. Generally speaking it may be said that tajga species occurring in the Forest during spring are adapted to lower temperatures. Summer species, chiefly Central European, find the best conditions for flight in the highest temperatures occurring in this area.

A knowledge of thermal reactions and their specific qualities may be of great importance in analysing the origin of fauna in the areas examined. It would appear, for instance, that the *Tabanus miki* B r a u. is not a typical Central European species, since its thermal adaptation indicates a Southern European origin. More searching examination is also required with regard to *Chrysozona hispanica* (S z i l.), which has only comparatively recently been described and is difficult to distinguish from the *Ch. pluvialis* (L.). and which may be a permanent inhabitant of the European lowlands, hitherto not distinguished from the *Ch. pluvialis* (L.).

A knowledge of the dependence of the flight of individual species on air temperature also indicates that attention should be paid to the comparability of numerical data. Tests taken at an air temperature of 26°C are not comparable as far as the *Tabanus miki* Brau. and *T. maculicornis* Zett. are concerned, as one of these species attains its iptimum flight at this temperature, and the other its pessimum flight activity. In tihs connection data collected at comparable temperatures for the species examined should be used for the purpose of numerical comparisons.

Light as an ecological factor for the *Tabanidae*

Light is one of the factors, which in view of the visual recognition of their environment by these insects may play a part in its ecology, and its influence on them has not so far been investigated. The manifestation of its influence on the flight activity of *Tabanidae* is attended with great difficulties on account of the simultaneous action of other elements of the environment, such as temperature, atmospheric moisture etc., the effect of which is far stronger.

Choice of nocturnal resting place by *Tabanidae* depending on direction in which light falls

Wybieranie miejsca nocowania przez *Tabanidae* w zależności od kierunku padającego światła

Tab. IV

Number of individuals in experiment / Liczba osobników w doświadczeniu	Direction of light / Kierunek światła; % of settled individuals / % osobników siedzących; Species / Gatunek	From top / Z góry		From bottom / Z dołu		From side / Z boku		Total / Ogółem	
		in light / przy świetle	away from light / od światła	in light / przy świetle	away from light / od światła	in light / przy świetle	away from light / od światła	in light / przy świetle	away from light / od światła
35	*Tabanus fulvicornis* Meig.	100	0	100	0	75	25	94,5	5,5
90	*Chrysozona hispanica* (Szil.)	64	36	90	10	87	15	80	20

Investigation of the influence of light on the behaviour of *Tabanidae* was carried out under laboratory conditions, in thermal conditions lower than the threshold temperature for commencement of flight. The individuals on which the experiments were carried out could not, therefore, fly. The influence of the direction in which light falls on the distribution of the *Tabanidae* was investigated. Observations were carried out in 20-litre jars coverd with gauze, from which blades of grass reaching to the bottom of the jar were suspended. The insects forming the subject of the experiments settled on these grasses and on the sides of the jars. The observations were made in a darkened room, the only source of light being a lamp. The widely separated species, from a systematic point of view, *Tabanus fulvicornis* M e i g. and *Chrysozona hispanica* (S z i l.). were used for the experiments. The results obtained (Table IV) indicate that the direction in which the light falls influences to a large extent the choice of a nocturnal resting-place. In all the experiments, irrespective of whether the rays of light were directed on the jar from the top, bottom, or side, the insects always moved in the direction in which the rays fell, and on reaching the edge of the jar remained motionless. In the case of the *Tabanus fulvicornis* M e i g. 94,5% of the total number of individuals moved in the direction of the light, and of the *Chrysozona hispanica* (S z i l.). 80%.

Influence of atmospheric moisture on the flight activity of the *Tabanidae*

A large amount of thermal energy is formed by the *Tabanidae* during flight. The organism rids itself of this excess heat by the evaporation of water. As the rate of evaporation depends on the amount of water vapour in the air, it may be expected that similarly as in the case of temperature, corresponding adaptations will take place for flight in various conditions of relative atmospheric moisture. Investigation of this dependence was carried out in a similar manner to the investigation of the dependence of temperature. Moisture was measured by means of Asmann's psychrometer and calculated according to tables. The rest of the work was carried out as for the temperature investigations.

The dependence of the flight activity of the *Tabanidae* on the relative atmospheric moisture is far less distinctly expressed than the dependence on temperature. Certain species belonging to the genus *Tabanus* L. — i.e. *T. bromius* L. (Fig. 20), *T. tropicus* P a n z. and *T. fulvicornis* M e i g. do not exhibit any regular connection between flight activity and relative atmospheric moisture. In the

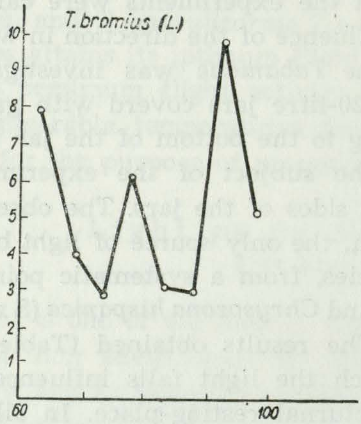


Fig. 20

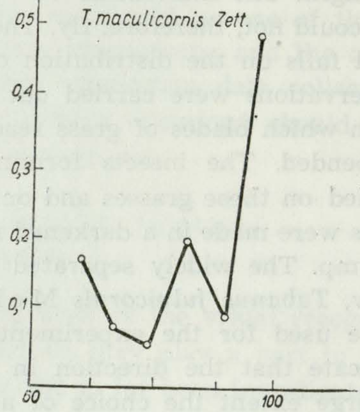


Fig. 21

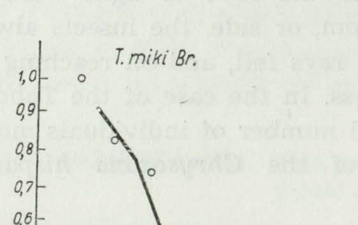


Fig. 22

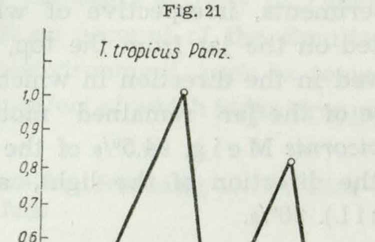


Fig. 23

Fig. 20—23. Dependence of flight activity of *Tabanidae* on relative atmospheric moisture: horizontal axis — scale of relative moisture, vertical — flight activity indicator

Zależność aktywności lotu *Tabanidae* od wilgotności względnej powietrza: oś pozioma — skala wilgotności względnej, pionowa — wskaźnik aktywności lotu

case of the *T. tropicus* P a n z. (Fig. 23) it may be suspected that flight activity is greater in lower values of relative atmospheric moisture, whereas the optimum flight activity of the *T. fulvicornis* M e i g. (Fig. 25) takes place at 85% relative atmospheric moisture.

A group of hygrophobic species is formed by *Chrysozona hispanica* (S z i l.), *Ch. pluvialis* (L.) and *Tabanus miki* B r a u. (Fig. 22). The data obtained, especially in the case of *Chrysozona pluvialis*

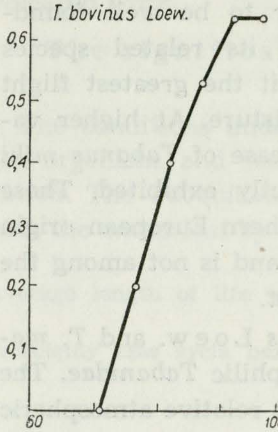


Fig. 24

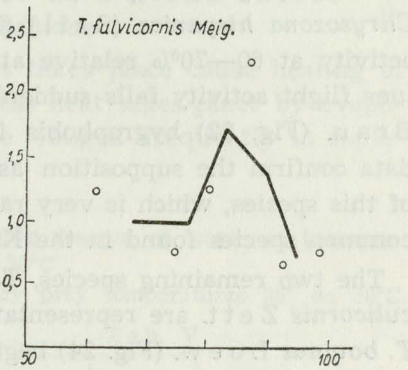


Fig. 25

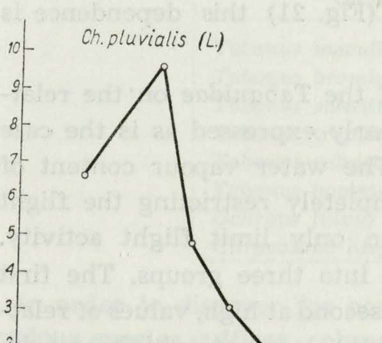


Fig. 26

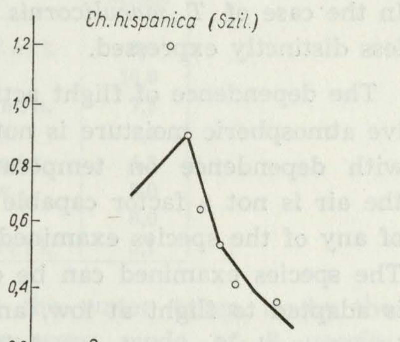


Fig. 27

Fig. 24—27. Dependence of flight activity of *Tabanidae* on relative atmospheric moisture: horizontal axis — scale of relative moisture, vertical — flight activity indicator

Zależność aktywności lotu *Tabanidae* od wilgotności względnej powietrza: oś pozioma — skala wilgotności względnej, pionowa — wskaźnik aktywności lotu

(L.) (Fig. 26) are relatively unexpected, for over 100 years the opinion has been accepted that this species is outstandingly moisture-loving, and that it specially likes to attack during rain, when the atmospheric moisture is greatest. This view has not, however, been checked even once by accurate investigation on a basis of measurements of the relative atmospheric moisture. The results obtained have been checked in two successive years on extensive quantitative material, so that they would appear to be well founded. The *Chrysozona pluvialis* (L.), and also its related species *Chrysozona hispanica* (Szil.) (Fig. 27) exhibit the greatest flight activity at 60—70% relative atmospheric moisture. At higher values flight activity falls suddenly. In the case of *Tabanus miki* Brau. (Fig. 22) hygrophobia is most distinctly exhibited. These data confirm the supposition as to the Southern European origin of this species, which is very rare in Poland, and is not among the common species found in the Kampinos Forest.

The two remaining species, *Tabanus bovinus* Loew. and *T. maculicornis* Zett. are representatives of hygrophilic *Tabanidae*. The *T. bovinus* Loew. (Fig. 24) begins its flight at relative atmospheric moistures of over 90% and the flight optimum is reached at 100%. In the case of. *T. maculicornis* Zett. (Fig. 21) this dependence is less distinctly expressed.

The dependence of flight activity of the *Tabanidae* on the relative atmospheric moisture is not so clearly expressed as is the case with dependence on temperature. The water vapour content of the air is not a factor capable of completely restricting the flight of any of the species examined, it can only limit flight activity. The species examined can be divided into three groups. The first is adapted to flight at low, and the second at high, values of relative atmospheric moisture, while the third does not exhibit any definite influence of atmospheric moisture on flight activity. Hygrophobic species exhibit simultaneously great flight activity at the highest temperatures which are encountered in this area. Hygrophilic species exhibit a simultaneous adaptation to flight at low temperatures. Adaptation to flight in varying conditions of atmospheric moisture may be interpreted in connection with evaporation of water from the surface of the insects' bodies. An analysis of the results obtained is, however, attended with great difficulties. Certain species fly in conditions facilitating evaporation, e.g. *Chrysozona pluvialis* (L.), others, e.g. *Tabanus bovinus* Loew. prefer to fly when evaporation from the organism is more difficult. It is possible that these forms of adaptation to a definite degree of moisture are only derivative thermal adaptations. The solution of these problems is only possible, however, after carrying out more detailed research work.

The significance of water as a niche factor for the *Tabanidae*

The conditions under which flight takes place cause heating of the organism, and cooling from excess heat takes place by evaporation. The *Tabanidae* are therefore obliged frequently to replenish the water lost by evaporation.

Average length of life without replenishing reserve of water at temperature 35° to 30°C

Przeciętny czas życia bez pobierania wody przy temperaturze 35° do 30°C

Tab. V

Species Gatunek	Minutes Minut
Tabanus maculicornis Zett.	5,8
Tabanus bromius L.	10,0
Tabanus solstitialis Schin.	7,3
Tabanus tropicus Panz.	6,4
Tabanus fulvicornis Meig.	4,3
Tabanus bovinus Loew.	5,0
Ochrops fulvus Meig.	6,0
Chrysozona hispanica Szil.	5,7

In order to discover for how long the water taken up by the various species suffices, observations were made of 8 species (Tab. V), 10 individuals of each species being introduced into jars after they had taken up water. The jars were than subjected to the action of the sun's rays at a temperature of about 30 — 35°C. The length of life of the various individuals was noted. These experiments were repeated several times, but the results obtained for the various species were not always identical. A great influence is exerted on the course of the experiments by the air temperature, the intensity of the sun's rays, the period over which the insects are kept in captivity, etc. The figures given are therefore provisional in character, but indicate the part played by water in the life of the *Tabanidae*.

The life-period of these insects during the experiment varied within the limits of 4,3 — 10 minutes. During these experiments the insects had not, of course, any opportunity of escaping, even temporarily, from the influence of the prevailing temperature, which was usually higher than the optimum flight activity temperature, and a little higher than the highest temperature in a zone of up to 2 m. above the surface of the ground, where the penetration flight takes place. When free, the rate of evaporation of these insects should be considerably lower, nevertheless, especially on hot days, when flight activity is very high, the insects have to take up water at frequent intervals to replenish their reserves.

Influence of accesibility of water on occurence of *Tabanidae* in various environments in the Kampinos Forest at the end of June and beginning of July 1955

Wpływ dostępności wody na występowanie *Tabanidae* w różnych środowiskach Puszczy Kampinoskiej na przełomie czerwa i lipca 1955 r.

Tab. VI

Species Gatunek	Water in environment Woda w środowisku	
	Accessible throughout whole day Dostępna przez cały dzień %	Inaccessible, dew drying very rapidly Niedostępna, rosa szybko wysycha %
Tabanus fulvicornis Meig.	99	1
Tabanus tropicus Panz.	100	0
Tabanus solstitialis Schin.	100	0
Tabanus maculicornis Zett.	87,9	12,1
Tabanus bromius L.	78,2	21,8
Tabanus bovinus Loew.	63,2	36,8
Chrysozona hispanica (Szil.)	74,2	25,8
Chrysozona crassicornis (Whlb.)	100	0

This is not an easy matter in the Kampinos Forest. The insects search for water by sight only, as they probably do not sense the smell of water. The species belonging to the *Tabanus* L. and *Chrysops* Meig. genera search for puddles, ponds, canals, even troughs filled with water in yards, and hit the surface of the water with their entire bodies, the water being taken up at the moment of impact. They do not distinguish between water and pools of petroleum, towards which they dive with the same eagerness as to water. There are, of course, other sources from which under natural conditions they can obtain water, since it is known that they do so, on occasion, from dew, damp ground, moss etc. Searching for hidden sources of water is, for these insects, a difficult matter. In forest areas water can easily be obtained from bogs, ponds, and wet meadows, but in a pine forest growing on dry ground dew dries quickly, and if there are no pools etc. the insects are sometimes forced to fly considerable distances. For this reason the chances of these insects remaining permanently in dry forests are not great, and as a rule only individuals on through flights, and not living in the area, are encountered. This is illustrated by Table VI, obtained from quantitative collections in numerous phytosociological environments of the Forest, distinguished from the point of view of one factor only — accessibility of water.

The results are synonymous, as 85% of the *Tabanidae* occurring in this area gathers in those parts of the Forest where drinking water is accessible. Skufin (1952) obtained similar results when investigating the distribution of the *Chrysops relictus* Meig. in various biotopes. This distribution of the insects in the area confirms the results obtained as to the significance of water as a niche factor.

Food as an ecological factor for the *Tabanidae*

The importance of food as a factor defining the ecological niche has been emphasised from the very start when this idea was first introduced. Turow (1953) and Skufin (1952) put it forward when carrying out research on the *Tabanidae*. The following are mentioned as forming the food of the *Tabanidae:* various categories of liquid and semi-liquid substances, especially sweet ones, and blood. In my investigations I drew attention only to the food forming the object of systematic search by the insects, that is, large mammals. Collections were carried out in a pine wood with more or less uniform conditions for obtained water and similar relative atmospheric moisture, and the species most commonly encountered here in the summer season, the *Chrysozona pluvialis* (L.) (Tab. VII) was chosen as the subject.

Influence of the occurrence of host-mammals on the distribution of *Chrysozona pluvialis* (L.) in the Kampinos Forest, in July 1954. *Pineto-vaccinetum myrtilli* with more or less uniform conditions of moisture

Wpływ występowania ssaków żywicieli na rozmieszczenie *Chrysozona pluvialis* (L.) w Puszczy Kampinoskiej, lipiec 1954 r. *Pineto-vaccinetum myrtylli* o mniej więcej jednakowych warunkach wilgotności

Tab. VII

Place / Miejsca	
Constant or very frequent occurrence of large mammals O stałym lub bardzo częstym występowaniu ssaków	Infrequent occurrence of large mammals Duże ssaki występują rzadko
83,3 %	16,7 %

The results obtained show that the population of the *Ch. pluvialis* (L.) congregates in areas where large mammals, chiefly humans and domestic animals, are frequently encountered. Similar regularity is exhibited by other species of the *Tabanidae*.

When carrying out ecological research it is usual to take into consideration a series of other factors influencing the physiology of flying insects, amongst which the most important are atmospheric pressure and wind. Discussion of their significance was under taken by Uvarov (1929). Both these factors were taken into account at the beginning of these researches, but it was not possible to demonstrate their unmistakable influence on the flight activity of the *Tabanidae*.

Wind is of fundamental significance with regard to evaporation from the body-surface of animals, and their distribution in a given area. A stronger wind facilates evaporation. In the case of the *Tabanidae*, the influence of slight winds is unimportant, the air eddies formed by wing action being far stronger than the action of moderate winds. When investigating the influence of wind force on the flight of the *Tabanidae*, the main aim is to discover the threshold wind force value, below which flight ceases. In the case of medium wind force the flight of the *Tabanidae* is not impeded, but the establishment of the limit at which flight is possible where high wind forces are involved proved very difficult. In the Kampinos Forest strong winds in the summer as a rule accompany a fall in air temperature, and it is impossible to decide which of the two factors, wind or temperature, is the impediment to the flight of the *Tabanidae*.

The factors investigated as influencing the activity of the *Tabanidae*, the most important of which are temperature, atmospheric moisture, water and food, form the ecological niche of the various species of *Tabanidae*.

B. ANALYSIS OF THE DISTRIBUTION OF *TABANIDAE* IN A TYPICAL ENVIRONMENT

Determination of the ecological niche by definition of ecological factors does not afford an exhaustive description of the connection of the population with its environment. Niche factors act jointly in every situation. In a given area we are not always dealing with optimum conditions for the species, their composition being dependent on the properties of the environment itself.

The next stage of research work consisted in making an analysis of the behaviour of the *Tabanidae* population in marshy alder-groves, this being an area which we may consider as a typical environment for the *Tabanidae*. Investigation of the conditions under which flight takes place is one of the main points of their ecology, as flight forms one of the chief phenomena of their life. During flight aggregations are formed and later copulation takes place. During flight they search for large mammals, whose blood is essential for the development of the ovaries in females of the majority of the species (O ł s u f i e w, 1940). In the first place an attempt was made to determine the areas of food penetration in the areas over which flight takes place.

In the environment certain niche factors change regularly over the course of 24 hours. The vertical scheme of temperatures in the air strata immediately above ground level is more or less constant for the individual environments, and changes regularly during the day. The *Tabanidae*, being flying insects, are able to choose for their flight that particular air stratum most suitable for their optimum flight activity. Only in this way it is possible to explain the phenomena referred to in literature on the subject, and observed in the Kampinos Forest, of their active flight at dawn over the top of the forest. Within the forest the temperature at this time is still far below the activity threshold, but there is a layer of warm air over the top of the forest (G e i g e r, 1927). Differences in the vertical distribution of flying *Tabanidae* is connected with the search for the particular air layer providing the insect with the thermal and moisture conditions which suit it best. On the other hand the continuation of its flight must take place at the distance from ground level permitting of the best penetration of the environment.

Investigation of vertical distribution was carried out by the use of panes, and collection by the Skufin trap method. The panes consisted of 2 series of 12 mm. each, the first being placed at a level of 1,5 m. and the other hung at the level of the bush-tops (5 — 8 m.) The Skufin trap was placed at various heights above ground level. A second trap, placed on the ground, collected material for comparison. In these collections only individuals caught on fly-papers were taken into account. It may be stated that in general (Tab. VIII) flight takes place mainly in the area up to 2 m. above ground level. Percentage ratios in the vertical distribution of two species systematically distant from each other, the *Tabanus bromius* L. and *Chrysozona pluvialis* (L.) are similar (about 20%) of individuals fly at the top, and 80% at the bottom). These percentages are good indicators of the vertical distribution. Comparison of arithmetical averages indicates the probability, in the case of *T. bromius* L., and the statistical reality, in the case of *Chrysozona pluvialis* (L.), of the ratios observed.

Vertical distribution of flying horse-flies during the 24-hour period; results obtained based on material collected by the "pane" method

Rozmieszczenie pionowe latających ślepaków w okresie dobowym; wyniki uzyskane na podstawie materiałów z szyb

Tab. VIII

Species Gatunek	Numerical ratios Stosunki ilościowe % %		Difference between averages Różnica średnich $\frac{M_1 - M_2}{\sqrt{m_1^2 + m_2^2}}$
	5 — 8 m. above ground level 5 — 8 m nad poziomem ziemi	up to 2 m. above ground level do 2 m. nad poziomem ziemi	
Tabanus bromius L.	21,7	78,3	2,03
Chrysozona pluvialis (L.)	19,9	80,1	22,33

Division into day and night collections makes it possbile to confirm that the numerical distribution of insects flying during the day is similar to the summarized scheme for a period of 24 hours, but a far greater number of insects fly among the tree tops (Tab. IX) during the day. Flight does not cease completely at night (Tab. X) but takes place only in the strata immediately above ground level.

Vertical distribution of horse-flies flying during day; results obtained from material collected by the "pane,, method

Rozmieszczenie pionowe latających ślepaków w ciągu dnia; wyniki uzyskane na podstawie materiałów z szyb

Tab. IX

Species Gatunek	Numerical ratios Stosunki ilościowe % % 5 — 8 m. above ground level 5 — 8 m nad poziomem ziemi	Numerical ratios Stosunki ilościowe % % up to 2 m. above ground level do 2 m nad poziomem ziemi	Difference between averages Różnica średnich $\frac{M_1 - M_2}{\sqrt{m_1^2 + m_2^2}}$
Tabanus bromius L.	33,2	66,8	0,9
Chrysozona pluvialis (L.)	23,0	77,0	2,92

By dividing tests into day and night in the upper and lower air stratas, it is possible to discover the intensity of flight in the various air strata during a period of 24 hours. Flight takes place in the layer up to 2 m. above ground level throughout this period (Tab. XI) but at night is far less intensive, and constitutes only 15—20% of the daytime flight. The flight of the *Chrysozona pluvialis* (L.), a species with less exacting thermal requirements, is more active during the night time than that of the *Tabanus bromius* L. In the upper air strata (5—8 m. above ground level) flight ceases entirely during the night, the insects only flying here during the day (Tab. XII).

Vertical distribution of horse-flies flying during the night, results obtained from material collected by the "pane" method

Rozmieszczenie pionowe ślepaków w okresie nocnym, wyniki uzyskane na podstawie materiałów z szyb

Tab. X

Species Gatunek	Numerical ratios Stosunki ilościowe % % 5 — 8 m. above ground level 5 — 8 m nad poziomem ziemi	 up to 2 m. above ground level do 2 m nad poziomem ziemi	Difference between averages Różnica średnich $\frac{M_1 - M_2}{\sqrt{m_1^2 + m_2^2}}$
Tabanus bromius L.	0,0	100	17,15
Chrysozona pluvialis (L.)	0,0	100	1,80

Intensivity of flight of horse-flies in the layer immediately above ground level during the day and at night. Results obtained from material collected by the "pane" method

Intensywność lotu ślepaków w warstwie przyziemnej powietrza we dnie i w nocy. Wyniki uzyskane na podstawie materiałów z szyb

Tab. XI

Species Gatunek	Numerical ratios Stosunki ilościowe % % day dzień	 night noc	Difference between averages Różnica średnich $\frac{M_1^2 - M_2^2}{\sqrt{m_1^2 + m_2^2}}$
Tabanus bromius L.	85,7	14,3	8,70
Chrysozona pluvialis (L.)	80,6	19,4	3,43

Intensivity of flight of horse-flies in treetops during the day and the night, results obtained from material collected by the "pane", method

Intensywność lotu ślepaków w koronach drzew we dnie i w nocy, wyniki uzyskane na podstawie materiałów z szyb

Tab. XII

Species Gatunek	Numerical ratios Stosunki ilościowe % % day dzień	 night noc	Difference between averages Różnica średnich $\frac{M_1 - M_2}{\sqrt{m_1^2 + m_2^2}}$
Tabanus bromius L.	100	0,0	1,5
Chrysozona pluvialis (L.)	100	0,0	2,6

Flight activity is greatest in the daytime during which period the population becomes partly dispersed in a vertical direction. The difference in numerical results between flight during the daytime and at night shown by collections made by means of panes and the Skufin trap, affords confirmation that the insects' flight is not always connected with food penetration. In further work on this problem collections were made by means of the Skufin trap, tests being taken from the lower strata (up to 2 m. above ground level) and from the tree-top level. From the material collected (Tab. XIII) it was possible to confirm that over a height of 2 m. from ground level attacks on the trap ceased completely, thus there is no question of food penetration here. About 30% of *Tabanidae* flying at tree-top level during the day are not intent on obtaining food, and therefore on this basis it is possible to separate the area of food penetration from the general flight area. These data are, of course, only significant with regard to European species.

The results obtained are set out in a diagram illustrating the vertical scheme of insects flying in the alder-grove area (Fig. 28) under examination. The composition of numerical ratios for day and night time are shown on this diagram.

Investigation of the vertical distribution of individuals not in flight, that is, having settled on grass and leaves of trees, has not yet been carried out. Insects when not actually flying are in practice difficult to find, and their nocturnal resting-places under natural conditions are unknown. Even an extensive series of sweeps carried out in meadows and alder-groves where the insects appeared in masses during the daytime did not succeed in catching any, or only very few individuals. It was impossible to draw any conclusions from material obtained in this way.

A guide to the correct arrangement of collections on the spot was supplied by experiments on the nocturnal habits of these insects, carried out in this laboratory, and deschribed in the previous section. During the hours of evening the flight of the *Tabanidae* slackens, and the insects fly off to their nocturnal resting-places, choice of which is decided by the direction in which the light falls. The insects bred in the laboratory

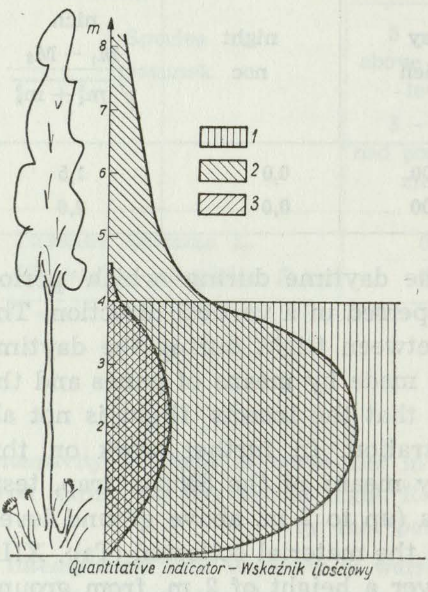


Fig. 28. Vertical distribution of horse-flies in flight. 1 — area of food penetration, 2 — daytime flight, 3 — night flight

Rozmieszczenie pionowe latających ślepaków. 1 — Obszar penetracji pokarmowej, 2 — lot dzienny, 3 — lot nocny

Attacks on Skufin trap by horse-flies depending on distance from ground level

Atakowanie pułapki Skufina przez ślepaki zależnie od odległości od powierzchni ziemi

Tab. XIII

	Numerical ratios Stosunki ilościowe % %		Difference between averages Różnica średnich $\frac{M_1 - M_2}{\sqrt{m_1^2 + m_2^2}}$
	treetops korony drzew	ground ziemia	
Tabanidae combined łącznie	0,0	100	2,8

Choice of nocturnal resting-place by *Tabanidae* with light falling from top and from side, July 1955

Wybór miejsca nocowania przez *Tabanidae* przy kierunkach światła górnym i bocznym, lipiec 1955 r.

Tab. XIV

Species Gatunek	Individuals in experiment Osobników w doświadczeniu	Top Góra (%)	Bottom Dół (%)
Tabanus fulvicornis Meig.	55	100	0
Chrysozona pluvialis (L.)	60	65	35

most often, with the approach of dusk, settled on the gauze covering the top of the jar. If light exerts the same influence on the insects in conditions of freedom, they ought to be found by sweeps, as this method is very effective in collecting material from the blades of grass and leaf surfaces. Another guide was afforded by observations of the direction of flight of individuals set free during the day and at dusk (Tab. XV). Individuals released during the day disperse haphazardly, whereas in the evening they first of all fly rapidly away from the person releasing them, then a large percentage flies in the direction of the nearest group of trees.

Direction of flight of *Tabanus fulvicornis* Meig. when released in different times of the day

Kierunek odlotu *Tabanus fulvicornis* Meig. wypuszczanego w różnych porach dnia

Tab. XV

	Daytime Dzień		Evening Wieczór	
	Fortuitous flight Odlot przypadkowy	Flight to treetops Odlot w korony drzew	Fortuitous flight Odlot przypadkowy	Flight to treetops Odlot w korony drzew
Number of individuals Liczba osobników	18	3	5	13

Distribution of individuals of *Chrysozona pluvialis* (L.) after settling, during daytime and at night. Data obtained from material collected by a scoop

Rozmieszczenie siedzących osobników *Chrysozona pluvialis* (L.) w dzień i w nocy. Dane uzyskane z materiałów czerpakowych

Tab. XVI

	Daytime Dzień (%)	Night Noc (%)
Grass Trawa	16,5	83,5
Treetops Korony drzew	4 5	95,5

Using these observations as a basis, night collections by means of a scoop were carried out in a large group of trees adjoining the meadows which, during the day, formed an area of intensive food penetration by these insects. At the same time collections for purposes of comparison were carried out in the grass. A general comparison of the numbers of individuals settled in the grass and on the tree-tops (Tab. XVI) shows that over 92% of the individuals caught comes from nocturnal collections. The majority of the population does not fly actively during the night. During the day there is only a very small percentage of individuals in the places in which they gather for night. Practically the entire population carries out penetration flights. At night the majority of individuals, about 80%, settles on the tops of trees, the remainder — about 20%, in the grass, whereas during the day neither trees nor grass attract these insects. The numbers of individuals caught during daytime sweeps are so small that it is impossible to draw any statistical conclusions from them.

As regards the species of *Tabanidae* occurring in the Kampinos Forest, it is not always possible, on the basis of a knowledge of their requirements only, to state whether the given species will be encountered or not. The important point here is the period of occurrence which, in the case of certain species, is very short. It is possible only to make a general statement, that as the flight of the respective species as a rule begins with the commencement of optimum flight conditions, so the end of flight is usually preceded by the change of optimum conditions for worse. It is impossible therefore to link the occurrence of the respective species with the niche factors discussed. Probably these matters are regulated by predaceous animals or it is a question of physiological death. This second possibility appears to me to be very probable under the conditions prevailing in the Kampinos Forest. There are not many predaceous species which attack the *Tabanidae* in this area. The *Odonata, Asilidae* or *Bembex* Fabr. are not very common here, and in spite of the special search which was made for them, I was not able to confirm a single instance of an attack by predaceous species considered as enemies on the masses of *Tabanidae* in flight.

Seasonal dynamics have their own characteristic course for the species concerned. As a rule species systematically closely related have separate periods of occurrence, and there are no cases of the beginning of one flight and ending of another coinciding. This is especially true of the *Tabanus bromius* L. group represented here by 3 species: *T. bromius* L., *T. miki* Brau. and T. *maculicornis* Zett., differing mainly in the shade of colouring. The time of of occurrence of these species (Fig. 29) varies considerably. Similar differences can be observed in the occurrence of two related species of the *Chrysozona* Meig., *Chrysozona hispanica* (Szil.) is a spring species, with its peak period of occurrence at the end of June, while the peak period

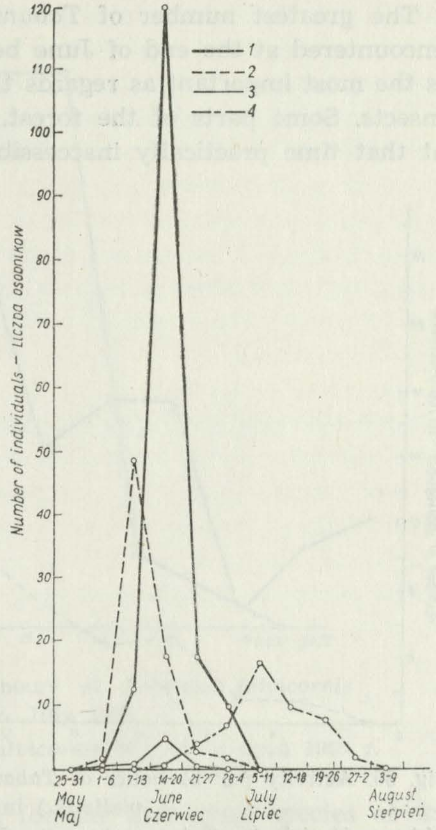


Fig. 29. Seasonal dynamics of commonest species of the *Tabanus* L. species in Kampinos Forest in 1955
Dynamika sezonowa pospolitych gatunków z rodzaju *Tabanus* L. w Puszczy Kampinoskiej w 1955 r.
1 — *T. maculicornis* Zett, 2 — *T. fulvicornis* Meig, 3 — *T. tropicus* Panz., 4 — *T. bromius* L.

for the *Chrysozona pluvialis* (L.) is the end of July. Differences in the period of occurrence can also be observed in the group of species belonging to the subgenus *Tylostypia* End.

The greatest number of *Tabanidae* in the Kampinos Forest is encountered at the end of June beginning of July, and this period is the most important as regards the economic significance of these insects. Some parts of the forest, especially the alder-groves, are at that time practically inaccessible to cattle and horses. Grazing

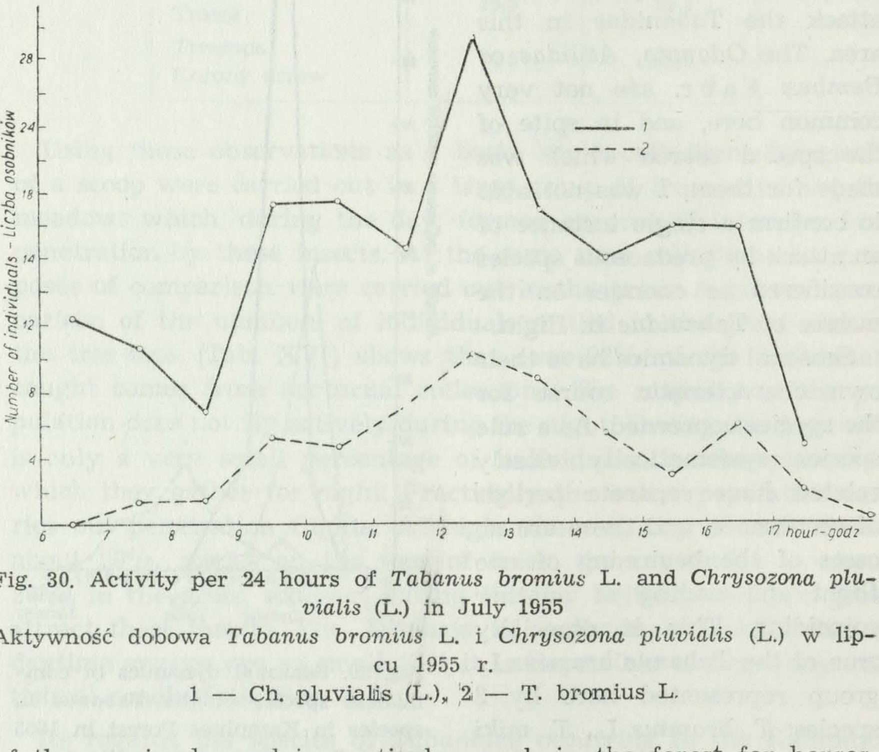


Fig. 30. Activity per 24 hours of *Tabanus bromius* L. and *Chrysozona pluvialis* (L.) in July 1955

Aktywność dobowa *Tabanus bromius* L. i *Chrysozona pluvialis* (L.) w lipcu 1955 r.

1 — Ch. pluvialis (L.), 2 — T. bromius L.

of these animals, and in particular work in the forest for horses, which have thin skins and are very sensitive to the stings of horse-flies, is rendered very difficult during this period. These areas are not, however, dangerous to the same degree throughout the day. Species occurring in the Forest during the summer season are capable of flying practically the entire day. This indicates a far smaller degree of specialisation than that observed in Africa by Haddow (1950, 1952) for certain species of *Tabanidae* occurring there. The active flight of *Tabanidae* in the Kampinos Forest begins about

6.30 a.m. and increases gradually with the rise in temperature, attaining a maximum between 12 noon and 4 p. m. In the afternoon as the temperature gradually drops, the flight activity of these insects gradually decreases.

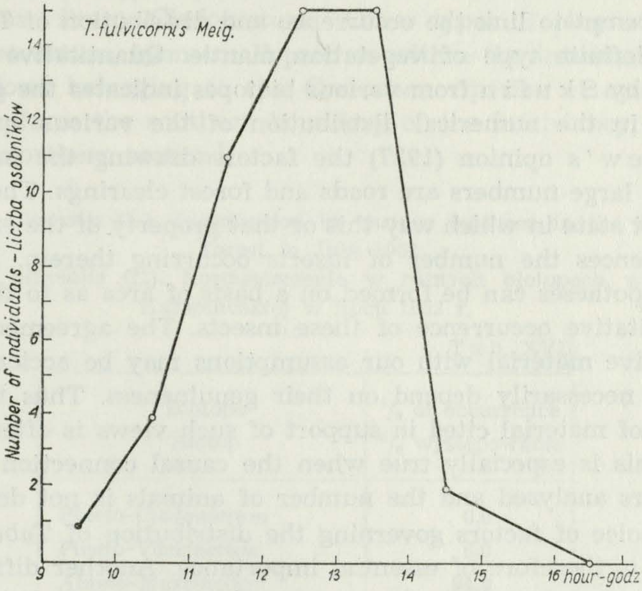


Fig. 31. Activity per 24 hours of *Tabanus fulvicornis* Meig. in July 1955

Aktywność dobowa *Tabanus fulvicornis* Meig. w lipcu 1955 r.

The Figs. 30 and 31 obtained for the individual species of the activity of the insects over a period of 24 hours do not differ materially from the results obtained by Soviet research workers. Gucewicz (1947) obtained more regular curves of the course of flight activity over a 24 hour period during his research in the Far East, on account of the longer period during which tests were taken. The course of the 24 hour activity of *Tabanidae* in the Kampinos Forest does not indicate that this phenomenon is specific to any one species. This makes it possible to establish the period during the 24 hours during which the insects can come into contact with domestic animals or humans. These data may have a practical significance in the event of infectious diseases, which are carried by the *Tabanidae*.

V. REGULARITY OF DISTRIBUTION OF THE *TABANIDAE* IN THE KAMPINOS FOREST AREA

The fact of the unevenness of distribution of the insects in this area has been known for a considerable time, and many authors have drawn attention to this. Skufin (1952) and Crosskey (1955) attempt to link the occurrence and distribution of *Tabanidae* with a definite type of vegetation mantle. Quantitative material obtained by Skufin from various biotopes indicates the great differences in the numerical distribution of the various species. In Olsufiew's opinion (1937) the factors drawing the insects together in large numbers are roads and forest clearings. These authors do not state in which way this or that property of the environment influences the number of insects occurring therein. Differentiation hypotheses can be formed on a basis of area as to the causes of quantitative occurrence of these insects. The agreement of the quantitative material with our assumptions may be accidental and does not necessarily depend on their genuineness. Thus the value as proof of material cited in support of such views is often problematic. This is especially true when the causal connection between the factors analysed and the number of animals is not defined.

The choice of factors governing the distribution of *Tabanidae* in the area is therefore of essential importance. Another difficulty in making this analysis is to demonstrate the mechanism of the action of a particular environment (usually understood as a given vegetation group) on the numerical distribution of the insects. The statistical picture of distribution percentage in various biotopes does not completely explain the area distribution to us, as it may be assumed that the numerical scheme of the *Tabanidae* in certain environments changes over a period of time.

The analysis of the area distribution of the *Tabanidae* was carried out on the Kampinos forest district. Here we meet several phyto-sociological groups distinctly separated from each other. The northern part of the area is occupied by marshy ground, covered by alders. belonging to the *Alneto-muscinetum* association. The alder groves are adjoined by extensive meadows forming a separate association of *Caricetum ripariae* et *acutiformis*. Further to the south is a pine wood — *Pinetum*, constisting of plantations of young trees and part of the old forest forming the Reserve. The pine wood is not uniform from the phyto-sociological point of view.

K o b e n d z a (1930) distinguishes several associations in this area, the most common being the pine and cranberry wood *(Pineto-Vaccinetum myrtilli)* on the dunes in the western section of the forest intendancy area. The cranberry does not grow in the dryest parts of the forest. The ground is covered with lichens. These areas are classified as *Pineto-Cladonietum*. Other types of pine wood, e.g. *Pineto-Festucetum,* form small patches within the intendancy area. The meadows belonging to the *Caricetum ripariae* et *acutiformis* association form the southern boundary of the intendancy, as they do in the northern section[1].

Chrysozona pluvialis (L.). Distribution in various biotopes in the Kampinos Forest in July 1952

Chrysozona pluvialis (L.). Rozmieszczenie w różnych biotopach w Puszczy Kampinoskiej w lipcu 1952 r.

T a b. XVII

Biotope Biotop	% of occurrence % występowania
Pineto-Cladonietum	0,0
Pineto-Vaccinetum	6,0
Alneto-Muscinetum	94,0

During the first stage of the work we succeeded in obtaining a picture of the distribution of certain species in the section of the Forest examined. In 1952, after a long period of drought, certain environments, especially those sections of the pine wood situated on higher ground (*Pineto-Cladonietum*) were completely devoid of *Tabanidae*. The distribution of the commonest species at this time of the year, *Chrysozona pluvialis* (L.), is illustrated by Tab. XVII. A similar picture of distribution in the respective biotopes of the Forest is exhibited by *Tabanus bromius* L. The result obtained indicates that differences exist for the *Tabanidae* in the area examined, and is similar to the schemes drawn up by S k u f i n (1952). Further research on the area distribution consisted in the comparative collections made from environments similar as regards the phyto-sociological standpoint. I devoted particular attention only to the

[1] According to K o b e n d z a's classification (1930).

commonest type of pine forest within the Forest area, the *Pineto-vaccinetum myrtilli.* It became clear that the numerical distribution of *Chrysozona pluvialis* (L.), is not even throughout this environment. Some sections of the forest are fairly densely populated, and others almost entirely devoid of these insects. Similar results were obtained when examining the meadow environment — *Caricetum ripariae* et *acutiformis.*

Fig. 32. *Chrysozona pluvialis* (L.). Degree of occurrence in various types of *Pineto-Vaccinetum myrtilli;* material obtained from roads and cross-sections of the area in July 1952: 1 — plantation of young trees, 2 — old wood without undergrowth, 3 — old wood with dense undergrowth

Chrysozona pluvialis (L.). Stopień występowania w rozmaitych typach *Pineto-Vaccinetum myrtilli;* materiały uzyskane z dróg i przekrojów terenowych w lipcu 1952 r. 1 — młodniak, 2 — stary bór bez podszycia, 3 — stary bór z podszyciem

Results obtained by the research work do not agree with data so far published (S k u f i n, 1952) on the dependence of numerical distribution of the *Tabanidae* on the vegetation mantle. The causes of unevenness in area distribution must therefore lie in other properties of the area.

When investigating the regularity of distribution of the *Tabanidae* in the Kampinos Forest, all the environments encountered were divided into two categories. This division is only significant with regard to the *Tabanidae.* In the first type are included all environments, regardless of their vegetation mantle, where development of the *Tabanidae* larve takes place — these are the banks and fringes ponds and bogs. This type of environment may be termed the producer environment, as the entire adult insect population originates here. The second type is the receiver environment, embracing a most varied range in a phyto-sociological respect — of environments in which the larvae of *Tabanidae* do not develop. All *Tabanidae* occurring here have entered from other environments.

Classification of the area under examination in this way made it possible to consider the phenomenon of the numerical distribution of individual species of *Tabanidae* in the area as the result of the process of radiation of the *Tabanidae* from one environment to another. The dispersal itself of the horse-flies from the hatching environment to other areas is the result of their biology. On account of their rapid flight, a relatively short time is sufficient for the insects to scatter from their hatching rounds to the adjoining areas. This phenomenon is not, however, governed by a chance direction of flight. If that were so, our observations vould give us a picture approaching diffusion, i.e. the number of horse-flies in the producer type areas would gradually decrease, and increase in the receiver type environment. Actually we have to do with two phenomena. The numerical distribution of the various species is never even, certain places are more attractive to the *Tabanidae*, and this attractiveness can alter regularly. The need therefore arises to search for factors attracting, or perhaps merely influencing, the occurrence of *Tabanidae* in the various sections of the Forest. As both preliminary and further investigations preculded the possibility of connecting these matters with the phyto-sociological character of the environment, it remained to search for the factors, less striking indeed to the human eye, but distinctly perceptible to the *Tabanidae*.

In the first part of this work I attempted to define the fundamental factors deciding in the first place on the phenomena of life of the various species. When investigating the area distribution I accepted some of them as factors governing the process of distribution in the Forest. Micro-climatic factors were not taken into consideration, on account of their extensive variations during the day, and their relatively slight ones in the area, especially as regards the essential factors for flight activity, temperature. With variability of this kind they cannot systematically influence the numerical distribution of the horse-flies, as in the area of the Reserve covered by the pine-cranberry wood, where a comparatively uniform microclimate prevails, the differences in the distribution of the *Tabanidae* is completely unrelated to the chlimate. As a result three factors were chosen as capable of influencing the congregation of insects in the various parts of the Forest.

1. T h e o c c u r r e n c e o f t h e h o r s e-f l i e s h o s t s. Large mammals, as only these form the object of attacks by the *Tabanidae*, do not belong to the category of animals remaining in one place bu move over the entire area of the Forest, particularly in the

case of wild animals. The numbers of deer cannot therefore form the basis of the characteristics of a small section of the area. Similarly in the case of domestic animals, such as horses and cows, there can be no question of such connections. It is, however, relatively easy to determine the frequency with which horses in harness or cattle are driven along the various forest roads, and establish a comparative scale of accessibility of host mammals in the respective places.

2. Accessibility of water. The significance of water for the physiology of *Tabanidae* has already been discussed. With their particular way of penetrating the environment, replenishment of water reserves is essential. The conditions under which water can be obtained is therefore an important factor influencing the accessibility of the given environment for this insects. The matter is simple in marshy environment, but in pine woods where there are no stretches of water, where dew dries quickly, the possibility of permanent habitation by the insects is limited, and they are obliged to fly away to other areas to search for water.

Way in which *Tabanus bromius* L. penetrate the forest. Observations carried out in July 1955 in the dry, compact plantation of young pine trees, 200 m. from belt of alders

Sposób penetracji lasu przez *Tabanus bromius* L. Obserwacja przeprowadzona w lipcu 1955 r. w suchym, zwartym młodniku sosnowym, 200 m od pasa olszyn

Tab. XVIII

	Number of individuals Liczba osobników	%
Penetration through forest Penetracja lasem	4	19
Penetration through paths Penetracja duktem	17	81

3. Method of penetration of the area. Not every environment is uniformly suitable for the flight of these insects. As appears from the observations carried out (Tab. XVIII) the areas

densely overgrown by bushes or compact plantations of young trees are not frequented by the *Tabanidae*, and penetration takes place almost entirely by means of the forest paths and clearings. Penetration in open spaces, meadows and fields is far more intensive than in dense woods and forests.

When investigating the distribution per area the following methods were employed: "human as bait", the Skufin trap, quantitative scoop and "observations". Collections using a human as bait were practised in the initial years of research work, and later this method was replaced by the use of the Skufin trap. The way in which the tests were made was varied. Comparative series were made on stations set up in seven different parts of the forest intendancy. Collection took place almost simultaneously on all stations, always at a temperature over 20°C. Twelve 5-minute tests were taken on each station. In order to compare the stations with each other, and calculate the indicators of occurrence, arithmetical averages from the respective series were used. In addition to the comparative series the area distribution was investigated by means of roads and cross-sections. Routes were marked out which passed through various types of environment through the area under investigation. The Skufin trap was moved along these routes, and collection was carried out not in units of time, but in units of area. The trap was moved and set up again at intervals of 20 steps, and the insects flying into it caught. The individual tests were collected in series, depending on the type of site. Arithmetical averages were also used for purposes of comparison. The quantitative scoop was used in accordance with the methods recommended for ecological collections. The observations were concerned with the method of penetration of the insects, the direction of their flight to and from the Skufin trap.

The material obtained by means of collections on the stations established enabled the numerical distribution in the section under observation to be determined. Spring species of small and medium sizes such as the *Tabanus fulvicornis* Meig., *T. maculicornis* Zett., and *Chrysozona hispanica* (Szil.) (Tab. XIX) congregate mainly in damp environments, or in those where drinking water is accessible from ponds or canals. About 50% of the *Tabanidae* in these areas occur in the alder-groves, and over 20% in the open wet meadows, where water is accessible. The remainder occur in dryer areas, such as the different types of pine wood. The distribution in the pine forests is very uneven. Roads frequented by people, or places where horse-drawn carts often pass, etc. in spite of their being without accessible water for the horse-flies have a relatively high occurrence indicator, this being particularly the case with the road leading to the forest, the insects penetrating here even during the longest period of drought. The occurrence indicator on much-frequented roads, despite the lack of water, is very close to the indicator for the wet meadows where there is no pasture for cattle or horses.

Quantitative* distribution of some *Tabanidae*-species on the respective stations of the Kampinos Forest intendancy, at the end of June and beginning of July, during a period of drought

Rozmieszczenie ilościowe* kilku gatunków *Tabanidae* na poszczególnych stanowiskach leśnictwa Kampinos na przełomie czerwca i lipca, w okresie posuchy

Tab. XIX

Station / Stanowisko — Species / Gatunek	Alder-grove / Olszyna	Village Nart / Wieś Nart	Reserve in depth of forest / Rezerwat w głębi	Reserve at edge of forest / Rezerwat na brzegu	*Pineto-Cladonietum*	*Caricetum* near forest intendancy house / Przy leśniczówce	*Caricetum* near alder-groves / Przy olszynach
Tabanus fulvicornis Meig.	1,63	0,04	0,00	0,04	0,00	0,84	0,91
Tabanus maculicornis Zett.	13,96	0,67	0,00	2,40	0,08	0,28	3,06
Tabanus bovinus Loew.	0,00	0,04	0,17	0,04	0,00	0,06	0,26
Chrysozona hispanica Szil.	0,17	1,46	0,00	1,70	0,00	2,70	0,56

* Indicative figures correspond to arithmetical averages obtained from comparative series. Cyfry wskaźnikowe odpowiadają średnim arytmetycznym uzyskanym z serii porównawczych.

Within the pine wood, unfrequented roads in the middle of the forest and especially dry parts of the wood are almost completely devoid of these insects, and the occurrence indicator in these places is always, near, or equal to zero.

The picture of the distribution of *Tabanus bovinus* L o e w, a representative of the large-bodied species, is slightly different, since the distribution remains more or less even whatever the type of forest, accessibility of water or food. The surface of its body in relation tc the total mass is smaller than in the case of small species, and therefore evaporation takes place more slowly. It is also possible that its rapidity of flight permits this species to penetrate the area freely, and renders it independent of factors strongly influencing the smaller species.

Quantitative distribution of the two main summer species on the respective forest stations at Kampinos at the end of July 1955 during a period of drought
Rozmieszczenie ilościowe dwóch głównych gatunków letnich na poszczególnych stanowiskach leśnych, Kampinos w końcu lipca 1955 r. w okresie posuchy

Tab. XX

Station / Stanowisko — Species / Gatunek	Alder-gove Olszyna	Village Nart Wieś Nart	Reserve in depth of forest Rezerwat w głębi	Reserve at edge of forest Rezerwat na brzegu	*Pineto-Cladonietum*	*Caricetum* near forest intendancy house Przy leśniczówce	*Caricetum* near alder-groves Przy olszynach
Chrysozona pluvialis (L.)	3,76	0,75	0,00	0,67	0,17	1,00	4,16
Tabanus bromius (L.)	0,67	0,50	0,00	0,58	0,25	3,56	0,08

The species occurring in the greatest numbers in the summer are the *Chrysozona pluvialis* (L.) and *Tabanus bromius* L. During the dry summer period the distribution of these species is similar to that of the spring species (Tab. XX). The interior of the forest, and also the completely dry sections of it (chiefly pine- and cranberry wood) are devoid of horse-flies. Only damp spots or those frequented by large mammals are areas of food penetration.

Material obtained from cross-sections and roads yields similar results. The correspondence of the numerical distribution of the *Tabanidae* with the factors described make it possible to interpret the causes and regularity of the numerical distribution of the insects in forest environments in a different way. It should not, however, be forgotten that the same objections can be made regarding these factors and reasoning as were put forward regarding other methods of analysing the area distribution of *Tabanidae*. It is often possible to obtain results which can be interpreted both from the point of view of the dependence of the numerical distribution of this insects on the vegetation mantle, and on other factors. Discovery of the correlation makes it possible to assume that causal connections exist between two phenomena examined, but it is not proof of their existence. The correlative connection becomes a picture of the causal phenomenon when based on a knowledge of the causal connections forming the basis of the phenomena investigated.

At the beginning of this work I demonstrated that attempts at indicating the dependence of the occurrence of *Tabanidae* on the character of the vegetation mantle lack foundation. It is easier, on the other hand, to accept the view that this insects are linked with forests or trees in general, chiefly as nocturnal resting-places. This may, of course, be o question of settling for the night on the highest point in its immediate surroundings, and not on a tree as a tree. Settling for the night at a height may be of importance from another aspect, e.g. protection from nocturnal enemies, chiefly the frogs occurring in great numbers in damp areas, or making sure of being warmed as rapidly as possible by the sun's rays in the morning. The layer of air above the treetops becomes warm far sooner than the layer immediately above ground level. Although we may assume the existence of a biological link between this insects and trees, we cannont consider their link with open areas, meadow and trees as other than very doubtful. We may even risk the statement that a meadow is a "non-typical" environment for the *Tabanidae*. As data obtained by means of collection using the Skufin trap show, meadows are the scene of far more intensive flight penetration than the interiors of forests. The numerical occurrence indicator in meadows is usually several times higher than that deep in the forest. Is it therefore, in view of this, impossible to link the *Tabanidae* ecologically with the meadow? One of the commonest species of *Tabanidae Chrysozona pluvialis* (L.). also occurs in the meadows. At the end of July, in the belt of meadowland lying on the southern boundary of the Forest, the number of individuals caught in a Skufin trap was approximately equivalent to 1 individual per 5 minutes. With flight activity such as this, scoop collections carried out in meadows and in the tops of trees in the group bordening the meadows give negative results Almost entire population of the *Chrysozona pluvialis (*L.) in this area takes part in penetration flights. As darkness falls and the temperature is lowered to the bottom limit of light activity of this species, penetration ceases, and the insects search for nocturnal resting places. In such cases numerical connection of the insects with the meadow or any other environment would be incorrect. Another phenomenon is important here: certain areas are temporarily inhabited by *Tabanidae*. Flights to the meadows take place during the daytime, and as night falls the insects withdraw.

An analysis of the numerical distribution of *Tabanidae* in the Forest area can therefore be carried out in another way, treating the numerical occurrence indicators as pictures extracted from the continuous process of re-distribution of the insects from one place to another in the Forest. It may be assumed that a change in any of the three factors determining the numerical distribution of the *Tabanidae* causes the insects to be re-distributed from one place to another. This would be expressed by a change in the numerical occurrence indicators on the various stations. Three such factors have been given, the first and third of which (accessibility of large mammals, and means of penetration) do not undergo change. It would be difficult to cut off access by humans or animals to the Forest. On the other hand, a change in the second factor (accessibility of water) takes place frequently in this area. Every heavy rainfall causes temporary retention of a large quantity of water, in the form of raindrops on leaves, in the moss, hollows in the ground etc. If the assumption of the influence of water on the distribution of the insects is correct, we shonld be able to observe a change in the area distribution. Where more or less uniform conditions of water accessibility exist throughout the area, the congregating points should be the places most attractive from the food aspect. In the summer of 1955, during the dry period, occurrence indicators for the various stations were determined. After several days of rain, a series of comparative collections by means of the Skufin trap (Tab. XXI) were carried out during the first hot afternon while the entire forest was still wet.

Chrysozona hispanica (S z i l.). Quantitative distribution* in the Kampinos Forest intendancy area depending on water accessibility at temperatures over 20°C

Chrysozona hispanica (S z i l.). Rozmieszczenie ilościowe* na terenie leśnictwa Kampinos w zależności od warunków dostępności wody, przy temperaturach powyżej 20°C

T a b. XXI

	Alder-grove Olszyna	Village Nart Wieś Nart	Reserve in depth of forest Rezerwat w głębi	Reserve at edge of forest Rezerwat na brzegu	*Pineto-Cladonietum*	*Caricetum* near forest intendancy house Przy leśniczówce	*Caricetum* near alder-groves Przy olszynach
In drought period W okresie posuchy	2,58	22,12	0,00	25,76	0,00	51,10	8,44
After rain Po deszczu	3,12	4,19	2,08	59,40	3,12	5,19	22,90

* Numbers correspond to percent of occurring individuals.
Liczby odpowiadają procentom występujących osobników.

During the dry period the population was chiefly concentrated in three places — around the ponds near the village of Nart, in the wet meadows in the southern part of the Forest, near the drainage canal, and on the main entry road to the middle of the forest. The actual interior of the forest was practically inaccessible for the *Tabanidae*. The *Chrysozona hispanica* (S z i l.) may serve as an example, this species being at the peak period of its numerical occurrence at this time. After rain the occurrence indicators for this species underwent a change. The number of individuals occurring near the ponds at Nart was approximately five times less, while the number of individuals concentrated on the meadows near the canal was approximately eight times less. At the same time the number of individuals on the main entry road to the forest was doubled, and the occurrence indicators for the interior of the forest increased. It is difficult to find a different interpretation for

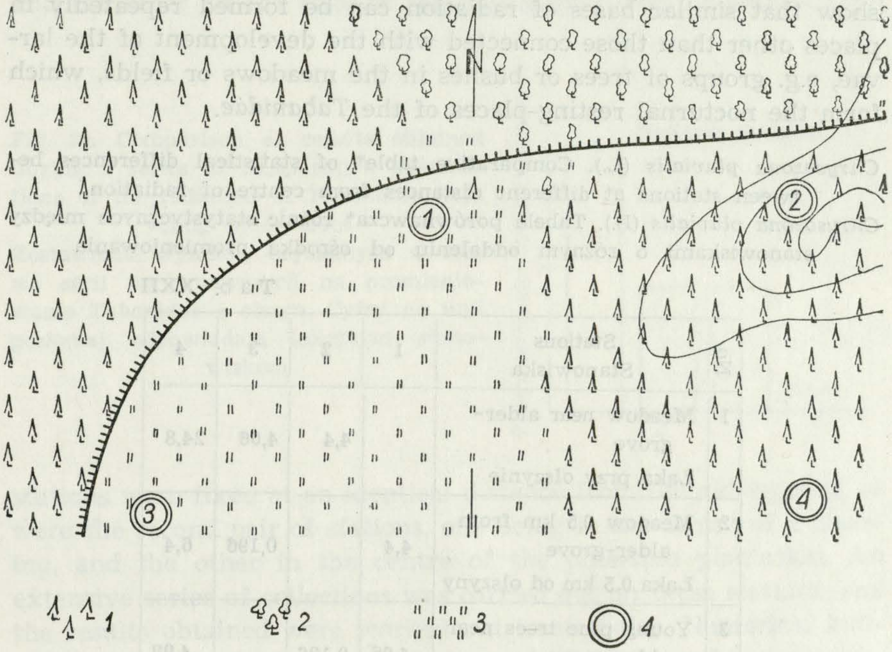


Fig. 33. Plan of distribution of stations during the series of comparative observations of radiation from the alder-groves of *Tabanidae:* 1 — pine forest, 2 — alder-grove situated on marshy ground, 3 — clearing, 4 — successive stations

Plan rozmieszczenia stanowisk przy seriach porównawczych nad promieniowaniem *Tabanidae* z olszyn: 1 — las sosnowy, 2 — olszyna położona na bagnach, 3 — poręba, 4 — kolejne stanowiska

this than that the insects which congregated by the main sources of water during the dry period scattered over the entire area, gathering in the places most attractive from a food aspect. The lack of water had proved the greatest impediment to settling in this area. During this period almost 60% of the total number of individuals caught on all stations were caught on the main road to the Forest. Evaporation of the water which took place after a few days caused another change in occurrence indicators, their value being similar to those obtained during the dry period.

The influence of the way in which the environment is penetrated on the area distribution of the *Tabanidae* remains to be discussed. The producer environment forms the base from which the *Tabanidae* spread to the adjoining areas. The observations carried out show that similar bases of radiation can be formed repeatedly in places other than those connected with the development of the larvae, e.g. groups of trees or bushes in the meadows or fields, which form the nocturnal resting-places of the *Tabanidae*.

Chrysozona pluvialis (L.). Comparative table* of statistical differences between stations at different distances from centre of radiation

Chrysozona pluvialis (L.). Tabela porównawcza* różnic statystycznych między stanowiskami o różnym oddaleniu od ośrodka promieniowania

Tab. XXII

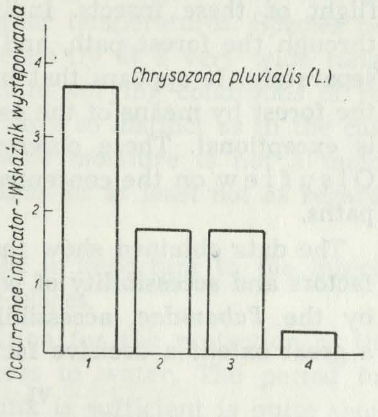
No.	Stations Stanowiska	1	2	3	4
1	Meadow near alder-grove Łąka przy olszynie		4,4	4,06	24,8
2	Meadow 0,5 km from alder-grove Łąka 0,5 km od olszyny	4,4		0,196	6,4
3	Young pine trees near alder-grove Młodnik sosnowy przy olszynie	4,06	0,196		4,98
4	Young pine trees far from alder-grove Sośniak w głębi	24,8	6,4	4,98	

* Compared by formula
Porównano przy pomocy wzoru $\frac{M_1 - M_2}{\sqrt{m_1^2 + m_2^2}}$

Investigations of the means of penetration and permeability of certain areas for the *Tabanidae* were carried out in the northern part of the Kampinos forest intendancy. The base from which the insects radiate in this section of the Forest are the wet alder-groves, bordered by meadowland, a former clearing now overgrown to a height of about 1 metre, and dense plantation of young pine trees, situated on sand dunes. The undergrowth consists partly of ground vegetation and partly of heather. A plan of this area is given in Fig. 33. Four stations, in two pairs, on which Skufin traps were set up, were established in the area under examination. The first pair differed only as regards site — one station being in an open space, in a clearing, and the other on the edge of the young pine tree plantation. Both

Fig. 34. Comparison of results obtained during a series of comparative observations of the radiation of *Tabanidae* from young alder trees

Zestawienie wyników uzyskanych w czasie serii porównawczych na promieniowanie *Tabanidae* z olszyn. Cyfry na linii poziomej odpowiadają kolejnym stanowiskom



stations were fixed at an identical distance from the alder-grove, as were the second pair of stations, one being in the centre of a clearing, and the other in the centre of the pine-tree plantation. An extensive series of collections was carried out on these stations, and the results obtained were worked out in statistics. Numerical indicators are given in Fig. 34 and comparison of the values of arithmetical averages in Tab. XXII.

All the *Tabanidae* caught on these stations could only originate in the alder-grove, as the areas further to the south, within the reserve, were devoid of these insects during this period, and the areas in which the stations were situated were too dry to permit of the insects settling there permanently. The results obtained make it possible, therefore, to state the "transit capacity" of certain environments for the *Tabanidae*. It appears that the wall of dense, but low, forest, about 20 metres wide, is equivalent to the insects being approximately 0,5 km distant from their base in open speces. Numerical indicators on station No. 3 (pine trees near alders) and No. 2 (clearing about 0,5 km. from alders) are identical from a statistical point of view. Penetration is most intensive in open spaces near the base of radiation. Station No. 4 (centre of pine trees) situated in a ry wood, on a forest path, about 0,5 km from the alder-grove, requires special discussion. A half-kilometre belt of dense forest forms an insurmountable obstacle to the *Tabanidae*. On account of the very small number of horse-flies approaching, additional observations were carried out here on the means of penetration of the *Tabanus bromius* L., a species easy to recognise during flight even at a distance of several metres. The observations concerned the approach flight of these insects. Individuals approaching the Skufin trap through the forest path, and through the forest itself, were noted separately. It appears that over 80% of the individuals penetrate the forest by means of the paths, and flight through the dense area is exceptional. These observations confirm the data supplied by Olsufiew on the concentration of insects in clearings and forest paths.

The data obtained show that in addition to the influence of food factors and accessibility of water on the occupation of a given area by the *Tabanidae*, accessibility for flight penetration is also to a great extent a decisive factor.

VI. SUMMING-UP

Investigations carried out on the ecology of *Tabanidae* in the extensive forest complex of the Kampinos Forest near Warsaw yielded a series of results both as regards collection technique and information on the ecology of these insects.

Two methods were applied with the aim of investigating the numbers of the *Tabanidae:* "panes" — covered with orchard adhesive lime, and the quantitative scoop. The selectivity of the respective methods in action, and size of tests necessary to solve the problems involved was also discussed.

The populations of flying insects of several of the most common species of *Tabanidae* have a definite structure and composition. The structure of the population was examined as regards flying insects — it is of an aggregational character. The *Tabanidae* move about the area in groups consisting of about 7—15 individuals, both males and females usually forming the groups. It has been confirmed that all the females lead a similar life, irrespective of their physiological state, and in view of this it may be assumed that a population belonging to the *Tabanidae* family form a whole from the ecological point of view.

The factors included in the composition of the ecological niche of the *Tabanidae* were defined in general terms — they are, temperature, relative atmospheric moisture, light, water and food.

Adaptation to flight in definite air temperatures and relative moisture are very distinct. It may be generally stated, that in the genus *Tabanus* L. the spring species, on account of their tajga origin, are adapted to flight at lower temperatures, summer species, Central European and especially those originating in South Europe, exhibit greatest flight activity at higher temperatures. Species belonging to the *Chrysozona* M e i g. genus fly at a very wide range of temperatures. Adaptation to flight in varying conditions of relative atmospheric moisture is not always so distinct as in the case of temperature adaptation. Atmospheric moisture is not a factor clearly limiting the possibilities of flight, or at least not as regards the majority of species examined.

The direction and intensity of light is important to the insects when searching for nocturnal resting-places.

Amongst others, an essential condition for the protection of the organism against overheating is access to water. The period for which the water taken up at one drink is sufficient is quite short in the case of the individual species, and therefore the need for constant replenishment arises.

The species of *Tabanidae* occurring in the Forest do not exhibit food specialization, and in practice they are capable of taking blood from all the large mammals found there. Detailed examination of food selectivity (T e r e t e r j a n, 1954) establishes that certain species of the *Tabanidae* usually attack definite parts of the animal's body. Differentiation of feeding places on the host therefore occurs.

Taking the factors forming the ecological niche as a basis, the distribution of *Tabanidae* in a typical environment — alders — was examined. The area of flight and its vertical extent both during the day and at night, was examined. The zone of penetration flight was also defined.

A hypothesis as to choice of nocturnal resting-place by the *Tabanidae* was put forward. An analysis of the distribution of *Chrysozona pluvialis* (L.) on the basis of material collected by the scoop method showed that tree tops are the chief nocturnal resting-place of these insects.

In the case of European *Tabanidae*, no differentiation as to the time of penetration flight during the day by the various species could be confirmed. Period of occurrence and seasonal dynamics, especially of species closely related systematically, varies markedly. Beginning, peak period and end of flight never coincide.

In investigating the regularity of area distribution of the *Tabanidae* on the basis of quantitative material coming from an environment phyto-sociologically uniform, the connection, proposed by certain authors, between the numbers of *Tabanidae* occurring and the vegetation mantle was held to be incorrect. The differences in the numbers of *Tabanidae* occurring in various parts of the pine and cranberry wood were found to be greater than the corresponding differences between the alder-groves and meadows.

The environments varying from a botanical point of view were divided into those which produce horse-flies and those in which the insects settle. Factors attracting these insects to an area are: water, food and nocturnal resting-places. The number of *Tabanidae* in a given place depends on a combination of these factors, and on the space structure of the environment itself, which influences the possibility of penetration flight. Numerical distribution undergoes constant changes in time.

The following were demonstrated on a basis of quantitative material:

1) influence of these factors on the number of *Tabanidae* occurring,

2) variations in distribution caused by a change in one of the factors — accessibility of water,

3) existence of the radiation of *Tabanidae* from one environment to another, and possibility of formation of further centres of radiation,

4) influence of the space structure of the environment, defined by the height and density of the vegetation mantle, on the possibility of penetration flight by the *Tabanidae*.

The collection of material for this work and analysis of the material was aimed at checking whether a definite group of environment conditions — the ecological niche — plays a real part in the ecology of the *Tabanidae;* on the basis of these factors a series of hypotheses were formed and examined regarding the course of ecological phenomena and the mechanism governing them.

A knowledge of the ecological niche of the species (the material collected clearly indicates the specific character of the niche for the species concerned) is not only an instrument for investigation of ecology, but may also have great significance for other sciences. In zoogeography a knowledge of the ecological niche of the given species gives the key to the discovery of the origin of the species. In taxonomy investigation of the ecological niche is the means whereby it is possible to check the connections of taxonomical solutions, usually based on morphology.

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NISZA EKOLOGICZNA KILKU GATUNKÓW ŚLEPAKÓW (*DIPTERA, TABANIDAE*) W PUSZCZY KAMPINOSKIEJ KOŁO WARSZAWY

Streszczenie

W trakcie badań przeprowadzonych w latach 1951—1955 w Puszczy Kampinoskiej pod Warszawą zebrano dane, dotyczące ekologii pospolitych europejskich gatunków *Tabanidae*. Na wstępie omówiono sposoby badania związku populacji ze środowiskiem. Przeprowadzono krytykę kierunku, który jako punkt wyjścia do badań przyjmuje właściwości środowiska i opartą o nie klasyfikację czy podział środowiska na jednostki mniejsze. Uzasadniono celowość przyjęcia w badaniach środowiskowych jako punktu wyjściowego wymagań gatunku. Jeśli chodzi o *Tabanidae*, badania te zostały oparte na rozszerzonej koncepcji niszy ekologicznej oraz analizie podstawowych zjawisk fizjologicznych, wynikających z budowy i trybu życia *Tabanidae*.

Opis Puszczy przyjęto za podstawę do wyjaśnienia genezy fauny, która wykazuje duże pokrewieństwo z fauną tajgi niziny rosyjskiej. Ponad 40% występujących w Puszczy Kampinoskiej *Tabanidae* to typowi przedstawiciele tajgi. Gatunki te stanowiące genetycznie element wcześniejszy występują głównie wiosną. Latem miejsce ich zajmują gatunki środkowoeuropejskie.

Omawiając literaturę, główną uwagę zwrócono na metody zbierania materiału, ilości osobników, ujęcie zagadnień ekologicznych oraz powiązanie ich z ogólną problematyką ekologiczną. Stwierdzono, że na skutek wybiórczości poszczególnych metod oraz stosowania dużych prób możliwości uzyskania pełnego obrazu życia gatunku były ograniczone. Dlatego też podejmowana tematyka często miała charakter wycinkowy.

W części poświęconej metodyce omówiono szczegółowo technikę połowów, wybiórczość działania poszczególnych metod oraz wpływy rozmaitych czynników na uzyskany przy ich pomocy materiał. Wprowadzone zostały do badań nowe, nie stosowane dotychczas metody: szyby pokryte lepem sadowniczym oraz czerpak ilościowy. Specjalny nacisk położony został na wielkość prób i wartość dowodową otrzymanych materiałów. W miarę możliwości autor stosował krótki czas połowu, tzw. próby małe. Pozwoliło to na zebranie dużej liczby powtórzeń i dzięki temu dało możność kontroli statystycznej poprawności uzyskanych wyników. W trakcie badań te-

renowych zebrano około 3 000 prób ilościowych przy pomocy rozmaitych metod. Ogółem złowiono około 7 500 osobników *Tabanidae*.

We wstępnej analizie materiałów stwierdzono, że przy pomocy pospolicie stosowanych metod, odławiających selektywnie tylko określone kategorie osobników, możemy pracować nad zagadnieniami dotyczącymi całej populacji. W tym celu przeprowadzono porównanie materiałów uzyskanych za pomocą rozmaitych metod połowu. Pozwalają one stwierdzić, że gatunek w rodzinie *Tabanidae* stanowi ekologiczną całość. Nie zachodzi tu rozbicie populacji na grupy o odrębnym trybie życia. Wyniki te pozwalają na stosowanie prostej, lecz działającej selektywnie metody połowów na pułapkę Skufina i wnioskowanie na podstawie uzyskanych materiałów o całości populacji.

W dalszym ciągu przeprowadzono analizę struktury populacji w oparciu o badanie frekwencji wariantów ilościowych w jednominutowych połowach na pułapkę Skufina i kałużę śmierci. Przez porównanie uzyskanych rozkładów z rozkładami Poissona za pomocą kryterium X^2 stwierdzono wyraźną tendencję do tworzenia skupień. Na podstawie tych danych stwierdzono, że populacja owadów latających *Tabanidae* ma strukturę agregacyjną. W skład skupienia wchodzą zarówno samce, jak i samice. Agregacyjność tę stwierdzono w różnych sytuacjach życiowych. Również penetracja pokarmowa ma charakter stadowy. Wnioski te uzupełniono obserwacjami terenowymi.

We wstępie do analizy wpływu rozmaitych czynników środowiska na ekologię *Tabanidae* przedyskutowano zjawiska termiczne i bilans wodny oraz możliwy związek fizjologii lotu z warunkami środowiska. W trakcie badań ustalono wartości progowe temperatur, powyżej których rozpoczyna się lot. Zbadano wpływ temperatury powietrza na aktywność lotu. Krzywe obrazujące tę zależność są charakterystyczne dla gatunku i wskazują na dużą specjalizację termiczną. Z rodzaju *Tabanus* L. gatunki z pochodzenia tajgowe rozpoczynają lot przy temperaturach 14—16°C. Maksimum aktywności lotu jest u nich zwykle przy temperaturach niższych niż u gatunków środkowoeuropejskich lub pochodzących z Europy południowej, u których dla rozpoczęcia lotu potrzebna jest również wyższa temperatura. Gatunki należące do rodzaju *Chrysozona* M e i g. wykazują mniejszą specjalizację i latają przy temperaturach 14—30°C.

Doświadczenia nad wpływem światła na *Tabanidae* przeprowadzono w warunkach laboratoryjnych. W doświadczeniach wykazano, że ślepaki przemieszczają się zawsze w kierunku padającego światła. Dane te potraktowano jako wskazówkę przy poszukiwaniu miejsc noclegowych *Tabanidae* w przyrodzie.

Związek lotu *Tabanidae* z wilgotnością względną powietrza jest wyrażony dużo słabiej niż związek z temperaturą. Niektóre gatunki nie wykazują żadnej zależności lotu od zawartości pary wodnej w powietrzu. U szeregu gatunków hygrofobność występuje zupełnie wyraźnie, dwa ze zbadanych gatunków przystosowane są do lotu przy wysokich wartościach wilgotności względnej powietrza.

Badanie tempa zużywania pobranej przez ślepaki wody wskazuje na to, że muszą one często uzupełniać jej zapasy z otaczającego środowiska. Brak zbiorników wodnych, z których mogłyby korzystać, wyklucza możliwość zasiedlania pewnych terenów na stałe. Poważną rolę w rozmieszczeniu terenowym *Tabanidae* odgrywa również występowanie dużych ssaków. Wpływ innych czynników uznany został za mniej ważny.

Po analizie poszczególnych elementów tworzących niszę ekologiczną podjęta została próba zbadania rozmieszczenia *Tabanidae* w typowym dla nich środowisku — olszynach. Przede wszystkim określony został rozkład pionowy latających osobników. Zestawienie wyników wskazuje na zróżnicowanie pionowe obszarów lotu. Przestrzeń do 4 m nad ziemią stanowi teren, w którym odbywa lot największa ilość osobników. Lot w tej warstwie powietrza nie ustaje również w nocy. W warstwach wyższych, mniej więcej na poziomie koron drzew, lot odbywa się tylko we dnie. Dane dotyczące lotu ponad koronami drzew oparte są tylko na obserwacjach lotu o świcie. Osobniki latające poniżej koron drzew znajdują się w obszarze penetracji pokarmowej, latające wyżej nie reagują na przynęty pokarmowe.

W nocy większość osobników skupia się w koronach drzew, które stanowią typowe miejsca noclegowe *Tabanidae*.

Dynamika sezonowa ma przebieg charakterystyczny dla poszczególnych gatunków. Szczególnie u gatunków bliskich pod względem systematycznym nie ma wypadków pokrywania się początku oraz końca lotu. Początek lotu pokrywa się na ogół z nastaniem optymalnych warunków dla gatunku, natomiast koniec z reguły wyprzedza pojawienie się warunków nie sprzyjających. Przyczyny tego są trudne do ustalenia.

Aktywność dobowa lotu zgodna jest z wynikami, jakie otrzymali badacze radzieccy. Wskazuje ona na małą specjalizację poszczególnych gatunków. Zmiany w natężeniu aktywności lotu skorelowane są z wahaniami temperatury i natężeniem światła słonecznego.

Badania rozmieszczenia terenowego *Tabanidae* przeprowadzone zostały na obszarze leśnictwa Kampinos. Rozmaite pod względem szaty roślinnej środowiska podzielone zostały na dwa typy: środowisko — producent (gdzie odbywa się rozwój larwalny) i środowisko — odbiorca. Cała fauna w drugim typie środowiska jest wynikiem migracji *Tabanidae* z terenów typu — producent. Wskaźniki ilościowe mówią o nierównomierności i zmienności rozmieszczenia gatunków w środowisku typu — odbiorca. Działanie trzech czynników: dostępności pokarmu, wody oraz sposobu penetracji terenu, kieruje procesem rozmieszczenia *Tabanidae* w lasach. Wpływ wody i pokarmu wykazany został w eksperymencie terenowym. Wykazano także czasowe zasiedlanie terenów łąkowych w ciągu doby — przykład migracji. Zbadano sposób penetracji oraz przenikliwość rozmaitych środowisk roślinnych.