ANNALES AGRICULTURAE FENNIAE
Maatalouden tutkimuskeskuksen aikakauskirja
1967 Supplementum 2 Vol. 6
Seria ANIMALIA NOCENTIA N. 27 — Sarja TUHOELÄIMET n:o 27

BIONOMICS, ENEMIES AND POPULATION DYNAMICS OF JAVESELLA PELLUCIDA (F.) (HOM., DELPHACIDAE)

Selostus:

Viljakaskaan bionomiasta, vihollisista ja runsaudenvaihtelusta

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HELSINKI 1967

PREFACE

esent work is part of an extensive study leafhoppers of spring cereals and the they do to these crops. The study has by Professor Veikko Kanervo, the Department of Pest Investigation. ry work was started in 1955, and the vestigations were begun a year later. hor's part of this work pertained to er bionomics and the distribution of the while Osmo Heikinheimo, M. Sc., he nature of the injuries caused by leaf- and Aulis Tinnilä, M.Sc., was con- ith the control of these pests. A prelimi- ort of the work was published in 1957 o et al. 1957), and several brief com- ions have subsequently appeared. The publication is the first of three extensive planned on this subject.

the very start of these investigations, my , Professor Veikko Kanervo, has followed the progress of the work and seful suggestions during its different My colleagues Osmo Heikinheimo is Tinnilä have assisted me in the field nd examination of material. During the rtime at the Laihia field laboratory I re- valuable help, particularly from my wife, erttu Raatikainen, but also from ef field technician, Mr. Unto Rousku, as Miss Tellervo Ylipoti and Miss asarainen; the latter also assisted e examination of the material and analysis in the winter. Mr. Matti Honkavaara iss Marja-Liisa Potka helped to collect es.

The fungi of the family *Entomophthoraceae* were kindly identified by Dr. Magnus Gustafsson, the others by Dr. Heikki Roivainen. *Achorolophus gracilipes* was identified by Dr. Eero Karppinen and the spiders by Mr. Pekka T. Lehtinen, M.Sc.

In connexion with the statistical analysis, helpful advice was received from Dr. Jukka Koskimies and Mr. Erkki Mikkola, M.Sc.

Mrs. Hilkka Hakola, Mrs. Paula Keturi and Mrs. Taina Kuusela prepared most of the diagrams.

Laihia commune granted free use of the former Hulmi military area, several hundred farmers have allowed samples to be taken from their fields, and certain farmers, among them Mr. Väinö Rapila, have permitted field trials to be carried out on their land for many years. Both the Department of Agricultural and Forest Zoology of the University of Helsinki and the Department of Plant Husbandry of the Agricultural Research Centre provided working facilities durring two winters.

For many summers the South Ostrobothnia Experiment Station and the Korsholm Agricultural School collected samples, and the former also carried out certain trials.

The manuscript has been read by Professors E. A. Jamalainen, Veikko Kanervo, and Ernst Palmén as well as Dr. Martti Markkula.

These investigations were partically financed by special funds provided by the Finnish State in 1956—1962, while in the years 1961—1965 the United States Department of Agriculture awarded a grant for studying leafhoppers and the damage caused by them. In addition, the Emil Aaltonen Foundation, the Finnish Entomological Society and the University of Helsinki have offered financial aid.

The manuscript was translated by Mr. Edvin Risser with linguistic revision by M Margaret Perttunen.

To the above persons and institutio as to many others, I wish to express m appreciation for their valuable help w made this extensive 11-year work poss

Tikkurila, November 1966.

Mikko Raa

CONTENTS

I INTRODUCTION

purpose of this study was to determine
in aspects of the bionomics and fluctua-
numbers of *Javesella pellucida*, as well as
tors affecting these features in a region of
Finland where the species is abundant.
tudy, carried out at the Department of
vestigation of the Agricultural Research
is related to a more extensive research
dealing with the two virus diseases oat
dwarf (OSDV) and European wheat striate
(EWSMV), as well as their vectors and
Part of this overall project has been
hed earlier (e.g.: Heikinheimo 1957, Ka-
et al. 1957, Tinnilä 1957, Kanervo 1958,
nen 1958, Raatikainen and Tinnilä
and b, 1961, Raatikainen 1960 a, 1961 a
1962, 1966 a and b, Ikäheimo and Raa-
en 1961, 1963, Heikinheimo and Ikä-
1962, Heikinheimo and Raatikainen
Raatikainen and Raatikainen 1964,
kainen and Vasarainen 1964, Laurema
966).

he region of investigation, *J. pellucida* has
hown to cause damage to oats by its
either directly or indirectly (Kanervo
1957), and such damage has occurred
hout a wide area (Jamalainen 1957,
vo et al. 1957). In later studies, Nuorteva
958, 1959, 1962, 1965) showed that the
of the species is toxic, while Ikäheimo (e.g. 1960, 1961, 1964) demonstrated that the species transmits EWSMV and OSDV. In the region of investigation, the yield losses caused by OSDV have sometimes been very great, and at the same time a certain amount of damage has also been brought about by EWSMV (e.g. Heikinheimo and Ikäheimo 1962). On the other hand, the yield losses caused by the toxicity of the saliva have been very small.

In many other countries in Europe, *J. pellucida* is likewise a serious pest of cereals, particularly oats. The species transmits at least the following viruses: OSDV, EWSMV, Aster yellows virus and maize rough dwarf virus (e.g. Slykhuis 1958, Slykhuis and Watson 1958, Průša 1958, Vacke and Průša 1959, Klinkowski 1961, Blattný et al. 1965, Harpaz et al. 1965). The reduction of grain yield caused by the toxic saliva are apparently quite small in all countries, while those resulting from the viruses, especially OSDV, may be very large. Attempts to reduce such losses have been directed against the vectors, the viruses, or both (e.g. Kanervo et al. 1957, Tinnilä 1957, Vacke and Průša 1959, Lindsten 1961 b, 1964, Ikäheimo 1962, Jamalainen and Murtomaa 1966).

In this paper the plant nomenclature of Hylander (1955) and the leafhopper nomenclature of Ossiannilsson (1946—1947), Fennah (1963) and Wagner (1963) are mainly used.

II REGIONS OF INVESTIGATION

A. Location of field studies

The main region where these studies were carried out in the summers of 1956—1964 is situated in western Finland near the city of Vaasa (Fig. 1). This region includes the communes of Sulva, Mustasaari, Laihia, Vähäkyrö, Isokyrö and Ylistaro. The terrain is exceptionally level and well suited for crop production and dairy farming. The farms here are located along the banks of rivers. In general, the farm buildings lie close to the river itself and the fields are elongated strips extending away from the river. From the standpoint of agriculture, this region is made up of several zones parallel to the river. Bordering the river, usually on very fine sand or clay soil, is a zone of intensively cultivated fields adjacent to the farm buildings, while further back is an area of border fields on soil with a thin layer of peat. Behind this tilled land is a continuous zone of forests, beyond which lies a narrow zone of fields located on peat soil, at the back of which are extensive forests. In recent decades some farm buildings have been constructed in the distant fields, but their influence on the nature of this zone has been only of minor significance.

In the fields adjacent to the river, the main crops grown are those which are most profitable but demand the most labour, such as potatoes, root crops, and winter turnip rape. This first zone also includes pastures, sometimes with clover, and leys, as well as cereals, such as spring wheat and part of the barley, oats and winter rye. Further back from the river, in the area of border fields, there is less diversity in the crops cultivated, with emphasis on spring cereals and leys. The rotation scheme followed in this zone is often: rye, oats, barley, and 3—4 years of timothy ley.

In the zone of distant fields behind the first forest belt, grasslands become more dominant, since the soil here is usually acidic peat soil which is not well suited to the more exacting crops. The rotation scheme on these fields is often: oats or sometimes barley, followed by about 4 years of timothy ley. In this zone crops other than cereals and grass are seldom cultivated.

In the six communes within the region investigated, the total farming area on June 15, 1959, was 1 729 km², of which productive forest accounted for 50.6 %, unproductive forest 5.6, le land 33.6, waste land 8.1, cleared pasture natural meadow 0.5, garden 0.1 and misneous uses 0.9 %. The proportion of arable devoted to ley was 55 % and to cereals 35 %. he cereal area, the percentages of the different s were oats 39, barley 25, spring wheat 13, d cereals 7 and winter wheat 0.4 % (Official stics of Finland III: 54). Cereals and grass thus grown on about 90 % of the cultivated while the remainder was devoted to broaded crops or was lying fallow. Grasses were abundant on the cleared pastures, natural dows and wastelands, and they also occurred ome extent in other habitats as well. About % of the arable land was drained by open hes, and in these ditches and on their banks e were also many species of grasses (cf. TIKAINEN and RAATIKAINEN 1964). The vated land was divided into fields with s ranging from about 0.1 to 6 hectares. The age field was apparently about 1 hectare ize.

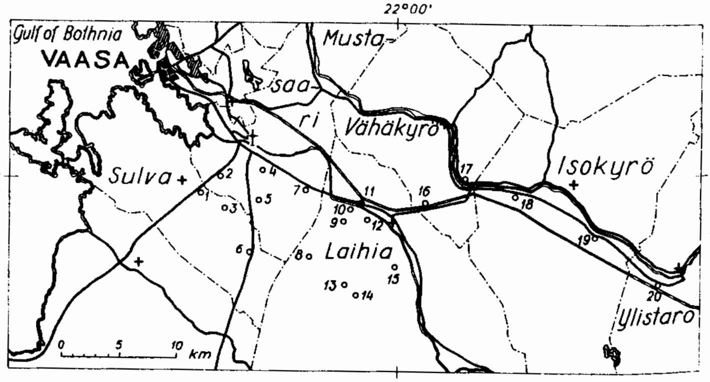


Fig. 1. Main region of investigation and sampling localities 1—20. Aeroplane symbol = airfield, + = church and center of settlement, dashed line = boundary of communes.

wenty localities in the region of investigation chosen for the field studies (Fig. 1). Howthe cereal fields and the first-year leys esshed under cereals, in which most of the ies were carried out, were seldom in exactly same sites in different years. Consequently, fields studied in each of the localities ingated were not always the same from year ear, although they were nearly always in the clearing. If it was not possible to use the clearing from year to year, another clearing chosen which was close, similar to the inal one in size, soil type and method of cultion. It was necessary to make such changes in certain of the small clearings, when OSDV and EWSMV caused large yield losses and the farmers consequently considerably reduced the area under oats.

Other regions of investigation. Data on the occurrence, abundance and enemies of the species were collected in different parts of Finland. Such data were gathered during numerous excursions made in the years 1956—1964. In addition the abundance of *J. pellucida* and *Panstenon oxylus* in leys of different ages was investigated in 9 communes in western Finland (cf. RAATIKAINEN 1960 a, p. 230).

B. Weather observations

In the western part of the main region of investigation is situated the Vaasa Meteorological Station, from where the data on mean monthly tempereture and humidity shown in Tables 1 and 2 have been obtained. Daily temperature and precipitation records are to be found in the periodical Kuukausikatsaus Suomen sääoloihin 50—58. The mean temperatures in the spring and autumn months during the period of these investigations were slightly higher than, or about the same as, the averages for the years 1921—1950, while the values for the summer months were slightly lower.

The summer of 1959 was particularly exceptional. In this year spring came early and was warm. Winter turnip rape began to flower around May 10, and *Prunus padus* blossomed about May 15. In the latter part of May and early June there were frequent night frosts, but the daytime tem-

1. Mean monthly temperatures (°C), April—November, at the Vaasa meteorological station in 1956—1964 (Kuukausikatsaus Suomen sääoloihin, 50—58)

	1956	1957	1958	1959	1960	1961	1962	1963	1964	Mean 1921—1950
il	—1.1	0.4	—0.1	3.4	2.1	1.6	2.5	1.8	1.3	1.0
	8.2	6.7	6.8	8.3	9.9	7.4	7.3	11.4	8.3	7.4
	13.6	11.2	12.7	14.0	15.0	15.8	11.4	12.3	12.0	12.3
	15.2	16.9	14.4	16.4	17.1	15.5	13.5	15.2	14.8	16.2
ust	12.3	14.1	13.9	15.1	14.4	13.2	11.9	15.0	13.3	14.3
mber	9.1	8.6	10.1	8.4	9.5	9.4	8.4	11.3	8.4	9.3
ber	3.5	4.3	5.5	3.9	1.1	8.5	6.3	5.3	6.7	3.6
mber	5.0	0.6	2.9	0.0	—1.9	2.3	0.5	—0.6	—0.7	—0.7

Table 2. Mean monthly relative humidity percentages, April—November, at the Vaasa meteorological statio 1956—1964 (Kuukausikatsaus Suomen sääoloihin, 51—58). The figures for 1956 as well as April 1957 were calcul from data of the Finnish Meteorological Office

	1956	1957	1958	1959	1960	1961	1962	1963
April	79	82	78	76	76	76	81	80
May	69	76	77	67	68	77	74	68
June	73	70	66	61	69	72	72	68
July	75	80	74	64	81	82	78	67
August	85	84	82	74	83	85	84	80
September	85	87	82	80	87	82	84	84
October	89	90	88	90	90	89	82	89
November	91	89	91	91	92	87	88	91

peratures were high. During June, July and August high pressure weather conditions prevailed, and September was the only month during the whole growing season with a mean temperature lower than the average for the years 1921—1950. That summer, cereals did not grow very tall; they ripened and were harvested earlier than usual. Other warm summers were those of 1960 and 1963, during which only one month had a mean temperature lower than that month's average during the period 1921—1950. The coolest summers were those of the years 1962, 1956 and 1957.

The figures showing mean monthly relative humidity percentages during the years of these studies were lowest in the early summer. At this time of year there is very little rain in the coastal districts, and drought periods lasting one month occur on an average once every three years, while droughts of at least two months' duration occur about once in 25 years (Keränen and Korhonen 1951, p. 108). The mean relative humidity percentages of the summer months were lowest in 1959, followed by the years 1963 and 1958. In the eastern area of the region, the early part of the summer of 1958 was also dry. For example, the June rainfall at the Ylistaro Experiment Station in 1958 was only 18 mm, and cereals did not attain a great height (see p. 43).

The meteorological observations relating to the insectary and laboratory were made with a Lambrecht thermohygrograph. The daily maximum and minimum values recorded with this device are not as extreme as the actual values.

C. Location of laboratory studies

The laboratory studies were carried out ev year during approximately the period May—Se tember in a field laboratory of the Departmen Pest Investigation situated in the commune Laihia (Fig. 1, locality 11). For experimental pu poses, a field insectary was constructed in th spring of 1957 having ground dimensions of 6.0 2.4 metres and a height of 2.5 metres (Fig The structure was designed by Mr. O. Heik heimo, after a model described by Peters (1955, Plates 2 and 3). The insectary was loca in the centre of a field 30 × 30 m in size su rounded by a grove of trees, which in turn wa situated in a larger cultivated clearing. The wa of the rearing section of the insectary were ma of wire screen, with the exception of the pa 65—125 cm above the ground, which was polythene film. The roof was painted silver. O sunny days the daily maximum temperature the table in the insectary was a few degress belo that in the open field, while the minimum slightly higher than outside.

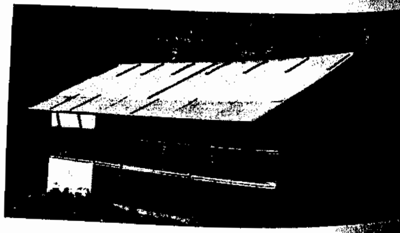


Fig. 2. Field insectary, where most of the cu were reared. Photo by Terttu Raatikaine

the species investigated differed in their habits, it was necessary both in the field the laboratory to use many different kinds pment and methods.

ring corks. A description of the corks is to be found in a publication by kula (1963, pp. 4, 5). Their outer dias 5 cm, thickness about 2 cm, and the diaof the inner rearing space 2.5 cm (Fig. 3). o open ends of the inner rearing space are d with either wide-mesh nylon gauze, fineterylene gauze or transparent cellulose film. While rearing adult Hymenoptera, a ops of water as well as dilute honey-water pplied daily to the gauze on the cork. rearing corks were used in the laboratory leafhoppers and their insect enemies, with ception of the first larval stage of *Elenchus nis*.

ri dishes. In some of the rearing trials nsectory, smooth-edged Petri dishes with de diameter of 9.5 cm and depth of 1.2 cm sed in the manner shown in Figure 4. gh the space between the lid and dish,

3. Rearing cork used for rearing *J. pellucida* nd its enemies. Photo by O. Heikinheimo.

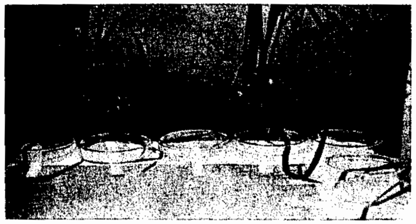


Fig. 4. Petri dishes used for rearing *E. tenuicornis* and *D. lindbergi*. Photo by Airi Rantanen.

usually two living leaves of oat plants were inserted into the dish. The leaves remained alive for several days. In the Petri dish was a strip of filter paper, one end of which extended outside the dish. When the air within the dish became too dry, it was moistened by applying water to the exposed end of the filter paper strip.

Such Petri dishes were used for rearing leafhoppers parasitized by *Elenchus tenuicornis* males and by *Dicondylus lindbergi*. Among other things, it was possible to observe the hatching times of the parasites and the durations of the different developmental stages. A maximum of ten leafhoppers was kept in a dish at one time. The final-instar larvae of *Dicondylus lindbergi* usually pupated on the walls of such dishes. The data presented later on the final-instar larvae, cocoons, pupae and adults of *D. lindbergi* were obtained mainly from such cultures.

Petri dishes lined with filter paper were also employed for mass cultures of pteromalid larvae during the winter. The filter paper was moistened when necessary, and the dishes were wrapped in paper which was kept moist. Furthermore, Petri dish cultures were used for determining the daily rhythm of emergence of pteromalids and *Anagrus atomus*.

Glass cylinders. To one end of a glass cylinder having a length of 9.5 cm and inside diameter of 1.6 cm, wide-mesh nylon gauze was fastened with insulation tape. Into the other end of the cylinder a short shoot of an oat plant was inserted. The space between the base of the shoot

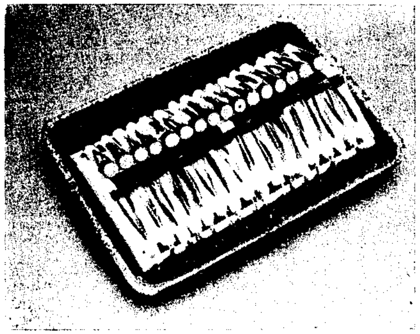


Fig. 5. Glass cylinders used for rearing *E. tenuicornis* females. Photo by Airi Rantanen.

and the walls of the cylinder was plugged with cotton wool. Such tubes were then placed in an inclined position on a rack standing in a water bath, in such a way that the roots of the oat plants were immersed in the water (Fig. 5). Such oat plants remained alive for more than a week.

Glass cylinder cultures were used for determining the discharging date of triungulinids of *Elenchus tenuicornis* as well as the subsequent survival time of the host.

Rearing boxes. Cardboard boxes 20 × 20 × 23 cm in size were provided with a glass tube 0.9 cm in diameter inserted into a hole made in the upper part of the box. Such boxes were employed for determining the number of insects in certain plant parts; the plant material was placed in the boxes and they were sealed with gummed paper tape. Such rearing boxes were placed in a shady spot in the insectary, and their contents kept moist. Every day between 8 and 9 a.m. the insects which had accumulated in the glass tube were removed. Not all the insects emerging from the plant parts were obtained from the glass tube, since some of the living specimens remained within the box. Moreover, some insects died inside the box. In the quantitative determinations, the insects remaining in the box were collected at the end of the trial. For example, about 5 % of the specimens of *Panstenon oxylus* emerging from oat stems remained in the box.

Rearing boxes were used in order to dete the annual emergence date of the first gene of *Anagrus atomus* and *Panstenon oxylus*, as their number per unit of surface area. The and living vascular plants from a ground 0.5 m² were generally placed in the rearing for these determinations.

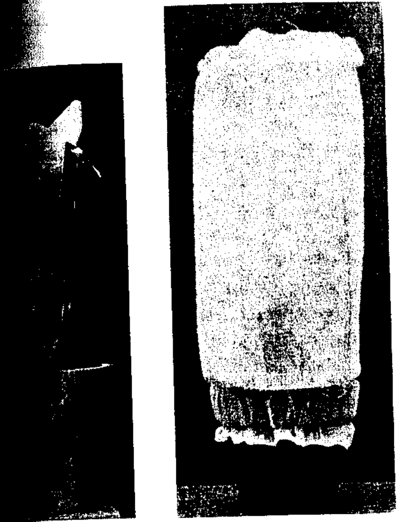
Glass tubes. In certain Hymeno cultures, use was made of glass tubes 6 long with an inside diameter of 0.9 cm bottom and inner wall of the tube were co with filter paper, which extended over abou of the wall, leaving the rest exposed as a window. The top of the tube was plugge cotton wool. A label was attached to the side of the tube with insulation tape, so keep the window upward. Such tubes were in a paperlined container in the insectary, an container was kept moist.

Such tubes were used for cultures of indi larvae and pupae of pteromalids and *A atomus*. They were also used for studying daily rhythm of emergence of the Hymenop

Glass tubes were also employed in de mining the number of triungulinids discha from *Elenchus tenuicornis*. In this case, afte first triungulinids had appeared, the parasi leafhopper and a piece of fresh oat leaf placed in the tube, which was plugged smooth rubber cork. When the triungulinid become attached to the wall of the tube and a pattern of small squares was drawn o outer surface of the tube, and the larvae cou with the aid of a microscope.

Plastic cylinders. Cellulose cylinders 29 cm tall and 9 cm in diamete used with 6″ flower pots, as shown in Two or four holes were made in the low of the cylinder and covered with nylon or gauze; the top of the cylinder was also co with the same kind of material. In some the plants inside the cylinder were allo grow out of the top, and the gauze carefully wrapped around the plants.

These cylinders were kept in the insecta used to rear leafhoppers.



nd 7. Plastic and gauze cylinder used for rearing *J. pellucida*. Photos by Airi Rantanen.

uze cylinders. From 6 to 10 plants own or planted in 6″ flower pots, and them was put white gauze attached to a cal wire framework (Fig. 7). The pots uried to their upper rim in the ground e insectary. Leafhoppers were reared in linders when studies were being made on ost plants, number of eggs, etc., as well n crossing trials were conducted.

es. Cages of three different sizes were these studies. The small cages had a basal 21 × 43 cm and a height of 26 cm. They ted of a wooden frame covered with galwire mesh No. 25—28 (Fig. 8). The top cage consisted of a removable lid. When ymphs of leafhoppers were reared in the the interior was lined with fine-mesh ylon fabric. The cages were placed either e insectary, or — when crossing trials onducted — in an open field protected he wind by a hedge. Leafhoppers were the small cages during the winter, and mes cultures were reared in them throughyear.

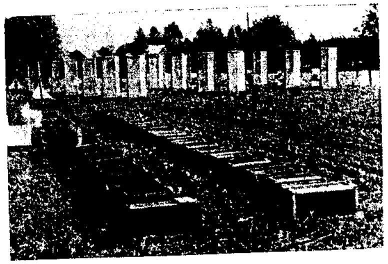


Fig. 8. Small cages in foreground and large ones in background, in which cultures of both healthy *J. pellucida* and those parasitized by *D. lindbergi* were reared. Photo by U. Rousku.

The medium-sized cages resembled the small ones, but their dimensions were 55 × 55 × 33 cm. They were placed in a cereal field, and seeds were sown or plants were planted at eight spots on the circumference of a circle about 40 cm in diameter within the cages. Selection experiments with host and oviposition plants were carried out in these cages. In the selection experiments there were four different plant species in one cage, and each species grew on two spots.

The large cages had ground dimensions of 56 × 56 cm and a height of 120 cm, and they were provided with a doorway (Fig. 8; cf. KANERVO et al. 1957, Fig. 11). In such cages the height of *Dicondylus lindbergi* cocoons in oats was investigated. *Javesella pellucida* leafhoppers parasitized by *D. lindbergi* were collected from the nearby field and placed in the cages.

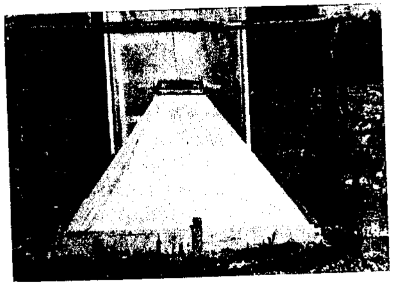


Fig. 9. Cloth funnel used for collecting pteromalids and *A. atomus*. Photo by U. Rousku.

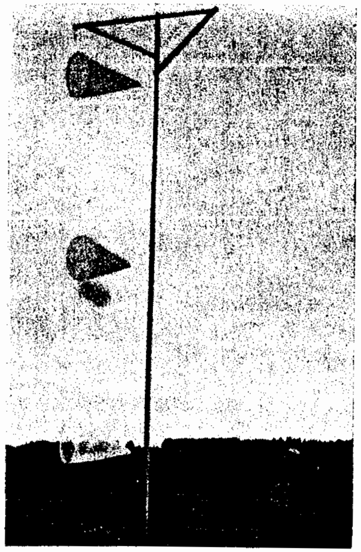


Fig. 10. Triple-level netting apparatus used for collecting migrating *J. pellucida* and pteromalids at different heights. Photo by M. Raatikainen.

Cloth funnels. These structures had a ground area of 0.5 m^2 and a height of 43 cm (Fig. 9). They were constructed in the following way: a square wooden frame was embedded in the ground and to it was attached a double layer of cloth in the form of a tetragonal pyramid. At the peak of the pyramid was a wooden frame to which two glass tubes were fixed. In some cases, small plastic cups were used in place of the glass tubes. These cloth funnels were kept on the field and the insects which had collected in the tubes or cups were removed every day around noon. The temperature within the funnels was considerably higher than that outside.

These funnels were used to determine the numbers of adult pteromalids and *Anagrus atomus.*

Netting apparatuses (cf. RAATIKAINEN 1960 a, Fig. 2). The circular metal-frame mouth of the apparatus had a diameter of 100 cm, and the funnel, made of white nylon fabric, was 165 cm long. At the base of the funnel was an opening formed by a circular metal ring 4.0 cm in diameter, through which the contents of funnel could be emptied. The centre of the mo of the apparatus was situated at a height 20 above the surface of the ground. The funnel rotatable and, like a weather vane, turned gether with its supporting arm into the direc of the wind. Three such netting apparatuses set up in first-year timothy leys, established un a spring cereal nurse crop, which were situ in the centre of clearings over 40 hectares in These three localities were at Mustasaari, on NW side of the airfield (cf. Fig. 1), at La (locality 9, Fig. 1) and at Ylistaro (locality The nets were emptied every evening betwe 8 and 9 p.m.

These netting apparatuses were used to vestigate the migration period of macroptero leafhoppers and those parasitized by *Elen tenuicornis* and *Dicondylus lindbergi* as well as pteromalids. In evaluating the results obtaine with these apparatuses, it must be borne in mi that 1) the apparatus operated only when a win was blowing; 2) the stronger the wind, the grea the flow of air and hence the more insects ente ing the net; 3) the animals collected were on those which were transported ± passively by wind or which for some reason voluntarily tered the net; 4) animals collected in the net cou leave it again (cf. the following apparatus).

Triple-level netting appara This device was similar to the previous one, it had three net funnels of 100-cm diameter pla at heights of 2, 6 and 10 (in 1959 only 9) met above the ground (Fig. 10). This apparatus placed in a second-year timothy ley on a clearing at Laihia (Fig. 1, locality 9), and the were taken down every evening at 8—9 p.m. emptying. This apparatus was used to investi the migration height of leafhoppers and th enemies. In interpreting the results obtained it, however, the same sources of error mu kept in mind as for the previous apparatus addition, during the periods when the wind blowing, the volume of air flowing through nets per unit time was greatest at the hig level and least at the lowest level. Conseque the numbers of insects collected in each of

nets are not fully comparable with one er.

eropterous leafhoppers and evidently also teromalids investigated are ± passively orted by the wind and readily accumulate net. When there is no wind, some of the ppers may escape from the net, but at s were made to empty the nets in the g before the wind had died down. During ytime period of operation, the weather was m so calm that the funnel collapsed.

nalysing these results, it would be desirable ow, for example, whether the daily numbers *stenon oxylus* obtained actually represent the sity of migration, or whether insects merely above their habitat could enter the net. lts obtained with these netting apparatuses previously been published by RAATIKAINEN a) and RAATIKAINEN and TINNILÄ (1961).

ction apparatus. Quantitative sam f leafhopper nymphs and adults as well as malid adults were taken with a suction atus. The use and reliability of this method previously been described (HEIKINHEIMO AATIKAINEN 1962). In each sample there three subsamples, each taken from an area 0 m^2. During sampling, the observer generally walked diagonally across the field from orner to the opposite one, and the first mple was often taken about 15 metres from dge of the field. According to HEIKIN and RAATIKAINEN (1962, p. 10), by using ethod 74.8 % of the nymphs of *J. pellucida* 7.5 % of the adults occurring in timothy ere obtained. The suction samples in the nt study were taken by the same person who cted the material for a previous study by NHEIMO and RAATIKAINEN (1962).

the years 1956 and 1957, suction samples of afhoppers in timothy leys (Fig. 17) were at weekly intervals at Ylistaro (Fig. 1, ty 20). In the autumn, similar samples were on the stubble of spring cereals containing dergrowth of young timothy ley (e.g. Table nd the following spring samples were again ted on the same leys (e.g. Table 90). In the 1958—1960, these samples were taken at localities 1, 3, 6, 9, 12, 17 and 20 and in the years 1961—1964 at all the localities 1—20 (cf. Fig. 1). The samples were almost always collected in the same fields where netting and plant samples had previously been taken. On the basis of the numbers of leafhoppers in the netting samples (Table 85), the approximate percentage of *J. pellucida* among all the *Javesella* nymphs can be calculated.

Sweep net. HEIKINHEIMO and RAATIKAINEN (1962) have described the sampling method and reliability of net sweeping. The samples were taken by the same person as in the investigation of HEIKINHEIMO and RAATIKAINEN (1962). Each sample usually consisted of either 3 × 20 = 60 or 60 + 140 = 200 sweeps. The subsamples were taken by walking across the field in the same way as for the suction samples. According to HEIKINHEIMO and RAATIKAINEN (1962, p. 19), the number of sweeps required in timothy ley to obtain a number of *J. pellucida* nymphs equivalent to the population of 1 m^2 is 396.2 ± 80.4 and that of adults 86.0 ± 18.8. In spring cereals the numbers of healthy adults equivalent to the population of 1 m^2 are obtained with 50.7 ± 11.8 sweeps and of parasitized adults with 39.5 ± 15.5 sweeps.

In the years 1958—1962, netting samples of leafhoppers and their enemies were taken at weekly intervals in oats and in first-year leys established under spring cereals (Figs. 18—20) at Laihia (Fig. 1, locality 9). At the end of June and beginning of July netting samples were taken in oats and spring wheat (e.g. Tables 64, 65 and 84). In 1958—1960, these samples were collected mainly in the same places where the suction samples had been taken, but in addition, sampling was done at localities 8, 11, 13—15 and 18 or in their vicinity. At the end of May and beginning of June netting samples were taken in leys (Fig. 1, localities 1—20), but in 1960 no samples were obtained from localities 7, 14 and 16 (Table 91).

Plant samples. The usual method used for sampling spring cereal plants was to walk through the field from one corner to the diagonally opposite corner. If the field was sufficiently large, the first sample was taken at about

15 metres from the edge. From this spot, 5—10 plants with their roots were collected. From there, a definite distance was walked, depending on the size of the field but usually 5—15 paces, and a second subsample of the same size was taken from immediately in front of the observer's shoe. This produce was continued across the field until about 10—20 subsamples and a total of at least 100 — or in some cases 200 — plants had been collected.

The plants were subsequently spread out on the floor, and from them every third or fifth plant was selected until 100 plants had been assembled. The plants containing eggs of leafhoppers weer separated by eye and later examined under the microscope. The initial separation of the plants was carried out by four persons, all of whom had been specially trained for this task and who were approximately equally careful in performing the work. Samples taken at weekly intervals from oats and spring wheat were always examined by the same person. Similarly, the same person always performed the microscopic examinations. The numbers of egg groups and/or eggs of delphacids as well as all stages of pteromalids and *Anagrus atomus* were counted in the plant samples.

In the years 1957—1960, plant samples were taken at weekly intervals at Laihia and Ylistaro, and in 1957 and 1958 also at Sulva (Fig. 1, localities 9, 20 and 3; cf. e.g. Fig. 16). In July, August and September samples were collected in oats and spring wheat (e.g. Tables 43 and 44). The oat and wheat samoles were taken at all the localities 1—20 (Fig. 1); however, in 1958—1960 wheat samples were not taken at localities 7 and 16, nor in 1959—1960 at site 14 either. During the entire period 1961—1964 and often in other years as well, sampling was done in the same fields where netting samples had been taken in late June or early July. From the numbers of delphacids in the netting samples (Tables 85 and 86), it was possible to calculate the approximate proportion of *J. pellucida* eggs among all the delphacid eggs present.

In the region of investigation, cereals were most always sown by drill. In August and Sep tember during the years 1957—1963, the numb of oat plants in an area of either 4 × 0.15 m 5 × 0.23 m^2 in 33 oat fields were counted. T average number of plants in these fields w found to be about 495 ± 16 per squ metre.

Mite counts. The numbers of leafhopper parasitized by *Achorolophus gracilipes* were count by inspection in the field. The observer crawle or lay on the ground, and counted all the pa sitized and healthy leafhoppers visible at severa sites in the field. The same person performed th counts which were used in year-to-year com parative studies. In certain other comparative studies, 1—4 persons participated. Since it wa easier to observe the leafhoppers parasitized b the red-coloured mites than the healthy spec mens, it is possible that the percentage of para sitized leafhoppers is somewhat too high. On th other hand, the percentage of parasitism ob tained by the netting or suction samples is likel to be still more erroneous, since the mites oft become detached during the sampling proce

Statistical calculations. In add tion to the mean value, the standard error of th mean (S.E.) is often given. The standard viation, on the other hand, is not reported the chi-square test the Yates correction w applied. If, according to analysis of varian there were significant differences, the signific differences between the means were computed the Tukey-Hartley method (cf. Snedecor 195 p. 251). In certain tables (for example Table the means which do not differ from one anot are indicated by the same letter written them. The levels of significance of differe used in this study are according to Sned (1959, pp. 126, 525). A single asterisk indic probabilities between 0.05 and 0.01, while asterisks show probabilities equal to or less 0.01. Three indicate probabilities equal to than 0.001. If the figures have been transfor this is reported in the text.

IV JAVESELLA PELLUCIDA (F.)

sella pellucida has been placed in over 10 nt genera (cf. Metcalf 1943, Fennah Wagner 1963). The generic names most only used are *Calligypona*, *Delphacodes*, *Del-* nd *Liburnia*. At present, the species is in the genus *Javesella*, the type species *J. pellucida* (Fennah 1963). This species the type species of the genus *Weidnerianella* bed by Wagner (1963), but since Wagner's was published about two months later than h's, the first-mentioned name is valid.

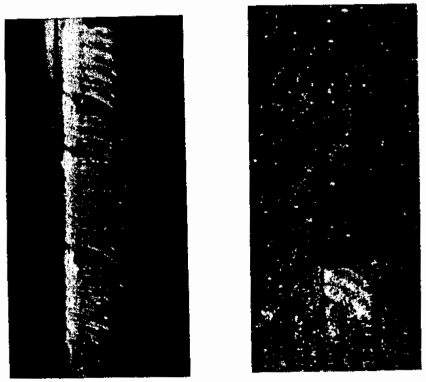


Fig. 11. Eggs of *J. pellucida* in the stem and leaf of oats. Photos by O. Heikinheimo (Kanervo et al. 1957) and M. Raatikainen.

A. Distribution

ella pellucida is a boreal-circumpolar species quite continuous distribution in both the ctic and nearctic regions. The northern- ocalities of the species are in the northern of Fennoscandia and Alaska, while the rnmost ones are in North Africa, East nd Central America (cf. Metcalf 1943). urope there are many reports concerning ribution and abundance of *J. pellucida*. It mon — and in many places abundant — British Isles (Le Quesne 1960, p. 44), ny (e.g. Haupt 1935, p. 142, Wagner . 7, 1939, p. 125, Kuntze 1937, p. 374, arpour 1960, p. 284, Remane 1958, er 1962, Emmrich 1966 b), Czechoslovakia la 1954, 1958, 1960, Okáli 1960, Vacke růša 1961), Denmark (Jensen-Haarup 51) and Fennoscandia (Sahlberg 1871). den the species has been encountered in every biogeographical province (cf. nilsson 1946—1947), but it appears to be ommon and abundant in the coastal dis- f northern and central Sweden (cf. Lind- 961 b, pp. 252, 253, Jürisoo 1964). Similar Finland *J. pellucida* has been found in all geographical provinces of the country, the north it occurs as far as the subarctic Lindberg 1947). With the exception of rthern districts, the species is common hout the country. It seems to be most abundant in the coastal region of the Gulf of Bothnia as well as in the interior of the country at the same latitude. In the southwestern, southern and northern parts of Finland it is not so plentiful as in the above-mentioned regions.

B. Developmental stages

Egg. The young eggs of *J. pellucida* are greyish-white in colour, but later turn pale reddish-brown. Their shape is typical of delphacid eggs, oval and slightly curved (Fig. 11). Both the length and the breadth of the eggs are smallest when the eggs are young. As the embryo develops within the egg, both dimensions increase (Fig. 12 and 13). The increase in thickness does not, however, take place evenly in all parts of the egg; it was found that when eggs were deposited in stems of plants, the increase in thickness was least at the anterior end and greatest at the posterior end. Both dimensions of the egg are at a maximum just before hatching. There are differences in size between eggs of different females which persist throughout the developmental period of the eggs. The length varies from 0.80 to 1.24 mm and the breadth

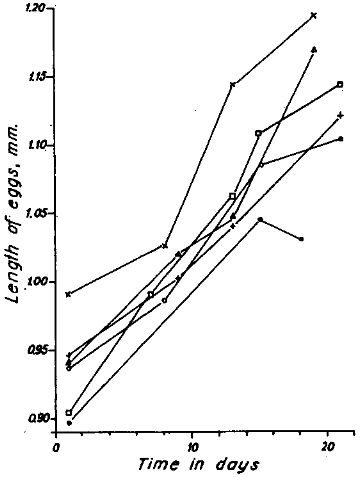


Fig. 12. Lengths of eggs of six *J. pellucida* specimens. Rearing temperature +18.5°C. Each point represents the mean of ten eggs. Same material as in Fig. 13.

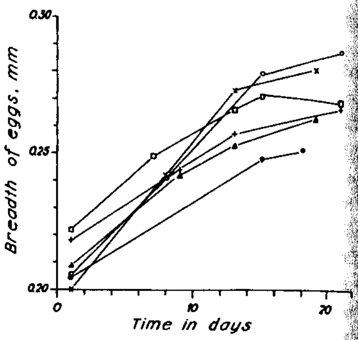


Fig. 13. Breadth of eggs of six *J. pellucida* specimens. Each point represents the mean of ten eggs. Same material as in Fig. 12.

from 0.17 to 0.29 mm (n = 400). The thickness of the anterior end ranges from 0.12 to 0.19 mm.

In the region of investigation the eggs of *J. pellucida* so closely resemble those of other delphacid species in the same region that it was not possible to distinguish them. The few statistical differences which are known in the egg length of, for example, *Megadelphax sordidulus* (Stål) (cf. Raatikainen 1960 a), *Dicranotropis hamata* (Boh.) (cf. Raatikainen and Vasarainen 1964), *Stiroma bicarinata* (H.-S.) and *J. pellucida*, are useless as distinguishing features in the field, since often the eggs have to be identified from the
alone or remnants after damage by Hymeno

N y m p h. Hassan (1939, pp. 356, 357
given a good description of the nymph
pellucida, while Tullgren (1925, pp. 54, 55
a brief description of five nymphal instars.
ever, the previous descriptions of the ny
instars were too incomplete to serve as
for distinguishing the different instars.
present work, the nymphal instars were
guished by the length of tne femur and
the hind leg as well as by the number of
on the spur (Table 3). These have been
to be good distinguishing features of ny
instars in several leafhopper species (c
Lindberg 1939, Williams 1957, Raati
1960 a, Raatikainen and Vasarainen

Table 3. Length (mm) of femur and tibia of hind leg of nymphs and adults of *J. pellucida* as well as number of spines on spur

	No. of specimens	Femur			Tibia			Spines on spur	
		Mean ± S.E.	Min.	Max.	Mean ± S.E.	Min.	Max.	Mean ± S.E.	Min.
1st instar ...	37	0.16±0.003	0.14	0.19	0.24±0.004	0.22	0.30	1.0±0.00	1
2nd » ...	37	0.25±0.003	0.24	0.29	0.36±0.005	0.33	0.43	1.0±0.00	1
3rd » ...	99	0.36±0.003	0.29	0.43	0.51±0.004	0.42	0.58	4.8±0.08	3
4th » ...	91	0.50±0.003	0.43	0.59	0.69±0.004	0.59	0.80	10.9±0.14	8
5th » ...	57	0.68±0.004	0.64	0.73	0.92±0.007	0.85	1.07	15.7±0.20	13
Male	27	0.91±0.009	0.75	0.98	1.29±0.014	1.10	1.41	20.2±0.54	15
Female	39	0.95±0.007	0.85	1.02	1.34±0.012	1.22	1.46	20.0±0.37	16

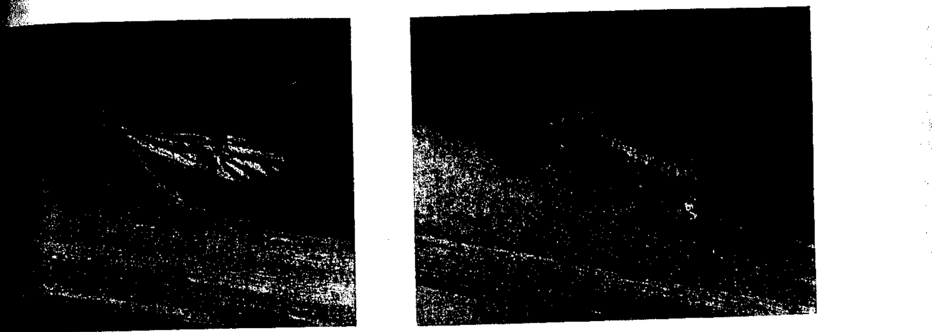


Fig. 14. Male and female of *J. pellucida*. Photo by L. Nordlund.

lear from Table 3, none of these features
ives a sufficiently reliable result, but when
e are used in combination, the nymphal
of each individual can be identified with
probability.

ult. The adult (Fig. 14) has been de-
in many works, but in general it was not
e to distinguish the female from those of
losely related *Javesella* species (cf. e.g. Le
1960). However, in the region of this
ation, the females could be identified ac-
since in that region virtually the only
pecies was *J. obscurella* (Boh.), which can
nguished from *J. pellucida* by the charac-
sented by Ikäheimo and Raatikainen
Distinguishing healthy specimens of *J.*
from those parasitized by *Elenchus tenui-*
as sometimes difficult on the basis of
logical characters, although in most cases
erences were clear (cf. Lindberg 1949,
rt-Behrisch 1960 a and b, Raatikainen
In the region of investigation there were
achypterous and macropterous (Fig. 14)
pers.

3 gives the lengths of the femur and
the hind leg of males and females as well
umber of spines on the spur. Both the
nd tibia of the female were found to be
than the corresponding parts of the male
2**, t = 2.94**), but no significant dif-
was found in the number of spines on
(t = 0.38, P > 0.05).

C. Life cycle

In Finland, Sweden and England, *Javesella pellucida* is univoltine (e.g. Kontkanen 1954, p. 152, Tullgren 1925, p. 56, Hassan 1939), while in Germany it is bivoltine (e.g. Kontkanen loc. cit., Remane 1958, p. 390, Afscharpour 1960, p. 285).

E g g s t a g e. The first eggs of *J. pellucida* were found at the end of June. In 1959 and 1960, when the spring and early summer were very warm, delphacid eggs were encountered as early as June 14. These eggs could not be identified as to species, but were evidently either *J. obscurella* (Boh.), or *J. pellucida*. In the years when the spring and early part of the summer were cool, eggs of *J. pellucida* were not found until the beginning of July.

In order to determine the duration of the egg stage, leafhoppers were allowed to oviposit for 24 hours in growing cereal stems in the insectary, after which a rearing cork was fixed to that place. Observations on hatching were made every morning at 8—9 a.m. The time elapsing between the deposition of the egg group and the hatching of the first egg is termed the minimum incubation period. At 17°C it was about one day less than the average incubation period, as seen from the following data on the hatching times of 17 egg groups:

Days after hatching of first egg in egg group	0	1	2	3	4
Number of nymphs hatched	36	42	9	6	2

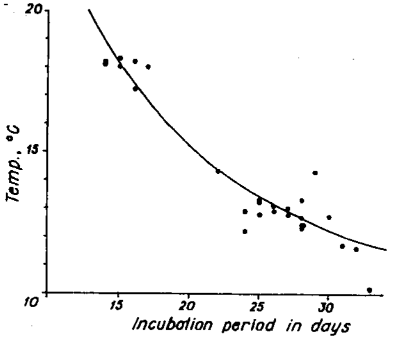


Fig. 15. Minimum incubation period of eggs of *J. pellucida* at different temperatures in the insectary.

In nature, the average duration of the egg stage appeared to be nearly 4 weeks. In calculating the duration of development, the following equation was used: t (T—c) = constant, in which t = egg period in days, T = mean temperature during the egg period, and c = constant to be calculated, which at the same time is the point of no development. For *J. pellucida* eggs, the equation is t (T—6.4) = 175.5 (Fig. 15). The equation is far from ideal and furthermore, it is based on the assumption that the temperature is constant (cf. ANDREWARTHA and BIRCH 1961, pp. 145—163). In the present work, however, the equation was used only to provide a general picture of development in conditions as natural as possible. The results of trials conducted at constant and variable temperatures did not differ appreciably from one another, as became evident from a parallel trial carried out indoors. Similarly, according to ANDREWARTHA and BIRCH (1961, p. 162), experiments made with different species at temperatures which varied within favourable limits as well as constant temperatures gave results that were in good agreement with each other. Discrepant results have also been reported, for example, by SCHWERDTFEGER (1963, p. 137).

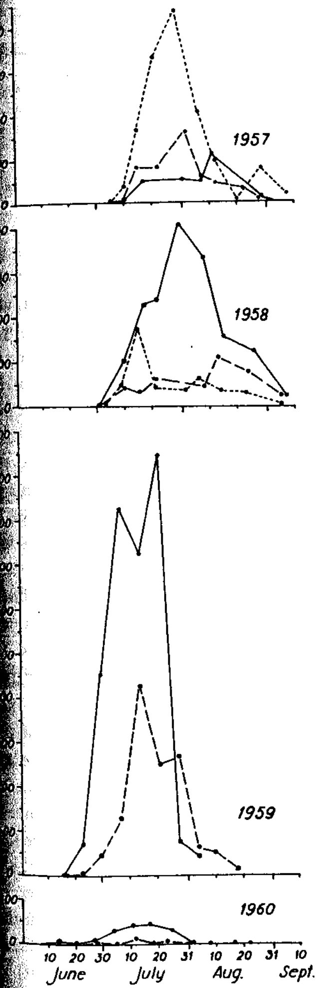
According to v. ROSEN (1956 b, p. 8), in most cases the incubation period of eggs indoors at about 23°C is approximately 13 (10—22) He found that the egg of this species hatch in as little as 8 days, and the longest in his trials was 29 days. His results, there are consistent with those obtained in the pr investigations.

In the years 1957—1960, the time o pearance of *J. pellucida* eggs was studied in so fields of spring cereals (Fig. 16). Weekly nettin samples (in 1957 suction samples) were tak from most of these fields, and the followin numbers of adult delphacids and *J. pellucida* we established.

Year	Date	No. of delphacids	% of J. pell
At Laihia			
1957	16. VI— 7. VIII	60	98
1958	2. VII—15. VIII	1 733	99.
1959	12. VI— 5. VIII	4 388	99.
1960	7. VI— 8. VIII	949	83.
At Ylistaro			
1957	25. VI—29. VIII	142	99
1958	1. VII—13. VIII	202	100
1959	18. VI— 7. VII	105	92
1960	7. VI—20. VII	181	86

In collections made at Sulva in spring whe fields in the period June 26—July 8, 1957, delphacids were obtained, 99 % of which we *J. pellucida*. The material in Fig. 16 thus gives fairly good picture of the numbers of *J. pellu* eggs, even though it was not possible to tinguish the eggs of this species from those other species. After the first eggs were lai natural enemies appeared, and destroyed a larg proportion of the eggs; after a few weeks, nymph hatched. Consequently, the maximum number healthy eggs which had not yet hatched occurre between mid-July and the beginning of Augus No data are available on the occurrence of last healthy eggs in the field. They were found even as late as September, and in the insecta the last nymphs hatched on October 2. In springs, eggs were still found occasionally, but they no longer hatched into nymphs.

Nymphal stage. The times of da which the nymphs hatched were investigat the insectary during the period August mber 2, 1957. According to the thermo- the mean temperature during the trial was 10—13°, with extremes of 8—18°C.



6. Number of healthy eggs of delphacids at Laihia ine), Ylistaro (dashed line) and Sulva (dotted line) -plant samples taken in 1957—1960. The 1958 from Sulva were from spring wheat, while all hers wete from oats. Same material as in Figs. 28, 29, 34, 61, 62, 75 and 78.

The number of hatched nymphs at two-hour intervals during this period were as follows:

Time (hours)	19—9	9—11	11—13	13—15	15—17	17—19	Total
No. of nymphs	375	219	131	84	30	0	839
% » »	44.7	26.1	15.6	10.0	3.6	0	100.0

According to these results, most of the nymphs hatched in the morning. Concerning the factors affecting the time of hatching, data are only available on the temperature. In a certain test, eggs kept at room temperature almost up to the time of hatching were placed in an illuminated refrigerator at a temperature of + 5—8°C. When the eggs were subsequently removed from the refrigerator, they hatched within a few hours. This reveals that it is the rise in temperature after the night that stimulates tbe hatching of the eggs, even in the insectary.

The first nymphs were observed in the field on July 22. It is to be presumed that nymphs were already present a week or two earlier, even though they were not found. According to HASSAN (1939, p. 353), under favourable conditions *J. pellucida* nymphs exist as instar I for an average of 8 days, as instar II to instar IV for four days each, and as instar V for nine days. In the region of investigation information was obtained only about the duration of nymphal instar V, which after overwintering as instar III lasted 6—8 days in the laboratory at +22°C. According to HASSAN (loc. cit.), the total duration of the nymphal instars was 29 days. In the present studies, the winter and the diapause caused an increase in the duration of the nymphal instars. In cages in the field, the average nymphal period lasted 314 days. In this test, the period was equally long for both males (27 specimens) and females (23 specimens).

The food consumed by the nymphs of *J. pellucida* may have an effect on the rapidity of their development, as has been shown by KISIMOTO (1956 b) for certain leafhopper species. In 1957, nymphs which hatched on August 18—19 were reared until August 26 on oats, after which they were put into small cages on different host plants. In two cages there were *Deschampsia caespitosa*,

Table 4. Development of *J. pellucida* nymphs on different food plants. The nymphs fed during the period Aug. 26, 1957—June 16, 1958

Plant	No. of nymphs on June 16, 1958			χ^2		
	Instar IV No.	Instar V No.	%	*D. caespitosa*	*E. repens*	*P. pra*
Deschampsia caespitosa	13	12	48	—	—	—
Elytrigia repens	13	18	58	0.24	—	—
Phleum pratense	7	47	87	11.92***	7.63**	—
Bromus inermis	3	31	91	11.41***	7.98**	0.04

Elytrigia repens and *Phleum pratense*, while in one there was *Bromus inermis*. Into each cage 110 nymphs were introduced, with the exception of the cage with *B. inermis*, in which 100 were placed. Attempts were made to keep the amount of herbage the same in all cages in relation to the number of nymphs. During the test period the mortality of the nymphs was high, and it was necessary to terminate the trial earlier than had been planned. The results obtained (Table 4), however, indicate that the nymphs develop more quickly on *B. inermis* and *P. pratense* than on *D. caespitosa* and *E. repens*, which are common weeds. Most of the *J. pellucida* nymphs live at first in cereals and later in pure stands of timothy, sown under a cereal nurse crop. Only a small proportion of the leafhoppers in the region spend their nymphal stage in leys, ditch banks or waste land where *D. caespitosa* and *E. repens* are abundant.

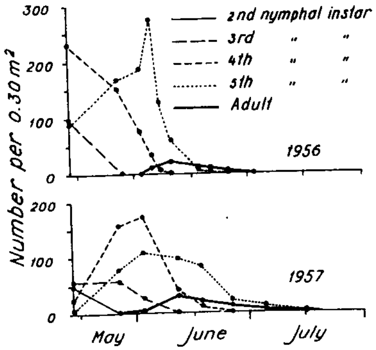


Fig. 17. Numbers of nymphs of 2nd—5th instars and adults of *J. pellucida* in suction samples taken in first-year timothy leys at Ylistaro in 1956 and 1957.

The time of appearance of nymphs in oats
in first-year timothy leys established unde
nurse crop of spring cereals was studied by mea
of suction and by netting samples. The maximu
nymphal density obviously occurred in Augu
after the main period of emergence, but in wa
summers, such as 1959 and 1960, it took pla
in early August and in cool summers, such
1958 and 1962, not until the end of this mon
or the beginning of September. In the win
the mortality was great, and in the course
the following spring and early summer the nu
bers of nymphs a further slight decline
place. After emergence had begun in May
June, the density of nymphs decreased rapi
and the last nymphs were encountered on Ju
15 (Figs. 17 and 18).

Adult stage. In all the years of inves
gation, special attention was paid to the app
ance of the first adults. During the years 195
1964, the average date at which emergence be
was found to be May 27, the earliest being M
15, and the latest June 3. In general, the em
gence of the first adults approximately coinci
with the onset of flowering of winter turnip
and *Prunus padus*. However, in years follo
warm summers and autumns, the leafhop
appeared to emerge before the flowering
winter turnip rape and *P. padus*, while in
following cool summers, emergence was
what later. Both in the field and in the labora
brachypterous adults emerged, on an avera
few days earlier than macropterous ones

The mean life-span of six *J. pellucida* fe
in the insectary was 48 days, and the longe
ceeded 66 days (cf. Fig. 26). The life-sp
females was divided into the three period

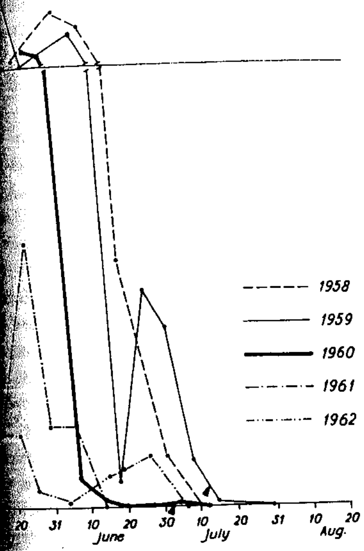


Fig. 18.

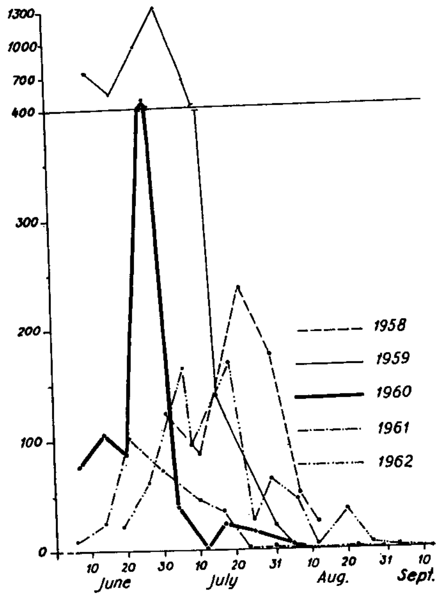


Fig. 20.

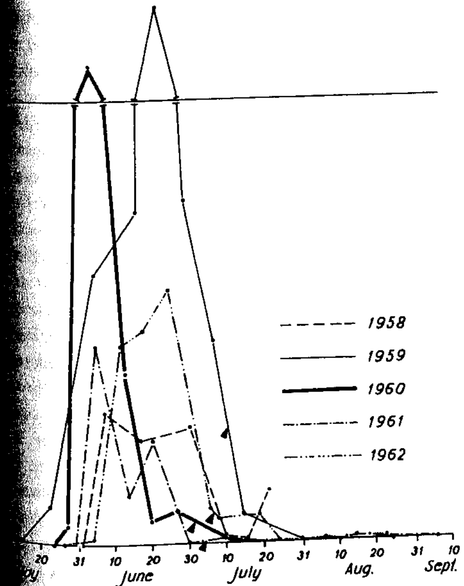


Fig. 19.

Fig. 18. Numbers of *Javesella* nymphs in netting samples (200 sweeps each) taken in first-year timothy leys established under spring cereals in 1958—1962. Nearly all the *Javesella* nymphs were *J. pellucida*. The black triangle denotes the time of cutting. Same material as in Fig. 19.

Fig. 19. Numbers of *J. pellucida* adults in netting samples (200 sweeps each) taken in first-year timothy leys established under spring cereals in 1958—1962. The black triangle denotes the time of cutting. Same material as in Figs. 18, 22 and 71 and Tables 15 and 70.

Fig. 20. Numbers of *J. pellucida* adults in netting samples (200 sweeps each) taken in oats in 1958—1962. Same material as in Tables 16 and 71 and Fig. 71.

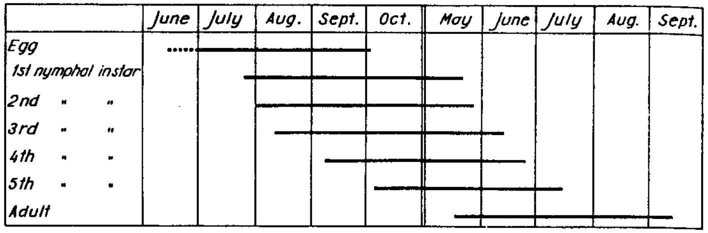


Fig. 21. Life cycle of *J. pellucida* in 1956—1964. The solid line denotes the known and the broken line the probable occurrence of the stages.

oviposition, oviposition and postoviposition. When 10 couples of macropters were kept after emergence at + 17°C in the insectary first for one week on timothy and later on oats, the average preoviposition time was found to be 19.3 days (range 18—22 days). The corresponding period of 10 couples treated in the same way but kept for the entire time after emergence on oats was 17.7 (13—22) days. The difference is not statistically significant ($t = 1.46$, $P > 0.05$). As for the couples kept after emergence on timothy and *Elytrigia repens*, not a single female oviposited, although there were 77 on the former plants and 19 on the latter. These plant species are poorer hosts than spring cereals for the period preceding and during oviposition.

The pre-oviposition period of brachypterous females ($n = 4$) on oats at 18°C was only about 62 % of that of macropterous females ($n = 4$), and this difference was significant ($t = 3.34^*$). The same difference has been observed in the leafhoppers *Nilaparvata lugens* (Stål), *Sogata furcifera* (Horváth) and *Laodelphax striatellus* (Fallén) (KISIMOTO 1957, MOCHIDA 1964).

In studies carried out in England, HASSAN (1939, p. 350) established that the females of five couples began to oviposit 30—33 days after emergence. Unfortunately, this worker did not present any data on the experimental conditions, but it is possible that the preoviposition period of *J. pellucida* is shorter in Finland than in England.

According to LINDSTEN (1961 b, p. 221), oviposition appears to commence about 2—3 weeks after the beginning of migration of *J. pellucida* to cereal crops. In the present studies, ovipositio began less than two weeks after migration in th warmest summers and in slightly less than thre weeks in the coolest summers.

The oviposition period of six macropterou females on Tammi oats averaged 27 (12—4 days (cf. Fig. 26) and the postoviposition perio of the same females was 3.5 (0—11) days.

The appearance of adults in first-year timoth leys sown under spring cereals was determine by means of suction and netting samples (Fig 17 and 19). In all the years studied, the adul reached their maximum density in timothy le during the month of June. Around the midd of July, which was the best oviposition tim only small numbers of *J. pellucida* remained i the leys; most of them had migrated before th time to fields of spring cereals. In netting sampl taken on oat fields, the maximum amounts of *J. pellucida* were found towards the end of June o in early July (Fig. 20). The maximum occurre after the main migration period, after which th numbers appeared to decrease rapidly. In a tuality, however, the decrease in leafhopper de sity was not as sharp as appears from Fig. 20 since during this time the oats elongated rapid and the leafhoppers became distributed throug out the different parts of the stand; furthermo they were particularly numerous in the lowe parts of the stand, where it is difficult to cat them with a sweep-net (cf. HEIKINHEIMO an RAATIKAINEN 1962, p. 15).

Life cycle in different regio The life cycle of *J. pellucida* is shown in Fig

ding to these data, the species hibernates nymphal instars but usually in instars IV I (cf. also Tables 31 and 32). In Sweden it nates mainly in instars III and IV (TULL- 1925, p. 56, LINDSTEN 1961, p. 221), or ding to JÜRISOO (1964, pp. 74—75) in in- —III. In Czechoslovakia the species hiber- mainly in instars III and IV, but also to extent in earlier instars (DLABOLA 1960, p. In England the species hibernates during s IV and V (HASSAN 1939, WATSON 1959), the adults appear there about a fortnight r than in Finland. Eggs and nymphs appear out the same time as in Finland, or some- later (cf. HASSAN 1939, p. 348). The reason his may be that the preoviposition period *pellucida* is long there, while in Finland it ort, as mentioned above.

Germany, in the region of Berlin, *J. pellucida* oltine and in general hibernates in instar IV in instars III or V (BAUMERT 1959, pp. 381, Near Kiel in northern Germany, the species wise bivoltine (AFSCHARPOUR 1960, p. 285). ppearance of the single adult generation of ecies in Finland apparently occurs between ppearances of the two generations in Ger- (cf. AFSCHARPOUR 1960, p. 283). The of occurrence of *J. pellucida* in Germany inland thus closely resemble the corres- ng situation in *Megadelphax sordidulus* (Stål) ese same regions (cf. KONTKANEN 1954, IKAINEN 1960 a).

the greenhouse it is possible in Germany to n at least four generations of *J. pellucida* ally (BAUMERT and BEHRISCH 1957, p. 435). inland two months are required to obtain generation. According to DLABOLA (1960), aximum temperature the species develops egg to adult in one month.

D. Dimorphism

acropterous adults of *J. pellucida* are more mon than brachypterous ones, at least in al Europe (HAUPT 1935, DLABOLA 1954), en (OSSIANNILSSON 1946—1947) and Finland (SAHLBERG 1871, p. 438, KONTKANEN 1947, p. 121, LINDBERG 1949, p. 26, KANERVO et al. 1957). In the region of investigation, macropterous specimens were likewise much more prevalent than brachypterous ones. This is clearly evident from samples collected at the beginning of emergence in first-year leys (Table 5). The brachypters emerged early. At the beginning of emergence as well as at the end of migration, the proportion of brachypters was evidently at a maximum in such leys (Fig. 22). More macropters were produced in such leys than brachypters, but they were more apt to move away from the leys, whereas a great proportion of the brachypters remained in the leys to reproduce. Therefore, after migration there were sometimes even more brachypterous than macropterous leafhoppers. One of the reasons for this may have been the presumed shorter life-span of the macropters (cf. KONTKANEN 1952, p. 31).

Table 5. Number of brachypterous *J. pellucida* in net samples taken at the beginning of migration in first-year timothy leys established under spring cereals. Each sample consisted of 200 sweeps (except 60 in 1958)

Period	No. of samples	Total adults	Brachypters No.	%
1958 8. VI—18. VI	5	330	3	0.9
1959 15. V— 4. VI	18	3 890	144	3.7
1960 25. V— 2. VI	8	1 193	0	0
1961 30. V— 6. VI	12	373	27	7.2
1962 2. VI— 7. VI	16	273	42	15.4
1963 23. V—31. V	20	441	75	17.0
1964 25. V—26. V	19	1 055	122	11.6
	98	7 555	413	5.5

Heredity. Among the factors which may affect wing dimorphism in insects are heredity, illumination, weather conditions, population density and nutrition. The proportions of brachypters were studied in leys of different ages at the beginning of emergence. It was found (Table 6) that as the ley aged, the proportion of brachypters increased. A test was performed in order to investigate the role of heredity in wing dimorphism. In this test, macropterous and brachypterous leafhoppers were crossed. The offspring consisted of both macropterous and brachypterous individuals of both sexes. Nor did the

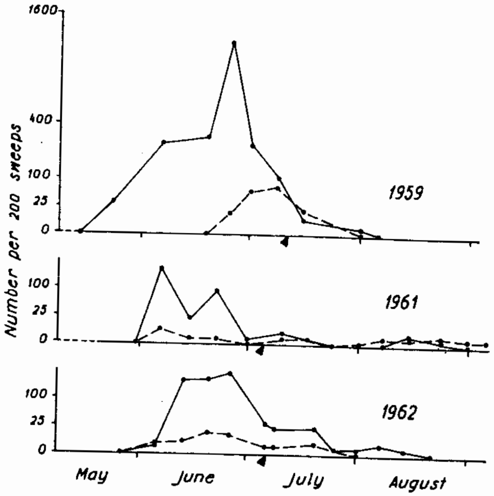


Fig. 22. Numbers of macropters (solid line) and brachypters (dashed line) of *J. pellucida* in netting samples (200 sweeps each) taken in first-year timothy leys established under spring cereal at Laihia in 1959, 1961 and 1962. Same material as in Fig. 19; this graph includes only the material having the most brachypters. The black triangle denotes the time of cutting.

results of crossing the F_1 generation (Table 7) suggest that wing dimorphism was inherited according to any simple rule. Similarly, Kisimoto (1956 b) did not find evidence of inheritability of leafhopper dimorphism.

Effect of weather factors. Sahlberg (1871, p. 21) and Kontkanen (1947, p. 122, 1952, p. 31) found that the proportion of brachypterous leafhoppers increased towards the north. In the present investigations, *J. pellucida* was collected after emergence in first-year leys established with spring cereal nurse crops located at different latitudes along the coast of the Gu of Bothnia. According to the data obtained, th proportions of brachypters may indeed incre towards the north (Table 8). However, additional data are needed in order to confirm th results. In his studies with the leafhopper *La delphax striatellus* (Fallén), Kisimoto (1956 d, p. 209) found that diapause in the nymphal period is an important condition for the appearance o the brachypterous male. Furthermore, Joh (1963) demonstrated that temperature and daylength affect the proportion of brachypterous

Table 6. Number of brachypterous *J. pellucida* in leys of different ages. Samples (200 sweeps each) taken between May 14 and June 4, 1959

Age of ley, years	No. of samples	Total adults	Brachypters No.	Brachypters %	χ^2 1st year	χ^2 2nd year	χ^2 3rd ye
1	26	5 080	121	2.4	—	—	—
2	26	1 068	42	3.9	7.52**	—	—
3	26	1 692	103	6.1	53.25***	5.68*	—
≥ 4	17	520	53	10.2	94.61***	23.29***	9.52

7. Results of crossing trial between macropterous (M) and brachypterous (B) *J. pellucida*

M ♀ × B ♂, 5 pairs

F₁	M♀ × M♂ 5 pairs	M♀ × B♂ 6 pairs	B♀ × M♂ 3 pairs	B♀ × B♂ 3 pairs
......	5	11	1	10
......	2	22	8	8
......	14	18	15	14
......	5	11	19	6

B♀ × M♂, 3 pairs

F₁	M♀ × M♂ 3 pairs	M♀ × B♂ 0 pairs	B♀ × M♂ 2 pairs	B♀ × B♂ 2 pairs
......	18	—	1	2
......	11	—	2	3
......	24	—	10	6
......	17	—	7	1

mens of *Nilaparvata lugens* (Stål). The factors h affect the relative numbers of brachypters *pellucida* in different geographical regions not clear.

ffect of parasites. According to BERG (1939, pp. 140, 141, 1949, pp. 34, 960, p. 5), the parasite *Elenchus* causes an ase in brachypterous individuals of certain hacids, including *J. pellucida*. In the region vestigation, an attempt was made to study aspect on the basis of the data in Table 9, there was no evidence that *E. tenuicornis* insed the number of brachypterous individuals *pellucida* ($\chi^2 = 3.10$, $P > 0.05$). Likewise, *ndylus lindbergi* was not observed to affect

Table 8. Proportion of brachypterous *J. pellucida* in net samples taken in first-year leys at different latitudes in West Finland during the period May 23—June 6, 1959

Latitude and biogeographical province	No. of leys	Total adults	Brachypters No.	Brachypters %	χ^2
< 62°; VS and St .	15	598	2	0.3	—
> 62°; EP	17	1 330	26	2.0	6.50*

wing dimorphism. Even if *E. tenuicornis* had caused a decrease in wing size, it cannot have been the sole factor responsible or even the most important factor in the region of investigation.

Effect of population density and nutrition. The influence of population density on wing dimorphism in *J. pellucida* was investigated in first-year leys established under spring cereal nurse crops. In the years 1958—1964, netting samples were taken at the end of May and beginning of June. Of the leafhoppers collected, about 90 % were *Javesella*, and of these over 99 % were *J. pellucida*. In order to calculate the population density, the number of adult *Javesella* in the samples was converted to number of nymphs by dividing it by 396/86 = 4.6 (cf. Heikinheimo and Raatikainen 1962, p. 19). This amount was added to the number of nymphs of the *Javesella* group, and the sum was regarded as a measure of population density. The result (Table 9) indicates that the proportion of brachypterous *J. pellucida* decreased as the population density of *Javesella* increased. Kisimoto

Table 9. Proportion of brachypterous *J. pellucida* in *Javesella* populations of different density

No. of *Javesella* nymphs per 200 net sweeps	No. of samples	*J. pellucida* Adults	*J. pellucida* Brachypters No.	*J. pellucida* Brachypters %	χ^2 1—40	χ^2 41—80
1— 40	42	601	76	13	—	—
1— 80	13	551	31	6	16.02***	—
1— 160	24	970	43	4	34.65***	0.84
1— 320	31	1 847	76	4	55.28***	1.92
— 640	23	760	59	8	8.43**	1.94
—1 280	18	3 125	78	2	127.96***	14.99***
—2 560	8	3 026	78	3	122.70***	13.62***
—5 120	3	1 066	30	3	60.81***	7.13**
Total		11 946	471	4		

(1956 a—c) has experimentally demonstrated with the leafhoppers *Nilaparvata lugens*, *Sogata furcifera* (Horváth) and *Laodelphax striatellus* that the population density during the nymphal period affects the proportion of brachypters. The proportion of brachypters among the females declined as the density of the leafhoppers increased. In the case of males of *Nilaparvata lugens*, the proportion of brachypters rose as the density increased to five per test-tube and subsequently diminished when the density increased still further (Kisimoto 1956 a and c). With the other species, there were no brachypterous males. Kisimoto (1959) later demonstrated that with *N. lugens* females, high densities during nymphal instars II—IV induced the appearance of the macropterous form. He also showed that determination of wing form takes place slightly earlier in males than in females.

According to the present field studies (Table 9), the effect of population density in shortening the wing length of *J. pellucida* females was similar to that found by Kisimoto (1956 a—c), and the effect on males seemed to be the same as on females. However, 3.7 % of the males were brachypters and 4.2 % of the females ($\chi^2 = 2.37$, d.f. = 1, P > 0.05), and at all densities the proportion of brachypterous males was lower but nevertheless statistically significant. According to Johno (1963), the mutual stimulation among individual nymphs of *N. lugens* played some part in determining the wing form, but visual stimulus was not the important factor.

In the cultures in cages and gauze cylinders, where *J. pellucida* was reared from egg to adult, there were considerably more brachypters than in the field under natural conditions, even though the population density in the cultures was many times greater than in nature. This shows that the population density is not, at least as such, the principal factor in wing dimorphism, but that evidently the kind of nutrition is very important. According to Kisimoto (1956 a—c), wilting of the host plant produces a definite effect, increasing the proportion of the macropterous form even in the absence of crowding, and according to Johno (1963) underfeeding during the nymphal period has an influence on the de- termination of wing form.

It is obvious that in studying the effect of population density on wing dimorphism, other leafhopper species must also be taken into con- sideration, and perhaps some other insect species as well, since they affect one another both directly and indirectly, for instance, by influencing nutri- tion. It has been shown by Johno (1963) that adults of *Laodelphax striatellus* have an effect on the determination of the wing form of *Nila- parvata lugens*.

E. Movement and migration

Ever since *J. pellucida* was established to be a pest, entomologists and plant pathologists have paid special attention to its migration. Thus far, Kanervo et al. (1957) in Finland as well as Taimr and Dlabola (1963) and Dlabola and Taimr (1965 a and b) in Czechoslovakia have done the greatest amount of work on the migra- tion of the species. Other investigators have also been concerned with the movement and migra- tion of the species (e.g. Tullgren 1925, Tinnilä 1957, Kanervo 1958, Raatikainen and Tin- nilä 1959 a, Vacke and Průša 1959, Jürisoo 1964).

1. *Nymphs*

In general, nymphs which have just emerged are able to move only a few centimetres from the site where they hatch. Later in the summer, however, they move on the ground. Observa- tions showed that during the time of cereal ripe- ning, nymphs were generally incapable of moving from the centre of a field strip to the bank of the ditch bordering the strip where there were many suitable host plants, a distance of about 5 metres. However, there were more nymphs along the ditch banks of field strips where cereals were growing than along those of other crops, be- cause the nymphs moved to the ditch banks from the strip proper, and in the ditch banks of fields ploughed after a spring cereal crop there ap- peared to be rather more nymphs than in

of spring cereal fields which had not been ghed but had been left for establishment of

the leys, the nymphs were generally to be d in the early part of the summer on the leaf hs or blades of timothy. Some of them were ad plant parts on the ground or in dicotyle- They moved by walking or hopping. The nces which overwintered nymphs hopped are ground were as follows (air temperature 8°C, soil temperature at depth of 2 cm 9°C):

l instar	No. of nymphs	Distance hopped, cm Mean ± S.E.
....	12	8.7 ± 1.36
....	25	14.0 ± 1.33
....	15	23.0 ± 3.65

hen nymphs in the field encounter a more ss erect plant part or other narrow object, often move to it and climb up it. Their viour was studied by means of the following carried out in the laboratory, in which hs were allowed to choose between vertical of different widths. The illumination con- of a 75-watt lamp placed 1.5 metres above ble. A cylinder 6.5 cm in diameter and 5 cm ght was used for the test. Its inside surface overed with white paper, on which seven al lines of varying width were drawn in ink al distances from one another. Nymphs of s III—V were placed one at a time in the e of the cylinder. The nymphs moved to- the lines, and 81 % of the 280 nymphs d began to climb up along the lines, while emainder climbed up between them. Often ymphs ascended the lines for several centi- s, and in many cases even those which d climbing between the lines shifted their ion toward the lines while ascending. The ers of nymphs which went to the lines of ent width were as follows:

line, mm	0.5	1.0	2.3	4.0	6.0	8.5	11.5
nymphs g to line	3	6	27	63	58	45	25

Even in the spring the nymphs of *J. pellucida* did not travel long distances. Generally they moved from one place to another by walking, and as a rule only hopped when they were disturbed. They usually walked in a serpentine fashion, and only rarely moved for several centimetres in a straight line. In growing stands of vegetation, they climbed up plants where, as was shown by marking tests, they remained for several days.

In the spring the nymphs from the banks of ditches or from first-year leys did not move more than a few metres into stands of spring cereals. This was seen particularly clearly in oat fields bordered by the hibernation sites of nymphs which were vectors of OSDV and EWSMV. In such fields there were numerous virus-infected oat plants along the borders of the fields, but as little as two or three metres from the edges only a few plants were diseased. Furthermore, netting samples no longer revealed nymphs at a distance of five metres from the border of the field.

In summing up the above observations and trials, it can be stated that the maximum radius of movement of *J. pellucida* nymphs is evidently only a few metres, at most a few dozen. According to Lindsten (1961 b, p. 222), nymphs only move very short distances.

2. *Brachypters*

Brachypterous leafhoppers move by walking or hopping. They were able to move more rapidly and hop for greater distances than the nymphs. In 1961, investigations were made on the movement of brachypterous leafhoppers from timothy to oats in two localities which had underground drainage. On June 14, July 1 and July 17, netting samples were taken in timothy leys 5 metres from the border between the ley and the adjoining oat field. In the oat field, netting samples were taken at distances of 5, 15, 25, 35 and 45 metres from the border. The samples obtained from both localities on the different dates were combined, since no significant differences were found between them. However, there were only a few brachypterous adults of *J. pellucida*. Eight were collected in the timothy leys, while in the oat fields two were found at 5 metres' distance and three at 15 metres' distance from the border between the two crops. The numbers of all the brachypterous delphacid leafhoppers in the samples, *Megadelphax sordidulus* (Stål), *J. pellucida*, *Xanthodelphax flaveolus* (Flor.), *Muirodelphax denticaudus* (Boh.), *Stiroma bicarinata* (H.-S.) and *Dicranotropis hamata* (Boh.), were counted, and the following figures were obtained:

Specimens in timothy ley	Specimens in oat fields. Distance from edge of oat field in metres				
	5	15	25	35	45
266	42	17	8	3	2

These data reveal that brachypterous delphacids were distinctly more numerous at the margins of the oat fields than in the centres ($\chi^2 = 75.92^{***}$). Numerous collections have similarly shown that the distribution of brachypterous *J. pellucida* individuals is about the same as that of all brachypterous delphacids. In relation to their numbers, brachypterous adults of *J. pellucida* were more numerous in the oat fields and were found farther from the field border than brachypterous nymphs.

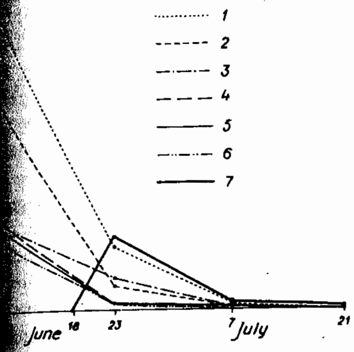
3. *Macropters*

During the present investigations, macropterous adults of *J. pellucida* were found to move by walking, hopping — which also included the use of their wings — and flying. The way they moved depended greatly on the age and sex of the leafhopper as well as on the weather. After emergence in timothy leys, macropters were found at all heights in the stand and were definitely higher than the nymphs (cf. Heikinheimo and Raatikainen 1962, p. 16). When disturbed, they readily jumped or flew for distances of several metres. If the temperature rose or the wind dropped, the distances covered by hopping increased from less than a metre to several metres. After the period of migration, the lengths of the hops decreased, and ovipositing females no longer hopped, or if disturbed hopped only a few centimetres.

Period between emergence and migration. No precise data were obtai
on the length of time elapsing between emerge
and migration, but apparently it was only a f
days. It appeared to be of longer duration if
weather after emergence was unfavourable
migration than if it was good. Field obser
tions showed that the average period between t
finding of the first adults and the first migrati
specimens was 8 days. However, the interval b
tween emergence and migration was probabl
actually shorter, since fewer observations we
made on migration than on emergence.

Cause of migration. Migration of
pellucida is generally associated with a change
host plant. In the area of investigation the speci
usually moved from timothy to cereals. In 195
a trial was carried out at Ylistaro, in which le
of the following species were established unde
a spring cereal nurse crop: *Lolium perenne*, *Phle*
pratense, *Bromus inermis*, *Dactylis glomerata*, *Fe*
pratensis and *Trifolium pratense*. The size of
ley was 15 × 20 metres. In the following ye
netting samples were taken from these leys
also from oats during the period June 9—July
The results (Fig. 23) show that most of the le
hoppers moved away from all leys, while th
was an increase in their numbers in the oats
same migration occurred even in a trial wh
oats had been sown in a first-year timoth
inhabited by leafhopper nymphs. It is thus
dent that migration of *J. pellucida* is governe
internal causes and that the ready availabili
suitable host plants is unable to prevent it
was also observed in cultures in which
hoppers which had not yet migrated were p
in cages containing spring cereals. When
leafhoppers reached the stage of maturi
which they normally migrate, they rose to
upper part of the cages and moved vigoro

Migration flight. *J. pellucida* was fo
to migrate between 6 a.m. and 10 p.m. *Me*
phax sordidulus, *Stiroma bicarinata* and *Dicra*
pis hamata also migrated during the day
Williams (1957, p. 77) mentions that *Perki*
saccharida (Kirkaldy) and *Dicranotropis mui*
kaldy migrate by day in the Mauritius Isl
but in Hawaii *P. saccharida* flies most frequ



ig. 23. Numbers of *J. pellucida* adults in dif-
ent kinds of first-year leys established under
spring cereal as well as in oats in 1959.
= *Lolium perenne*, 2 = *Phleum pratense*, 3 =
omus inermis, 4 = *Dactylis glomerata*, 5 = *Festuca*
pratensis, 6 = *Trifolium pratense*, 7 = oats.

et nights when air currents are at a mini-
Glick (1939, p. 27) captured leafhoppers
an aeroplane in Louisiana, U.S.A., and
that many species of delphacids occurred
air both by night and by day, but they
more abundant in the daytime.

he present investigations, the weather at
ne when migration began was very warm
ill. However, migrating specimens were
imes seen even though the temperature was
bout 10°C. When starting its flight, *J.*
da at first rose almost vertically upward for
nce of a few centimetres to a few metres.
height it was then carried by air currents,
tioned by Kanervo et al. (1957, pp. 14—
d Kanervo (1958, p. 127). Only when the
was very slight (ca. 0.5 m/sec.) did it fly
t the wind, but this was uncommon.During
tion the height of flight varied by several
At times the leafhopper flew at a height
ly about 1½ metres, but then it rose to
6 metres and later descended again. During
ne of descent to the field, the flying height
sed slowly and the leafhopper often made
ntal turns in its direction of flight. Finally
inated its flight by landing, usually on the
of plants in a cereal field.

Height of migration. The height of migration was investigated by means of a triple-level netting apparatus at Laihia during the periods June 3—July 20, 1958, and May 25—July 17, 1959. These results (Table 10) as well as direct observations show that *J. pellucida* usually flies at heights of about 2—6 metres. Only very few flew at less than one metre. According to these observations, the migration height of *J. pellucida* is greater than that of the related species *Laodelphax striatellus* (Fallén), which was balked by a gauze fence two metres high (cf. Sukhov and Petlyuk 1940, p. 484). Air currents, however, may carry *J. pellucida* considerably higher than the 10 metres detected by the triple-level netting apparatus. For example, Glick (1939, p. 27) encountered specimens of the genus *Delphacodes* at an elevation exceeding 5 000 feet (ca. 1 500 m). Forests constitute an obstacte for most of the migrating *J. pellucida* adults, and when they reach wooded areas many leafhoppers descend to the ground. This is clearly seen, for instance, in the greater numbers of virotic plants in the vicinity of forests, both in Finland and in Czechoslovakia (Vacke and Průša 1959). In the present study, similarly, in the vicinity of small woods isolated in open country, fewer migrating leafhoppers were found on the leeward side of the woods than on the other sides.

Table 10. Height of migration of macropterous *J. pellucida* according to samples taken with the triple-level netting apparatus. Migration height of males compared with that of females $\chi^2_{1958} = 3.82$, $P > 0.05$, $\chi^2_{1959} = 16.81^{***}$. Same material as in Tables 60 and 72

Year	Height of net above ground m	Males	Females	Parasitized	Total	% of ♂♂ among apparently healthy specimens
1958	10	37	28	32	97	57
»	6	102	73	62	237	58
»	2	· 73	41	46	160	64
Total		212	142	140	494	60
1959	9	194	208	105	507	48
»	6	330	338	205	873	49
»	2	567	462	261	1 290	55
Total		1 091	1 008	571	2 670	52

The height of migration of males (Table 10) was significantly lower than that of females.

Distance of migration. Only scanty information is available on the distance covered by migrating *J. pellucida.* According to KANERVO et al. (1957, p. 15), migration was followed for 0.5 km, whereas TAIMR and DLABOLA (1963, p. 331) and DLABOLA and TAIMR (1965 a, p. 416, 1965 b, p. 328) found that *J. pellucida* covered a distance of 835 metres. As for other delphacid species, *Euides speciosa* (Boh.) was indirectly shown to migrate about 15 km in the region of investigation (RAATIKAINEN 1960 b). During its migration *J. pellucida* does not descend to the first suitable cereal field which it encounters but often flies over it, as has also been established by TAIMR and DLABOLA (loc. cit.). In the region of investigation the distances covered by migrating *J. pellucida* were apparently several kilometres in length (cf. KANERVO et al. 1957, p. 15, KANERVO 1958, p. 127) and the time of flight some minutes. According to DLABOLA and TAIMR (1965 b, p. 328), *J. pellucida* had been found to spread over an area exceeding 2—3 km in diameter.

Period of migration. In the years 1957—1964, the dates of the annual period of migration were determined by means of netting apparatuses at Mustasaari, Laihia and Ylistaro. The numbers of leafhoppers obtained daily at each of the three localities were very similar, and thus the data from the three sites were combined every year. The results (Fig. 24) indicate that the average date when migration began in the years 1958—1964 was June 2 (range May 26—June 11). In 1957, the apparatuses were set up in the fields after migration had already begun; that year, migration was first observed on June 12, which in the calculations has therefore been taken as the starting date of migration. Among the first migration specimens of *J. pellucida,* no parasitized specimens were found in any of the years. On an average, half the specimens considered to be healthy were collected by June 14 (June 5—22) while half of all the leafhoppers of this species were collected by June 15 (June 5—25).

The beginning of migration appeared to be most strongly influenced by the daily temperature sum of the spring and previous summer. Of various equations tested, the following bes presents the starting date of migration: a/ b = 527, in which a = mean daily tempera sum during the period between the date of pearance of eggs, and October 2 in the year pr ceding migration (cf. Fig. 36), and b = m daily temperature sum in the year of migratio starting on May 1 and continuing until a tota 527°C is accumulated. When this equation w used, the difference between the calculated an actual dates when migration started in the yea 1957—1964 was 1.7 ± 0.5 days. If the tempera ture sum during the previous year was not take into consideration, the sum of b had to amou to 265°C before migration began. In this ca the calculated date differed from the actual o by 2.4 ± 0.8 days. These results are so good th by means of temperature sums in the region investigation it would have been possible to ma prognostications, for example, as to the ti at which chemical control measures should taken.

During the first part of the migration peri there were many leafhoppers, but towards th end the numbers gradually declined, and netting apparatuses were not kept in the fi long enough to establish the date of the migrating specimens (Fig. 24). However, the apparatuses had been removed, there we so few leafhoppers still flying that their numb would not have appreciably affected, for examp the migration half-time as seen in Fig. 24. migration period of the macropterous popula of *J. pellucida* lasted an average of at least 42 d (27—56) during the years of this study. migration period often consisted of two or phases lasting several days, during which the intensity of migration increased, reache peak and then declined. There appeared to positive correlation between the intensit migration and the mean daily temperature. rain fell, the leafhoppers generally ceased fly but after a brief shower they often resumed On days when migration took place the intensity varied between 1 and 12 m/sec. ever, no correlation was found between

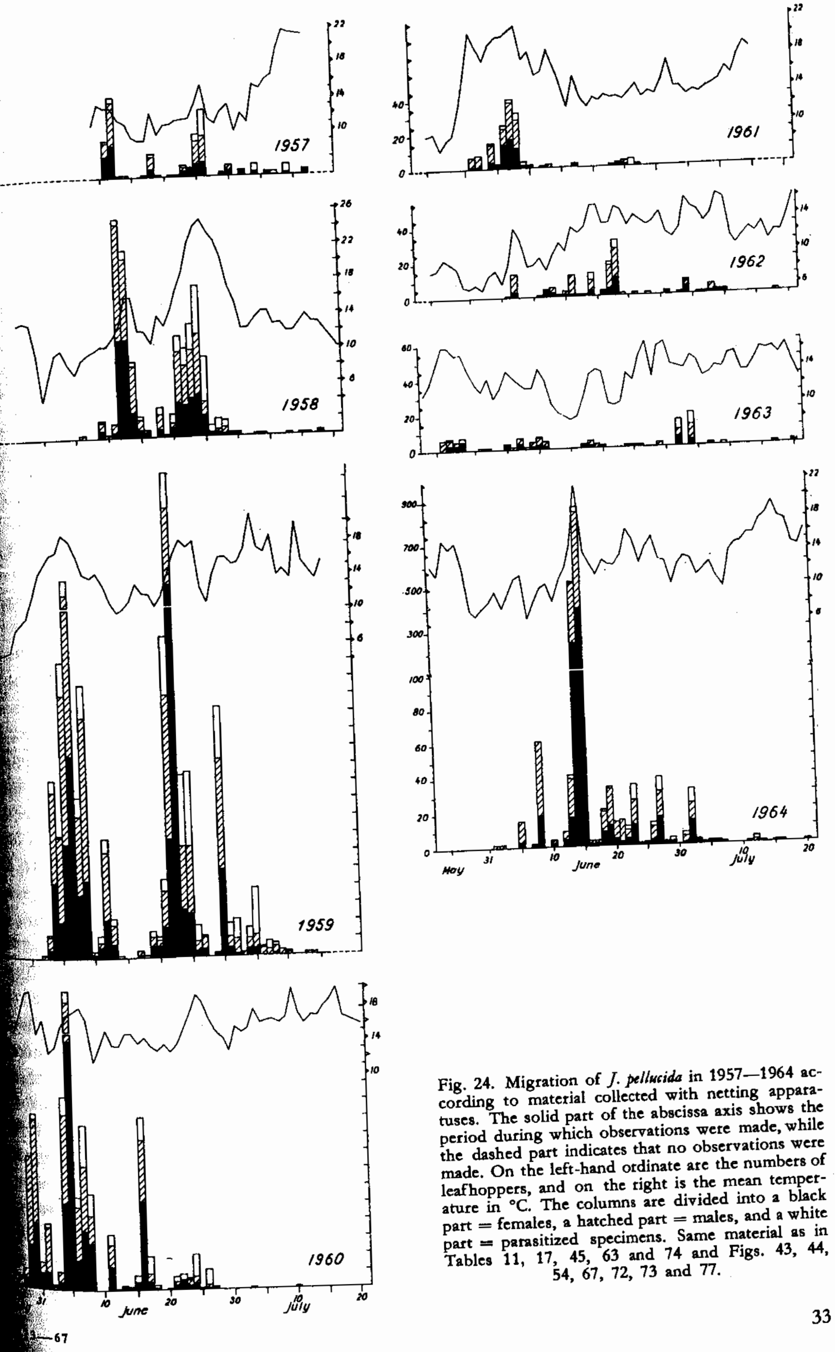


Fig. 24. Migration of *J. pellucida* in 1957—1964 according to material collected with netting apparatuses. The solid part of the abscissa axis shows the period during which observations were made, while the dashed part indicates that no observations were made. On the left-hand ordinate are the numbers of leafhoppers, and on the right is the mean temperature in °C. The columns are divided into a black part = females, a hatched part = males, and a white part = parasitized specimens. Same material as in Tables 11, 17, 45, 63 and 74 and Figs. 43, 44, 54, 67, 72, 73 and 77.

Table 11. Proportion of males among apparently healthy *J. pellucida* according to netting apparatus samples. The catches from each of the years 1957—1964 were divided into three periods comprising as similar numbers as possible, and the data of corresponding periods from the different years were then combined. Same material as in Fig. 24

Part	Total no. of specimens	Males No.	Males %	χ^2 1st third
First migrating third	2 041	1 186	58.1	—
Second » »	2 634	1 427	54.2	7.05**
Third » »	1 211	681	56.2	1.01
Total	5 886	3 294	56.0	

intensity and numbers of migrating leafhoppers. On windy days a larger volume of air enters the netting apparatus per unit time, and with it more leafhoppers are collected, than on calm days. Consequently, it is very difficult to determine the relation between wind intensity and strength of migration with such apparatuses.

In investigating the migration periods of males and females with these apparatuses, the leafhopper catches were divided into three periods comprising approximately equal numbers. According to the results (Table 11), there were more males in relation to the total numbers of leafhoppers presumed to be healthy in the first third of the migration period than in the second third.

F. Habitats

Table 12.. Numbers of *J. pellucida* in different ha
according to collections made by Linnavuori (195
Raisio (SW Finland). Out of the total material, the
taken in June and July were selected. + = *J. pel*
occurred, even though it was not in the sample

Habitat	No. of samples	No. of *J. pellucida*
Open fields and meadows .		
Dryish field	6	1
Moist sloping meadow ..	6	5
Drier peaty meadow	3	11
Wet peaty meadow	5	18
Cultivated field	4	7
Seashores		
Phragmites zone	4	2
Scirpus tabernaemontani-S. maritimus zone	4	4
Heleocharis zone	4	4
Juncus gerardi-Spergularia salina zone	4	8
Drier meadow area	3	7
Wooded biotopes		
Sphagnous spruce wood	3	4
Rich swampy wood	5	1
Rich moist grass-herb wood	4	1
Moist *Oxalis-Myrtillus* spruce wood	3	2
Moist *Myrtillus* spruce wood	3	0
Dry *Vaccinium* pine wood	≥ 2	0
Calluna pine heath	4	0
Bogs and marshes		
Tall-sedge bog	3	0
Short-sedge bog	2	0
Wet »rimpi» bog	3	0
Quagmire marsh	3	0
Pine bog with undershrubs	4	0
Cloudberry-*Sphagnum fuscum* bog	3	0

Javesella pellucida is a eurytopic species (cf. e.g. Dlabola 1954),but it usually occurs in meadows, particularly moist grassy meadows (e.g. Sahlberg 1871, Haupt 1935, Kuntze 1937, Ossiannilsson 1946—1947, Lindberg 1947, Kontkanen 1950 a, Marchand 1953, Remane 1958, Dlabola 1960, Le Quesne 1960, Vilbaste 1965, Emmrich 1966 b). It often lives on bogs and fens and even in forests (e.g. Ossiannilsson 1946—1947, Kontkanen 1950 a, Linnavuori 1952, Remane 1958, Krogerus 1960, Emmrich 1966 b). On cultivated land it is most common in cereal fields and leys but also occurs in many other kinds of crops (e.g. Tullgren 1925, Kuntze 1937, Dlabola 1954, 1958, 1960, Kanervo et al. 1957, Raatikainen and Tinnilä 1959 a, Schober 1959, Afscharpour 1960, p. 284, Va
and Průša 1961, Tischler 1962, Jürisoo 19
In cereals it is often the most abundant spe
of leafhopper (e.g. Kuntze 1937, p. 374, Ka
nervo et al. 1957, Afscharpour 1960, p. 2
Jürisoo 1964).

Adults in different habi
The best quantitative data on the occurrenc
J. pellucida in different habitats have bee
tained from Finland (Kontkanen 1950 a, Li
vuori 1952), Germany (Marchand 1953,
mane 1958, Afscharpour 1960, Emmrich 19
and Sweden (Lindsten 1961 b, Jürisoo 19
Table 12 presents data on the abundance o
species in different habitats. It is seen th
species is most abundant in meadows, o
shores and in cultivated fields. In the regi

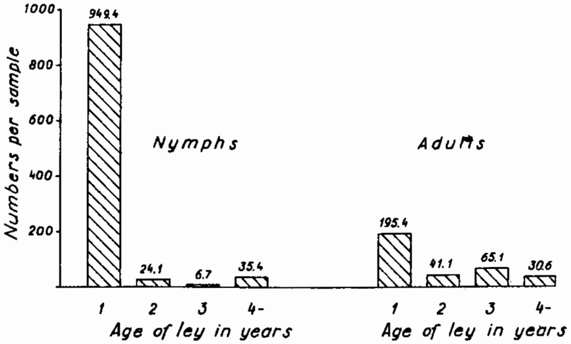


Fig. 25. Numbers of *Javesella* nymphs and *J. pellucida* adults per 200 net sweeps in samples taken on May 14—June 4, 1959, in leys of different ages. Total number of nymphs 26 087; adults 8 360.

gation, seashores are found only in the
districts, and their surface area is small
mpared with that of the other habitats.
are numerous meadows, but on the basis
ections the numbers of leafhoppers in them
to be about the same as, or smaller than,
leys.

numbers of *J. pellucida* on cultivated land,
ined in different crops, showed that this
pper was distinctly more abundant in the
and leys than in potatoes, winter turnip
d root crops, which were the three com-
crops in the region after ley and cereals.
region investigated *J. pellucida* was not so
distributed among different crops as it
und to be in Germany by Afscharpour
p. 284). Since the conclusions reached by
vuori (1952) and also by Kontkanen
) on the abundance of the leafhopper in
nt habitats seemed to apply well to the
region of investigation, the occurrance
llucida was investigated principally in leys
reals.

mothy leys before migration.
g samples were taken from leys of different
hich had been established under a cereal
rop. The leys were selected in such a way
the same clearing were located — at most
lometre from one another — first-year, second-year, third-year leys and if possible also leys four or more years old. In all, 95 leys were studied, of which there were 26 first-, second- and third-year leys but only 17 which had been established for four years or more. The sampling areas comprised 22 in South Ostrobothnia, 3 in Satakunta and one in Finland Proper (cf. Raatikainen 1960 a, p. 230). According to these samples (Fig. 25), nymphs of *Javesella* were most numerous in first-year leys. Comparisons between the second-, third- and fourth-year leys showed no statistically significant differences in the numbers of nymphs. Almost all the *Javesella* nymphs were *J. pellucida*. This was demonstrated among other things, by the fact that the proportion of *J. pellucida* among adult *Javesella* in first-year leys was 95.3 %, in second-year leys 94.4 %, in third-year leys 90.1 % and in fourth-year leys 91.5 %. Even a higher proportion of the nymphs were *J. pellucida*, since *J. obscurella* emerged earlier than *J. pellucida* and the other species were very scarce. In summarizing, it can be stated that about 47 times as many nymphs of *J. pellucida* were obtained in first-year leys as in older leys, and obviously this truly reflects the density of nymphs in leys of different ages. Not all species of leafhoppers showed the greatest numbers in first-year leys. For example, the numbers of *Megadelphax sordidulus* (Stål) in-

creased as the ley became older (Raatikainen 1960 a, p. 239).

Ditch banks before migration. In 1959, about 80 % of the fields in the region of investigation were drained by open ditches (Official statistics of Finland III: 54). The ditches were located slightly more than 10 metres from one another, on the average, and with their banks were approximately 1—2 metres wide. The ditch banks bore meadow vegetation, in which about one-third of the plant cover at the beginning of July consisted of grasses (Raatikainen and Raatikainen 1964). During the period May 6—9, 1962, the suction method was used to determine the numbers of leafhoppers on the ditch banks of the previous year's spring cereal fields as well as in first-year timothy leys established under a cereal nurse crop. A ley and a ditch bank were chosen from the same main clearing so that the distance between them was at most 100 metres. Fourteen such sample pairs were studied. Suction samples were taken from six spots in both the leys and ditch bank sites. It was found that there were altogether 1 638 *Javesella* nymphs in the ley samples and 491 in the bank samples. This difference is significant ($\chi^2 = 617.94^{***}$). If it is assumed that *Javesella* nymphs were obtained equally well from the fields and the ditch banks by the suction method, these quantities correspond to 261 nymphs per m² in the leys and 78 per m² on the banks, when the correction value calculated by Heikinheimo and Raatikainen (1962, p. 10) is employed. Here, too, most of the leafhoppers in both sampling places were *J. pellucida*, as was demonstrated by netting samples and visual observations made during the period of emergence.

It is thus evident that the ditch banks of fields, especially cereal fields ploughed in the autumn, are important habitats for the nymphs, since the ditches and their banks constituted about one-tenth of the total field area. However, about two-thirds of the ditch banks were in fields where crops other than cereals were growing, and on such banks the density of *J. pellucida* nymphs was found to be clearly less than on the ditch banks of cereal fields.

Table 13. Numbers of *J. pellucida* in oats and diffe aged timothy leys at the end of the migration perio according to netting samples taken July 1—4, 19 Logarithmic transformation. The means retransform

Crop	Total numbers	Means per 20 net sweeps	
Oats	1 981	318 a	
1st-year timothy ley	594	80	b
2nd-year » »	74	12	c
3rd-year » »	49	9	c
4th-year » »	37	4	c

F = 22.73***, d.f. = 4 and 16

Oat fields and timothy leys at the end of migration. Toward the end of the migration period, the numbers of *J. pellucida* were determined at Laihia in crops of different kinds. Netting samples were taken in five areas from each of the following crops: oats, and first-year, second-year, third-year and fourth-year timothy leys. The samples (Table 13) showed that *J. pellucida* was most abundant in oats. There were also considerable numbers of leafhoppers in first-year timothy leys, but a substantial proportion of them had not yet migrated (cf. Figs. 19 and 24). After the termination of the migration period, the quantities of *J. pellucida* were smaller than at the time of sampling (cf. Figs. 19 and 22).

Cereal fields at the end of migration. The numbers of *J. pellucida* in cereals at the close of the migration period were determined by means of netting samples (Table 14) taken from 7 sampling localities. The samples from the different cereal species are not completely comparable with one anothe particular, the numbers of leafhoppers ned from the tallest cereal, rye, were ously too small in relation to those of the cereals. However, direct examination also the impression that *J. pellucida* was less ndant in rye than in spring cereals. The area oted to winter wheat was especially small, in this crop the species seemed to be approximately as abundant as in rye.

Table 14. Numbers of *J. pellucida* in different cereals the end of the migration period, according to sample netted in the period June 27—July 1, 1960. Logarithm transformation. The means retransformed

Cereal	Total numbers	Means per 20 net sweep
Oats	1 014	104 a
Spring wheat	703	85 a
Barley	458	62 a
Rye	44	5

F = 42.11***, d.f. = 3 and 18

G. Host plants

ymphs. *J. pellucida* nymphs of instars IV were kept without food in plastic cylin- which were placed over moist soil in the tary. There were 10 nymphs in each treat- , and the number of replicates was four. temperature of +9 °C half the nymphs died in eight days, at +12° half died after five at +17° half died after three days. The num lifetime at 9° was 17 days and at it was 6 days. According to these results, ng warm periods in the late summer and mn nymphs cannot survive for many days out food, while in cool periods they are to survive for long periods without nour- ent. In the fields cereals were initially the important food source for the nymphs, s the grain ripened, the host plant changed. ever, in oats damaged by OSDV there were abundant green shoots available as food for nymphs even after the normal time of ning. In those fields where there were no cereal shoots, the nymphs principally fed grasses growing as weeds or on timothy h had been undersown with the cereal. e of the nymphs moved to the ditch banks, e grasses suitable for their nourishment abundant (cf. Raatikainen and Raati- en 1964). After the cereal fields and leys been ploughed, the host plants were con- ably depleted. However, in such fields there still some food source, and thus a proportion e nymphs were able to survive until the wing spring. In the spring the nymphs in fields were mainly on *Phleum pratense*, *ampsia cæspitosa*, *Elytrigia repens* and *Poa pratensis*. In general, the nymphs did not feed on dicotyledonous weeds (such as *Ranunculus repens*, *Chamaenerion angustifolium*, *Galeopsis bifida*), even though they were found in such plants from time to time.

Adults. Many investigators (e.g. Baumert and Behrisch 1957, p. 434, Heikinheimo 1958, Slykhuis and Watson 1958, Průša et al. 1959, Raatikainen and Tinnilä 1959 b, Vacke and Průša 1961, 1962, Lindsten 1961 b, Heskova et al. 1962, Nuorteva 1962, Ikäheimo 1964, Harpaz et al. 1965) have reared *J. pellucida* on scores of different grass species. When the leafhoppers were reared on different cereals and grasses, differences were noted in their longevity, rate of development (Table 4) and egg number (Table 18). Some workers have also tested other monocotyledons and dicotyledons (e.g. Heikinheimo 1958, Raatikainen and Tinnilä 1959 b, Průša et al. 1959, Vacke and Průša 1962, Heskova et al. 1962, Ikäheimo 1964). Such plants, however, are evidently less suitable as host plants than gramineous species. At least in the region of investigation, cereals and grasses were the most important food plants of *J. pellucida* adults.

Although the leafhopper was able to live on several different kinds of plants, it preferred certain species and individual plants in the stand and occurred most abundantly on them. In 1957, an experiment was carried out with *J. pellucida* adults which had been collected from oat fields after migration. They were placed in medium-sized cages in the field and allowed to choose from the different host plants during the period July 1—17 (cf. p. 13). The numbers of leafhoppers on the different plants were counted 10 times during the course of the experiment. As they were counted, the insects were removed from the plants. The numbers of leafhoppers from the different replicates and countings were combined.

When offered a choice of grass species, *J. pellucida* in the cages was found 148 times on *Phleum pratense*, 103 times on *Elytrigia repens*, 99 times on *Deschampsia cæspitosa* and 69 times on *Calamagrostis purpurea*. In the cages containing crops growing in cereal fields, the leafhoppers were found 178 times on oats, 149 times on *Phleum pratense*, 18 times on *Trifolium pratense* and 6 times on *T. hybridum*. In the cages containing weeds and red clover, it was found 34 times on *Stellaria media*, 18 times on *Trifolium pratense*, 18 times on *Galeopsis bifida* and 7 times on *Spergula arvensis*. All observations and experiments demonstrate that adults chiefly choose gramineous species as host plants. According to trials and observations in the fields, adults seemed to occur mainly in spring cereals, but also in winter cereals, timothy and other grasses. They also inhabited dicotyledonous plants, although obviously they did not generally use such plants as a source of nourishment. In forests and on seashores and boggy land, they appeared sparsely on grasses as well as on *Carex* and *Eriophorum*.

H. Reproduction

Sex ratio. The sampling method may influence the results relating to the ratio of males to females in *J. pellucida*. However, samples collected from both timothy leys and spring cereals by the suction and the netting methods did not give different results for the sex ratio (HEIKINHEIMO and RAATIKAINEN 1962, pp. 15, 16). Since on grounds of economy it was found best to employ the netting procedure, the results obtained with it will be discussed below.

The sex ratios of leafhoppers collected from timothy and oats as well as of migrating adults were studied at different times during the summer. The weekly netting samples obtained from first-year timothy leys were grouped into three consecutive categories of approximately equal size. In these samples (Table 15) the proportion of males declined toward the end of the period during which leafhoppers occurred. Likewise, weekly netting samples taken from oat fields were divided into three consecutive groups of equal size. In this case (Table 16) the proportion of males was greatest in the middle group and decreased, particularly at the end of their period of occurrence. These results may be interpreted to mean that the males emerged earlier than the females, and thus males were initially most abundant in timothy. It appeared that the males migrated slightly earlier than the females (cf. Table 11), and therefore their numbers in spring cereals were highest in the beginning. On the average, they apparently died sooner than the females, and during the period of oviposition the females were evidently at a lower level on the oat plants than the males.

From the various data obtained, it appears that the sex ratio varied during the summer, the proportion of males generally being highest at the beginning and lowest at the end of the period of leafhopper occurrence.

Table 15. Proportion of male *J. pellucida* in weekly netting samples taken from first-year timothy leys in 1958—1962. The samples for each year were divided into 3 consecutive groups containing about the same numbers of leafhoppers, and the corresponding groups of each year were then combined. Same material as in Fig. 19

Group	Total leaf-hoppers	Males		χ^2	
		No.	%	I	II
I . . .	635	340	53.5	—	—
II . . .	938	370	39.4	29.84***	—
III . . .	872	224	25.7	120.43***	38.21***
	2 445	934	38.2		

Table 16. Proportion of male *J. pellucida* in weekly ne samples from oats in 1958—1962. The samples w grouped in the same way as in Table 15. Same ma as in Fig. 20

Group	Total leaf-hoppers	Males		χ^2	
		No.	%	I	II
I . . .	1 320	704	53.3	—	—
II . . .	1 858	1 125	60.5	16.16***	—
III . . .	1 737	463	26.7	225.06***	416.90***
	4 915	2 292	46.6		

In view of the above facts, it is very difficult to determine the sex ratio from material collected in the field. The data for the entire period of leafhopper occurrence (Tables 15 and 16) presumably give too low a percentage of males (38 % in timothy and 47 % in oats), while the data from the early part of the period the proportion of males is probably too high (54 in timothy and 53 % in oats).

17. Proportion of male *J. pellucida* in samples ob- d with the netting apparatuses. Parasitized leaf- ers are not included. Same material as in Fig. 24

Year	Total leaf-hoppers	Males	
		No.	%
......	557	307	55.1
......	2 139	1 224	57.2
......	999	531	53.2
......	132	76	57.6
......	120	81	67.5
......	87	51	58.6
......	1 704	937	55.0
Mean			57.7

he sex ratio of migrating adults can be mined by counting the specimens collected the netting apparatuses in the years 1957— According to this material (Table 11), e were slightly more males (56 %) than les, the divergence from the theoretical atio being significant ($\chi^2 = 83.49$***). The uations from year to year were small (Table Of the macropters collected in the field le 9) 60.8 % were males, while 57.1 % he brachypters were males ($\chi^2 = 2.37$*). e crossing experiment between brachypters acropters, there were relatively more males %) among the macropterous offspring 275) than among the brachypterous ones n = 332). This difference is significant 12.97***). According to this, the pro- on of males captured with the netting atuses was presumably higher than among population in the field, where there were brachypterous and macropterous leaf- pers.

he sex ratio of *J. pellucida* was also investi- d by means of rearing experiments. In the g before emergence, nymphs were collected eep net from first-year timothy leys. Of the ealthy nymphs reared, 43 % developed into s. In a second experiment, *J. pellucida* was ed in the autumn and the nymphs were ed until they had become adults. A total of dult leafhoppers were obtained, of which % were males.

cording to all the material and observations red, the sex ratio of *J. pellucida* was close to 1:1, but under natural conditions it may tend to be dominated by females.

Copulation. According to KANERVO et al. (1957, p. 47), copulation probably takes place after migration. This is consistent with the fact that both sexes migrate (cf. Fig. 24). This assumption is supported by experiments in which leafhoppers were collected from timothy before migration and from spring cereals after migration, and were subsequently reared in gauze cylinders. Only the leafhoppers taken from the spring cereals congregated into groups, and of 89 leafhoppers 70 % were in groups. The 21 groups observed contained from 2 to 6 leafhoppers each (mean 3.0), and 16 of the groups consisted of both sexes. When leafhoppers were reared continually in the gauze cylinders, they were in active movement during the normal time of migration, but afterward they congregated into groups in the same way as leafhoppers which had actually migrated, as in the trials of HEIKINHEIMO (1964). At this stage they apparently copulate.

In the usual grouping of leafhoppers, the female was above and the male below. The male vibrated its wings and turned its abdomen sidewards. Such activity was most pronounced in the daytime and decreased at night. The chain of reactions preceding copulation was associated with sounds produced by the male at least. Copulation itself was only seen extremely rarely. During copulation on plants, the head of the female was upwards and that of the male downwards.

Under experimental conditions the male copulated with at least two females, since in cultures comprising one male and four females, two of the females produced fertile eggs. *J. pellucida* was not found to reproduce parthenogenetically. According to HALKKA (1959), the male in Finland is of the type XO and 2n = 29.

Oviposition and oviposition period. Before oviposition the female made a long fissure in the plant and deposited the eggs in it. (Fig. 11). She covered the anterior end of the egg, which remained at the level of the plant surface, with a thick white secretion;

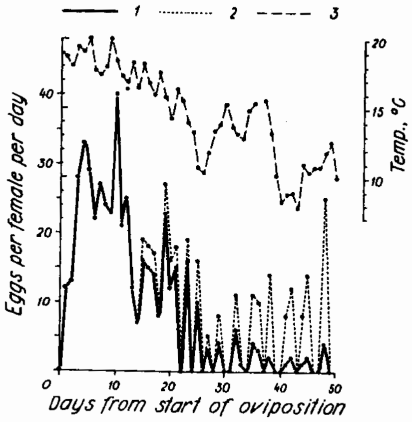


Fig. 26. Oviposition of six *J. pellucida* females in the insectary, July 14—Sept. 4, 1957. 1 = average fecundity per female, 2 = average fecundity per surviving female and 3 = mean temperature °C.

this secretion has been studied by STRÜBING (1956 b). The posterior end of the egg was usually within the cavity of the stem. If the stem wall was very thick, the posterior end was within the wall tissue. Sometimes the leafhopper oviposited in the sheath or blade of the leaf (Fig. 11).

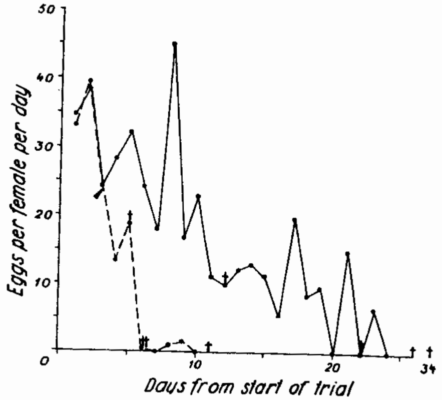


Fig. 27. Oviposition of four *J. pellucida* females on oats (solid line) and four *J. pellucida* females initially on oats and later on timothy (dashed line). Black triangle = leafhoppers transferred from oats to timothy; † = leafhopper died.

The oviposition of six females was stu by means of rearing corks placed on oat pla (Fig. 26). At first the number of eggs laid dai was small, but it rose to a maximum, whi averaged 40 eggs per day, and thereafter slo declined. This is typical of many insects (e ANDREWARTHA and BIRCH 1961, p. 37). I addition to the age of the female, at least th temperature had an influence on ovipositio In warm weather the number of eggs deposit per day was larger than in cool weather.

Eight leafhoppers in the same stage of ovipos tion were selected; four were transferred t timothy and four were left on oats. The numbe of eggs laid daily by the females transferred t timothy diminished and laying ceased complete within 1—6 days (Fig. 27). These females subsequently died on an average less than one day after oviposition ceased. The leafhoppers which remained on oats continued to deposi eggs and later died an average of 4 days afte oviposition had ended. The difference was no significant (t = 2.2, d.f. = 6, $P > 0.05$). When leafhoppers were transferred from oats t *Elytrigia repens*, they soon stopped producin eggs and died, while those transferred from oa to spring wheat continued to oviposit.

The oviposition of leafhopper populations o oat fields was investigated by means of 100-plan samples taken every week (Fig. 28). Ovipositio began during the period around June 10—July and 1 $^1/_2$ months after it had begun there was n longer any appreciable increase in the numbe of eggs.

Number of eggs per female. It ha been demonstrated that females are capable o reproducing on at least 17 different gramineou species and ovipositing on them after having been reared on such plants during their entire adult period (RAATIKAINEN and TINNILÄ 1959 b The number of eggs per female in the common grass species growing in fields (cf. PAATE 1953 c, RAATIKAINEN and RAATIKAINEN 1964 was studied by means of gauze cylinders (Tab 18). The largest number was laid in spring cereals and the smallest in grasses growing o leys and ditch banks. The number of eggs w

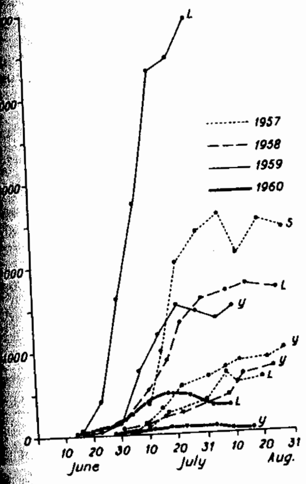


Fig. 28. Numbers of delphacid eggs per 100 oat plants in certain fields in 1957—1960. The curves are 3-point moving averages. Localities: L = Laihia, Y = Ylistaro, S = Sulva. Same material as in Fig. 16.

derably larger than had been presumed by GREN (1925, p. 56). In the laboratory trials ROSEN (1956 b, p. 8) the number of eggs ced was 500—1 000 per female, while in iments carried out by the writer in 1957 26 females reared on oats the average ber of eggs was 430 (HEIKINHEIMO 1958). data of all the cultures reared on oats in nd are combined, the average number of of *J. pellucida* is found to be 402 ± 38.5 per le (n = 48).

certain years macropterous leafhoppers gathered from the same clearing and placed oats in gauze cylinders to oviposit. The ber of eggs varied from year to year (Table The numbers produced in the cultures and he field evidently do not completely correspond to one another. For example, in 1959, n the number of eggs was small, the leafpers in the cultures died as a result of the conditions before oviposition had ceased. he open field the mortality was apparently so great, since there the leafhoppers could

Table 18. Numbers of eggs of *J. pellucida* in different host plants in 1960. On June 11, one female and two males were placed in each gauze cylinder; on Aug. 1—19 the eggs were counted. Twelve replicates. Same material as in Tables 20 and 24

Plant species	Ovi-positing females	No. of eggs per ovipositing female Mean ± S.E.
Triticum aestivum	10	536 ± 80.9
Avena sativa	7	455 ± 98.9
Hordeum vulgare	7	421 ± 93.6
Elytrigia repens	4	366 ± 37.0
Anthoxanthum odoratum	3	287 ± 81.5
Festuca pratensis	7	277 ± 63.7
Secale cereale	8	257 ± 81.8
Poa pratensis	6	240 ± 110.6
Alopecurus pratensis	4	225 ± 43.6
Phleum pratense	10	206 ± 33.0
Deschampsia caespitosa	4	204 ± 81.8
Agrostis tenuis	7	166 ± 48.2

more easily find spots with adequate moisture than inside the gauze cylinders.

Oviposition plants. In the trials carried out in cages and gauze cylinders, eggs of *J. pellucida* were found in the stems of the following grass species: *Festuca rubra*, *F. pratensis*, *Lolium perenne*, *Poa pratensis*, *Dactylis glomerata*, *Avena strigosa*, *A. fatua*, *A. sativa*, *Deschampsia caespitosa*, *Calamagrostis purpurea*, *Agrostis stolonifera*, *A. gigantea*, *A. tenuis*, *Alopecurus pratensis*, *A. geniculatus*, *Phleum pratense*, *Phalaris arundinacea*, *Anthoxanthum odoratum*, *Bromus inermis*, *Secale cereale*, *Triticum aestivum*, *Elytrigia repens*, *Hordeum vulgare* and *H. distichum*. Eggs occurred less frequently in the leaves than in the stems. However, they were found in leaves of all the above-mentioned cereals, and in addition in the leaves of *Avena strigosa*, *Deschampsia caespitosa*, *Calamagrostis purpurea*, *Phleum pratense* and *Elytrigia repens*. In the field, eggs of *J. pellucida* were established to occur in the stems

Table 19. Numbers of eggs of *J. pellucida* in Tammi oats

Year	Ovi-positing females	No. of eggs per ovipositing female Mean ± S.E.	t
1957	4	700 ± 68.4	}6.55**
1959	8	192 ± 36.8	
1960	7	455 ± 98.9	}2.50*

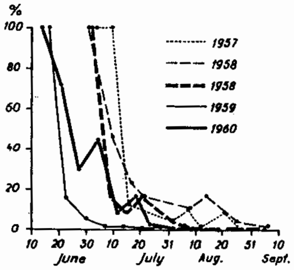


Fig. 29. Percentage of total delphacid eggs located in the leaves of oats, 1957—1960, and spring wheat, 1958 (double dashed line). Same material as in Fig. 16. The material collected at Laihia and Ylistaro was combined each year.

Table 20. Distribution of *J. pellucida* eggs between ste and leaves of different plant species in trials made in 19 Same material as in Table 18

Plant species	Eggs in stems No.	Eggs in stems %	Eggs in No.	
Avena sativa	3 123	98.1	61	[illegible]
Hordeum vulgare	2 908	98.6	42	[illegible]
Triticum aestivum	5 362	100.0	0	[illegible]
Secale cereale	2 058	100.0	0	[illegible]
Phleum pratense	2 055	100.0	0	[illegible]
Festuca pratensis	1 936	100.0	0	[illegible]
Elytrigia repens	1 464	100.0	0	[illegible]
Poa pratensis	1 440	100.0	0	[illegible]
Agrostis tenuis	1 221	100.0	0	[illegible]
Alopecurus pratensis	898	100.0	0	[illegible]
Anthoxanthum odoratum	861	100.0	0	[illegible]
Deschampsia caespitosa	816	100.0	0	[illegible]

and leaves of all cereals as well as in the stems of *Avena fatua*, *Apera spica-venti*, *Phleum pratense* and *Elytrigia repens*. Eggs of delphacids occur in many other gramineous species, but they were not reared, so that no species identification could be made. According to JÜRISOO (1964, p. 75), the proportion of plants of different grass species containing eggs of *J. pellucida* in relation to the total number of plants investigated is greatest in spring cereals, less in winter cereals, and least in *Phleum pratense*, *Elytrigia repens*, *Festuca pratensis* and *Poa pratensis*.

Under field conditions the eggs of *J. pellucida* are usually deposited in the stems of gramineous plants. In the cultures kept in cages and gauze cylinders, eggs were also laid in the plants of other families whose stem or petiole was hollow or contained porous tissue, such as *Trifolium pratense*, *T. hybridum*, *Galeopsis bifida* and *Plantago major*. Even under natural conditions eggs may occasionally be found in such plants (cf. RAATIKAINEN and TINNILÄ 1959 b).

The location of eggs and egg groups in the stems and leaves. *J. pellucida* oviposits in the stems and leaves of gramineous plants. The distribution of the eggs between the stem and leaves of cereals was found to vary during the course of the oviposition period. On oats and spring wheat, the eggs were initially located exclusively in the leaves, whereas at the end of the oviposition period only 1 % were situated in the leaves (Fig. 29). Not all the eggs, however, were those of *J. pellucida*, but at least during the middle and later phases of oviposition most of them were of this species (cf. te of Fig. 16).

The distribution of the eggs between the lea and stems differed according to the plant spec In trials, the eggs were only found in the lea of oats and barley but not in those of other pl (Table 20). The leaf sheaths of these two ce are thick and otherwise suitable sites for eg deposition, while the sheaths of spring wh are thin and consequently *J. pellucida* ra oviposits in them.

The distribution of eggs between the lea and stems of different cereal varieties was inve tigated in field trials. The plots, 6.7 × 2.4 m size, were sown on May 24, 1963, and there we four replicates. Netting samples taken on July 1 revealed that all the 274 delphacid specim collected from oats were *J. pellucida*, and li wise all the 193 specimens from spring wh belonged to this species. In this trial it is evid that all or nearly all the delphacid eggs were *J. pellucida*. The proportion of oat plants di tinctly infected with OSDV was 13—48 %, w those infected with EWSMV amounted to 3 %. All the plants located in an area 15 × cm in each replicate were taken and the num of delphacid eggs in them determined. The nu bers of eggs and egg groups in the leaves o

1. Distribution of delphacid eggs and egg groups stems and leaves of oats in field variety trial. ions made on Aug. 12—26, 1963. The varietal ces in egg distribution were not statistically ant (arc sin transformation, F = 1.07, d.f. 8 and Same material as in Tables 26, 29 and 53

	Eggs			Egg groups		
	In stems	In leaves No.	In leaves %	In stems	In leaves No.	In leaves %
	932	72	7.2	95	22	18.8
	3 105	228	6.8	276	57	17.1
	3 185	178	5.3	355	43	10.8
	5 647	228	3.9	449	32	6.7
	6 150	245	3.8	532	56	9.5
	4 649	159	3.3	418	39	8.5
	4 471	144	3.1	361	37	9.3
	4 409	81	1.8	354	22	5.9
	4 031	42	1.0	335	13	3.7
	36 579	1 377	3.6	3 175	321	9.2

arieties were very great (Table 21), but no ences in the distribution of the eggs between the leaves and stems of the different ies were detected. Only in one wheat y were eggs found in the leaves, and here were very scanty (Table 22).

developmental stage of the cereal at the of oviposition was the factor determining cation of the leafhopper eggs in the plant. g the early phase of oviposition, the stem ot always visible, and in such cases the opper deposited its eggs in the leaf sheaths. factors may lead to late emergence of the of spring cereals. One such factor was the drought prevailing in the spring and early part of the summer. The effect of dry conditions was studied at Ylistaro for two consecutive years in fields of Pendek oats growing on the same soil type. In June 1957, the weather was quite wet (precipitation 68 mm, temperature 11.5°C), while in 1958 it was very dry (precipitation 18 mm, temperature 13.8°C). According to suction samples taken in July 1957, 77 of the 81 healthy delphacid leafhoppers collected were *J. pellucida* and 4 were *J. odscurella*. Similar samples taken in July 1958 showed that all the 23 healthy delphacids were *J. pellucida*. These results thus clearly reflect the position of the *J. pellucida* eggs in the cereal stands investigated. According to plant samples taken at intervals of about one week during the perlod July 1—Aug. 24 (totalling 700 plants in each year), the following numbers of delphacid eggs were found:

22. Distribution of delphacid eggs and egg groups stems and leaves of spring wheat in field variety Inspections made on Aug. 14—26, 1963. No ant varietal differences in egg distribution were nd. Same material as in Tables 27, 30 and 53

	Eggs			Egg groups		
	In stems	In leaves No.	In leaves %	In stems	In leaves No.	In leaves %
	518	5	1.0	31	3	8.8
	4 030	0	0.0	234	0	0.0
	3 763	0	0.0	227	0	0.0
	3 548	0	0.0	213	0	0.0
	2 890	0	0.0	182	0	0.0
	2 440	0	0.0	128	0	0.0
	17 189	5	0.0	1 015	3	0.3

	Total eggs Number	In the leaves Number	In the leaves %
1957	3 440	277	8.1
1958	2 722	895	32.9

Oats growing under dry conditions, i.e. in 1958, were short and their stems emerged late. In such stands, oviposition of *J. pellucida* was concentrated in the leaves, and the drier the site, the higher the proportion of eggs in the leaves. Under natural conditions the largest number of delphacid eggs encountered in leaves was 32.9 %, as seen in the above tabulation.

When oats are infected with the virus diseases OSDV or EWSMV, their stems emerge later than normal, and OSDV-infected plants tiller profusely (VACKE 1960). In such virotic oats, there were indeed more eggs and egg groups in the leaves than in non-diseased oats (Table 23). Likewise, plants injured by certain flies, such as *Oscinella frit* L. and *Elachiptera cornuta* Fall., have many leaves and their stems emerge late. These plants, too, appeared to have larger numbers of *J. pellucida* eggs in their leaves than normal. Similarly, plants which were injured by frost at the end of May apparently had more eggs in their leaves than uninjured plants. On the other hand, the use of MCPA for weed control did

Table 23. Proportion of delphacid egg groups (mainly *J. pellucida)* in leaves of oat plants in fields distinctly
with OSDV and EWSMV in 1961. Number of plants examined 5 739. Same material as in Table 40

Condition of plant	Egg groups			χ^2	
	Total	In leaves No.	In leaves %	OSDV	EWS
Infected with OSDV	1 125	498	44.3	—	—
Infected with EWSMV ...	48	5	10.4	20.22***	—
Not visibly infected	2 317	27	1.2	1 084.98***	26.1

not have any appreciable effect in increasing the numbers of eggs in the leaves, since the treatments were carried out late and tillering of the plants likewise took place at a late date.

In both the trials and fields, most of the eggs and egg groups of *J. pellucida* at the end of the oviposition period were located in the stems of all the plants examined. In grasses the eggs were usually laid in the sheaths but occasionally in the blades as well. In leaves of dicotyledonous plants the eggs were deposited in the petioles.

Vertical distribution of eggs and egg-containing internodes. The height of cereal plant internodes containing delphacid eggs was studied by means of plant samples taken from cereal fields. *J. pellucida* probably made up more than half of the total delphacids in all the fields investigated and about 95 % on the average in oats and spring whe
Consequently, the results give a very good
ture of the height of the stem internodes co
taining eggs of *J. pellucida*. The level was dete
mined by measuring the distance between th
upper node of the internode in question and th
base of the plant. According to the results (Fig
30), in all of the cereals investigated, most o
the internodes containing delphacid eggs we
located at heights between 5 and 20 cm.

The eggs in the stems were generally situa
close to the upper node of the internode in whi
they were found, and for this reason this upp
node was selected as the height to be measur
Actually, the eggs were located below this heig
especially in the upper parts of the plant. Ho
ever, despite this minor discrepancy, the resu
are valuable, for instance, in allowing comp

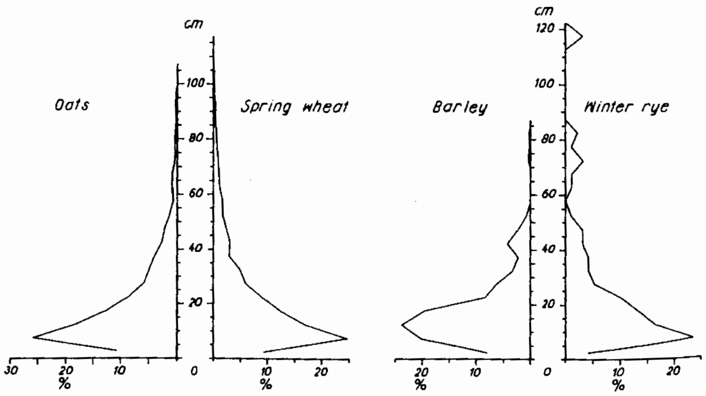


Fig. 30. Height of internodes containing delphacid egg groups, measured from the ground, 1958—1963. Total numbers of egg-containing internodes examined: oats 3 971, spring wheat 2 097, barley 429, winter rye 97.

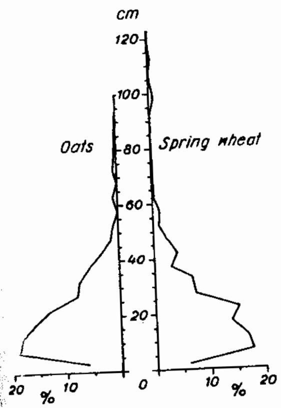


Fig. 31. Height of delphacid eggs in cereal stems, measured from the ground, 1958—1963. Total numbers of eggs examined: 58 715 in oats and 21 183 in spring wheat.

between different cereals and other plants
ards the vertical position of the eggs and
ymenoptera which fed on them. The height
eggs differed from the height of the egg-
ning internodes (cf. Figs. 30 and 31).

e of egg groups. Delphacids
y deposit their eggs in groups. For exam-
he egg groups of *Ditropis pteridis* (Spinola)
ise 1—5 eggs, while those of *Muellerianella*
irei (Perris) have 1—13 eggs (Morcos
pp. 413, 416, 417). The egg groups of *Megadelphax sordidulus* (Stål) in the stem of Tammi oats were found to consist of an average of 6.9 eggs (Raatikainen 1960 a, p. 235), and the groups of *Dicranotropis hamata* (Boh.) had 8.5 eggs (Raatikainen and Vasarainen 1964, p. 315). The size of *J. pellucida* egg groups on different plant species was determined in experiments carried out in gauze cylinders. It was found (Table 24) that the size of such egg groups in the stems varied according to the plant. In an even larger experimental material, the distribution of the egg group sizes was asymmetrical. On an average, there were 12.8 eggs per group in oat stems and 5.4 eggs in the leaves (Figs. 32 and 33).

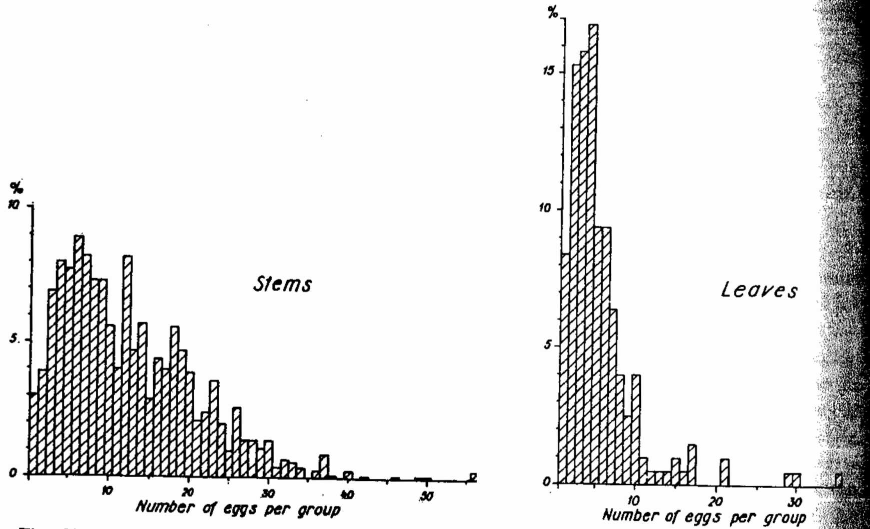
24. Size of egg groups of *J. pellucida* in stems of
nt grass plants. Same material as in Table 18. The
means are unweighted

Plant species	Eggs per group Mean ± S.E.
pratensis	19.0 ± 2.17
mpsia caespitosa	18.5 ± 5.16
m aestivum	16.0 ± 1.03
ia repens	15.6 ± 0.65
atensis	15.0 ± 1.39
rus pratensis	14.6 ± 1.40
m vulgare	13.0 ± 0.78
cereale	12.1 ± 0.54
s tenuis	11.5 ± 1.68
sativa	11.4 ± 1.37
pratense	11.3 ± 1.22
canthum odoratum	9.8 ± 1.58

The size of the egg groups of *J. pellucida* in cereal fields could not be determined. However, large numbers of delphacid egg groups were studied in samples of oats and spring wheat collected from the field, and most of them (about 95 %) were of the species *J. pellucida*. The distribution of egg group sizes in this material was asymmetrical (Table 25). However, the large-sized groups, which were uncommon, were sometimes made up of eggs deposited at different times, but it was not possible to distinguish them even on the basis of the developmental stages of the eggs. The sizes of the egg groups both in the trials and in the field were approximately equal. The field examinations showed that the egg groups varied in size according to the plant species; for example, the groups in the stems of spring wheat were larger than those in oat stems. The egg groups in oat leaves were usually in the sheath, but sometimes they occurred in the blade. The size of the delphacid egg groups in the blades was smaller than in the sheaths, as became evident from examinations made on material collected in 1964 and shown below:

	No. of eggs	No. of egg groups	Mean	Eggs/group Min.	Max.
Sheath	691	180	3.8	1	24
Blade	721	253	2.8	1	15

The size of the egg groups in different varieties of oats and spring wheat was investigated in the field. The size in both oat and wheat varieties was found to vary considerably (Tables 26 and



Figs. 32 and 33. The size of egg groups of *J. pellucida* in the stems (left) and leaves (right) of oats. A total of 12386 eggs and 968 egg groups in the stems and 1 095 eggs and 202 egg groups in the leaves were examined.

27), but in neither of these cereals were the differences between varieties significant. The difference between cereal species, however, was similar to that established in the material listed in Table 24.

There are obviously several factors influencing the size of the egg groups. A trial was carried out in which one female and two males were placed on oats in each of 21 gauze cylinders. After oviposition the plants were examined, and it was found that the egg groups were small in size if the stem wall was thick, whereas they were large if the wall was thin (Table 28). This resu is the same as was found in a trial perform with *Megadelphax sordidulus* (Stål) (Raatikain 1960 a, p. 235). The egg groups of leafhopp were apparently small-sized at the beginning oviposition and become larger as time elapsed This fact may partially affect the results presente in Table 28. At the beginning of oviposition this trial, the females deposited their egg exclusively in thick-walled stems, while at the end of oviposition they were able to selec between walls of varying thickness. In oat

Table 25. Size of delphacid egg groups in field samples of spring wheat and oats in 1957—1964

	No. of eggs	No. of egg groups	Eggs per group		
			Mean	Min.	Max.
Spring wheat, stems	40 332	2 341	17.2	1	54
Spring wheat, leaves	305	92	3.3	1	12
Oats, stems..	97 189	8 475	11.5	1	83
Oats, leaves..	9 429	2 886	3.3	1	35

Table 26. Size of delphacid egg groups in oat stems a variety trial in 1963. Same material as in Table

Variety	Eggs per group Mean	Variety	Eggs per group Mean
Marne	14.3	Kyrö	12.
Tammi	12.5	Eho	11.
Pendek	12.5	Kultasade II .	11.
Nip	12.4	Sisu	9.
Orion III ...	12.4		

F = 0.63, d.f. 24 and 8, P > 0.05

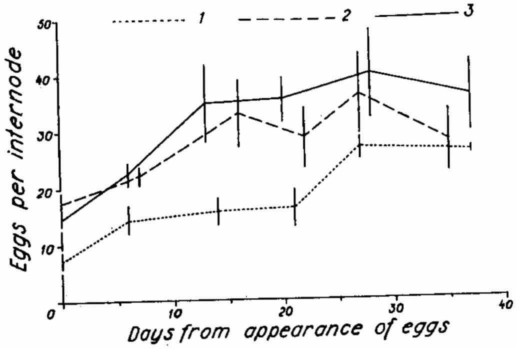


Fig. 34. Numbers of delphacid eggs per internode in oats at different times of the oviposition period. 1 = under 800, 2 = 800—1 400, and 3 = over 1 400 eggs per 100 plants. The vertical lines denote the standard error. Same material as in Fig. 16.

les collected from the field, the size of acid egg groups was small in thick-walled and large in thin-walled plants, just as in se of the experiment carried out in gauze ers. Other factors which affected the size egg groups were the hardness of the stem her structural features of the plant, as well turbance of the leafhoppers during the of oviposition.

mber of eggs per internode. estigating the egg-predatory pteromalids he ecology of their enemies, data were d on the numbers of delphacid eggs in the odes of the host plants. Therefore, in the 1957—1960 such information was obtained eans of plant samples (each consisting of lants) taken at weekly intervals from nine elds. The nine fields were divided into three ps of three each on the basis of the density of delphacid eggs in the plants. According to the results (Fig. 34) and to other field observations, the average number of eggs per internode rose toward the end of the oviposition period. This rise was similar in all three groups. Furthermore, the results seem to indicate that the numbers of eggs per internode were largest in those fields having a high density of leafhopper eggs and smallest in the fields with a low egg density.

The quantities of eggs in the internodes of different varieties of oats and spring wheat were determined in the field experiments. No significant differences were found as regards the number of eggs per internode between the oat varieties (Table 29) or between the wheat varieties (Table 30).

As the density of *J. pellucida* adults in the different fields rose, the density of their eggs also appeared to increase in most cases. However,

27. Size of delphacid egg groups in spring wheat in a variety trial in 1963.Same material as in Table 22

iety	Eggs per group Mean	Variety	Eggs per group Mean
o	19.3	Apu	17.1
.....	17.3	Norröna	16.4
l	17.1	Timantti	15.0

d.f. 5 and 15, P > 0.05

Table 28. Size of egg groups of *J. pellucida* in oat stems having walls of varying thickness

Thickness of stem wall, mm	No. of stems	No. of egg groups	No. of eggs	Eggs/group Mean ± S.E.
0.2	25	97	1 542	15.9 ± 0.7
0.3	32	93	1 290	13.9 ± 1.1
0.4	20	58	442	7.6 ± 0.7
0.5	21	60	531	8.9 ± 1.0
>0.5	11	46	396	8.6 ± 0.7

Table 29. Numbers of delphacid eggs in oat internodes in a variety trial in 1963. Same material as in Table 21

Variety	Eggs per internode Mean	Variety	Eggs per internode Mean
Kultasade II .	40.5	Pendek	33.7
Kyrö	36.0	Orion III ...	32.7
Nip	35.3	Sisu	31.5
Eho	34.3	Marne	22.8
Tammi	34.0		

F = 1.96, d.f. 8 and 24, P > 0.05

Table 30. Numbers of delphacid eggs in spring wh internodes in a variety trial in 1963. Same material a Table 22

Variety	Eggs per internode Mean	Variety	Eggs per internode Mean
Svenno	42.5	Tammi	32.5
Apu	33.2	Ring	29.5
Norröna	33.1	Timantti	29.1

F = 1.67, d.f. 5 and 15, P > 0.05

as the egg density increased, there was a change in the distribution of the leafhopper eggs in the stand. At the end of the oviposition period in the years 1957—1964, determinations were made of the numbers of delphacid eggs per 100 plants and per internode in oats growing in 36 different fields. Since there were no significant differences between the oat varieties (most common: Tammi, Pendek, Eho Nip, Orion) regarding the egg number per internode, the entire material was combined. Figure 35 shows that there was a distinct positive correlation between the number of eggs per internode and the density of delphacid eggs. As the density of the leafhopper population increased, apparently more and more leafhoppers oviposited in the same internode. Consequently, in such internodes there could be a considerable difference in the age of the egg groups, since the insects oviposited during a period of several weeks. This was advantageous for the larvae o *Panstenon oxylus* and *Mesopolobus aequus* whic inhabited the internodes, since there wer abundant delphacid eggs, and the nymphs fro the last eggs emerged late, so that even the lat appearing pteromalid larvae often had an ampl source of nourishment.

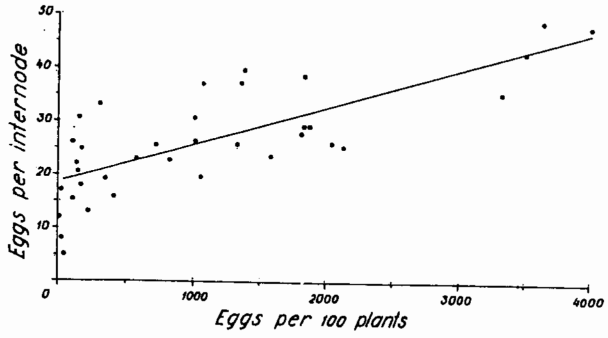


Fig. 35. Regression of number of delphacid eggs per internode on numbers of delphacid eggs per 100 oat plants. $r = 0.77^{***}$, d.f. = 34; $y = 18.4 + 0.007x$.

I. Overwintering

In the present studies *J. pellucida* was foun to occur mostly during the winter in leys whic had been established the previous summer unde a cereal nurse crop. The species also occurred some extent in older leys, as has been establishe by several investigators, including Kanervo e al. (1957), Heikinheimo (1959), Raatikain and Tinnilä (1959 a), Dlabola (1960), Lin sten (1961 b), and Jürisoo (1964). There we

31. Percentage of different nymphal instars of *Javesella* leafhoppers in suction samples taken in autumn on different fields. The material from the 4 fields was combined each year. Same material as in Table 89

Date of sampling	Total nymphs	Nymphal instars					
		Percentage					Mean ± S.E.
		I	II	III	IV	V	
19. IX—18. X	685	10.1	34.1	42.5	13.3	—	2.6 ±0.03
—8. X	1 039	1.0	18.0	61.9	19.1	—	3.0 ±0.02
5. X	541	2.2	37.5	50.9	9.4	—	2.7 ±0.03
20. X	826	—	1.7	31.6	66.7	—	3.7 ±0.02
—5. X	679	1.2	16.3	48.9	33.3	0.3	3.2 ±0.03
16.—17. X	295	8.8	51.5	22.1	17.6	—	2.5 ±0.05
—9. X	753	0.1	3.1	21.9	74.9	—	3.7 ±0.02
—8. X	826	0.6	13.7	28.7	57.0	—	3.4 ±0.03
Mean (1957—1964)		2.0	20.3	38.0	39.7	0.0	3.2

rous open ditches in the region of investin, and the ditch banks in cereal fields of the ous summer were similarly important overering sites of the species. *J. pellucida* also red to a minor extent in other ditch banks ll as in other places, especially where grasses growing. In autumn the nymphs only move ort distances, and they generally hibernate same place where they have hatched from ggs. There was some movement, however, the field itself to the ditch banks.

cording to Kanervo et al. (1957, p. 14), region of investigation *J. pellucida* hiberin nymphal instars I—IV but usually in III. As shown by suction samples taken tumn (Table 31) and spring (Table 32), nation may take place in all nymphal instars. lculating the average hibernating instar, the les taken in spring and autumn of 1956 could not be combined with the other years, since the samples were collected either too late or too early. On the other hand, the samples of spring 1958, despite the late time of sampling, were included with the others, since the spring was cool and very little development had occurred before the time of sampling. According to the results calculated in this manner, *J. pellucida* usually hibernates in nymphal instars IV and III. However, the nymph material used in these calculations was not completely uniform, since the nymphs of the genus *Javesella* belonged to at least two different species. On the basis of netting samples taken in the sampling site at the beginning of emergence, more than 90 % of the adults every year were *J. pellucida* and the rest were *J. obscurella*. Since *J. pellucida* emerged slightly later than *J. obscurella*, the nymph samples every year presumably consisted of over 99 %

32. Percentage of different nymphal instars of *Javesella* leafhoppers in suction samples taken in spring on The sampling fields and treatment of the material were the same as in Table 31. Same material as in Table 90

Date of sampling	Total nymphs	Nymphal instars					
		Percentage					Mean ± S.E.
		I	II	III	IV	V	
—28. V	1 593	0.1	0.8	23.4	57.5	18.2	3.9 ±0.02
25. IV—14. V	314	1.9	30.9	43.3	21.3	2.6	2.9 ±0.05
20.—21. V	581	0.7	20.6	59.4	19.3	—	3.0 ±0.03
16. IV	556	0.3	41.2	47.7	10.8	—	2.7 ±0.03
28.—29. IV	375	—	0.5	23.2	76.3	—	3.8 ±0.02
22.—24. IV	81	—	6.2	19.7	63.0	11.1	3.8 ±0.08
—9. V	207	1.9	18.9	48.8	30.4	—	3.1 ±0.05
23.—25. IV	237	11.0	64.5	15.2	8.9	0.4	2.2 ±0.05
27.—29. IV	316	—	2.2	22.8	75.0	—	3.7 ±0.03
Mean (1957—1964)		2.0	23.1	35.0	38.1	1.8	3.2

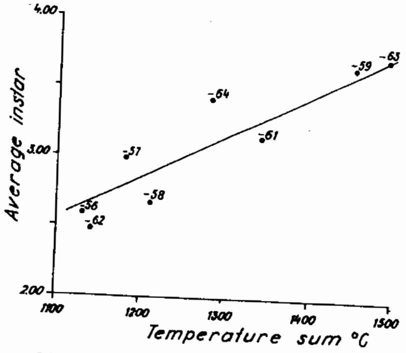


Fig. 36. Regression of *J. pellucida* average nymphal instar on the mean daily temperature sum during the period between the date of first appearance of eggs and October 2. The numbers denote the years of the study (1956—1964). r = 0.92**, d.f. 6; y = —0.753 + 0.003x.

J. pellucida. Owing to the possible errors due to the sampling method (cf. Heikinheimo and Raatikainen 1962, p. 15) and to the presence of *J. obscurella* nymphs, the actual nymphal instar of *J. pellucida* may have been slightly lower than the *Javesella* nymphal instar presented in the tables. This discrepancy, however, was probably very small and was masked by other variations.

In the wintertime the nymphs were in a "weak" diapause, as also mentioned by Dlabola (1960, p. 366). However, the diapause instar was not the same from year to year. According to the mean values of suction samples taken in the autumn (Table 31), it is seen that there was an annual fluctuation of 1.2 nymphal instars (t = 22.6***, d.f. = 1 046). The corresponding difference in the samples collected in the spring (Table 32) was 1.6 nymphal instars (t = 16.5***, d.f. = 316). The temperature during the summer evidently had a decisive influence in determining the instar which the nymphs reached before winter.

Since in many insects, diapause is initiated when the day-length becomes short (cf. e.g Lees 1955, p. 14, Schwerdfeger 1963, p. 144), it was assumed in the present study that diapause began at approximately the same time in all the years, and after testing different dates, October 2
was taken as the beginning date of dia
Furthermore, tests made with different tem
tures showed that the mean daily temper
sum during the period between the date of
appearance of eggs in spring cereals and Oc
2 had the highest correlation with the nym
instar established in the autumn (Fig. 36).
correlation with the nymphal instar found the
spring was slightly lower (r = 0.91**, d.f.
The difference is small, and chance factors or
continuation of development between the ti
of sampling in the autumn and spring may h
influenced it. The temperature sum during
period preceding oviposition probably also h
an effect on the hibernating nymphal instar,
this effect was presumably considerably sm
than that produced by the temperature
prevailing during the period following ov
position.

J. Discussion

Information was needed on the ecolog
J. pellucida in order to study the fluctuation
its abundance. In the early years of these stu
attention was mainly paid to those aspec
the life cycle which were most strongly influe
by natural enemies, man, or weather facto
the same time the effect of food supply
internal factors on the abundance of the sp
was also investigated.

One of the greatest difficulties was ide
fication of the species. Although careful stu
were made of the egg of *J. pellucida* and
variations in size, as well as the egg group
their position in the host plant, it was
possible to distinguish the eggs of this sp
with complete certainly from those of o
delphacids. The difficulty was greatest in attem
ing to identify the eggs which had been dam
by larvae of Hymenoptera, and such eggs
very numerous. For this reason, only the
to which the eggs belonged could be establi
with certainty. However, this did not caus
errors in studying the abundance of *J. pe*
since there were few other delphacids
localities. It was often possible to identif

pecies of the nymphs belonging to the
Javesella, but some specimens could not
nguished so accurately, and for this reason
cation of the genus was considered ade-
This caused only minor errors in deter-
the abundance of *J. pellucida*, since the
ommon species present in the area of
gation were *J. pellucida* and *J. obscurella*,
numbers of the latter were always small
species of *Javesella* were encountered only
ically (cf. Tables 85, 86). Although it is
to identify the females and parasitized
ens of the genus *Javesella*, nearly all the
of *J. pellucida* were identified as to their

udying the abundance of *J. pellucida*, it was
ered important to investigate the pro-
ns of brachypterous and macropterous
ppers in the region concerned as well as
ctors determining the ratios of these two
The results revealed that the proportion
chypters was generally less than 10 %.
oportion of macropters was found to rise
population density of the nymphs
ed. These field investigations thus con-
the results obtained by Kisimoto (1956 a
1959) in his laboratory experiments with
vata lugens (Stål), *Sogata furcifera* (Horváth)
odelphax striatellus (Fallén) on the effect of
tion density upon dimorphism. The popu-
density itself was probably not the basic
but it might have influenced the food
for instance, and this in turn might have
d dimorphism.

perennial crops, brachypters were re-
ble for the maintenance of the population
and macropters for its expansion. The
ations of *Megadelphax sordidulus* (Stål)
Dicranotropis hamata (Boh.) were simi-
omposed of two forms (cf. Raatikainen
Raatikainen and Vasarainen 1964).
haracteristic is evidently advantageous to
ecies in view of the crop rotation system
ced in the area. According to the Official
ics of Finland III, 54, in the year 1959 about
of the arable land in the area consisted of
and 55 % was leys. According to Paatela (1953 a, p. 52), some 97 % of the leys were established under a cereal nurse crop, and they were usually kept for 3—4 years (Paatela 1953 b, pp. 14, 15). By the beginning of the present study, the system of crop rotation and the areas devoted to different crops had changed somewhat from the figures presented above, and they continued to change during the years of this study, but such changes apparently had no great effect on *J. pellucida*. In cultivated areas the species generally hibernated in leys. From such leys it was chiefly the macropters which enabled the populations to expand every year into the entire area of cereals, comprising about one-third of the cultivated land. On the other hand, most of the brachypters and some of the macropters remained in the leys, but since the leys were ploughed up within a few years, the leafhoppers in them were destroyed, and only those which had moved to cereals and consequently to the new leys established under them, survived to maintain the populations.

The studies on the population of *J. pellucida* were concentrated on leys and spring cereals. The latter were evidently the most important sites of investigation; here attention was chiefly paid to macropterous leafhoppers and the formation of new populations in spring cereals.

During the period of migration, lasting about 1½ months, the macropters and some of the brachypters moved principally from leys to spring cereals, where new, generally dense, populations were formed. In general, *J. pellucida* had not previously been present in such fields. Moreover, its natural enemies had likewise not occurred here previously, so that the studies on population formation had also to be concerned with the arrival of natural enemies. This factor made the studies more difficult, but at the same time more interesting, and the results obtained may even have a wide, over-all application in studying the "zooms" of cultivated region (cf. Jürisoo 1964, p. 52). The economic importance of the species justified carrying out the investigations on oats, and since in normal years the bulk of the arable land under cereals was devoted to oats (Official statistics of Finland III, 54, pp.

106, 108), oat fields constituted good sites for investigations. Oats also proved to be a favourable host plant for reproduction of the species. From time to time, however, the virus diseases OSDV and EWSMV considerably reduced the yields, and in the following years the area devoted to this crop was greatly reduced (cf. KANERVO et al. 1957, RAATIKAINEN and TINNILÄ 1959 a, HEIKINHEIMO and IKÄHEIMO 1962). For this reason, populations of *J. pellucida* had to be studied in other cereals as well. The best of these was spring wheat, since there were many fields of this crop in the region. Furthermore since spring wheat differs considerably in its morphology from oats, studies on this crop could be relied on to provide other significant results pertaining to population dynamics. In addition, spring wheat appeared to be a very good host plant for ensuring the reproduction of the species.

The migration and oviposition periods of *J. pellucida* were long, and hence the determination of its abundance in spring cereals was difficult. The determination of adult abundance had to be made after the end of migration, but at that time the stand was quite high, and some of the leafhoppers were ovipositing in the lower parts of the stems, while others had died. The best time for sampling was at the end of migration and suction samples were suitable but difficult and expensive to carry out (cf. HEIKINHEIMO and RAATIKAINEN 1962).

Grasses and cereals, certain other mono tyledons and a few dicotyledons appeared to suitable as host plants of *J. pellucida*. In cer fields the species oviposited almost exclusiv in the cereal crop itself, so that during counting of egg numbers in the field it was gen rally unnecessary to investigate the wee growing in the field. Eggs were encounter in certain weed species, such as *Elytrigia rep* *Deschampsia caespitosa* and *Apera spica-venti*, how ever, such weeds were scarce among spri cereals (cf. RAATIKAINEN and RAATIKAINE 1964, pp. 148, 149) and furthermore *D. caespit* in cereal fields rarely formed a stem where *pellucida* could have oviposited. According experiments and observations, nearly all th eggs occurring in weeds growing in the field were in the stems. In the cereal plants, however it was necessary to ascertain the numbers o eggs in the leaves as well.

Before a complete study of the fluctuations i abundance of *J. pellucida* could be made, howeve it was necessary to obtain sufficient informatio on the natural enemies of this species as well on the other hosts of these. In the followi sections of this work, descriptions are given the ecology of the enemies of *J. pellucida*. addition, separate papers have already been pub lished dealing with the host species of certain these enemies (RAATIKAINEN 1960 a, IKÄHEI and RAATIKAINEN 1961, 1963, RAATIKAINEN an VASARAINEN 1964).

V NATURAL ENEMIES AND DISEASES OF JAVESELLA PELLUCIDA

According to the literature, the following species have been established to be natural enemies of *Javesella pellucida:*

Panstenon oxylus (Walk.) (*Hym., Pteromalidae*) has been found to be an egg-predator of *J. pellucida* in Sweden (v. ROSEN 1955 a and b, 1956 b, JÜRISOO 1964, p. 37) and in Finland (HÅRDH 1953, KANERVO et al. 1957, RAATIKAINEN 1961 b). Since HÅRDH (1953) employed various specific names for this predator as well as for its host, reference should be made in this connexion to the amendments made by ROSEN (1956 b) and RAATIKAINEN (1961 b

Mesopolobus aequus (Walk.) (*Hym., Pteromalid* has been shown to be an egg-predator of *pellucida* in Sweden (AHLBERG 1925, v. ROSE 1955 a and b, 1956 a and b, JÜRISOO loc. ci and in Finland (KANERVO et al. 1957, RAAT KAINEN 1961 b).

Mesopolobus graminum (Hårdh) (*Hym., Pte malidae*) has been mentioned as an egg-predato of *J. pellucida* in Sweden under the name *Ah*

longatus (Thoms.) (v. ROSEN 1956 b) and land under the name *A. graminum* Hårdh DH 1950 a, NUORTEVA 1959). The reader is ed to the amendments made by v. ROSEN b) and RAATIKAINEN (1961 b). These ts, however, have not been confirmed, t the present time the species is known a parasite of *M. aequus* and also possibly *oxylus* (RAATIKAINEN 1961 b, 1962). ng the present study, the species was d nine times to the adult stage from an ode in which only delphacid eggs were d. Of these, three occurred in 1958 in the ial mentioned in Table 49 and two in 1961, one was found in the 1962 material, for h data are presented in Table 50. However, uncertain whether in such cases the species n delphacid eggs or on other Hymenoptera h may have been in the internodes but were ooked. *M. graminum* may feed on all the s inhabiting internodes, just as do certain species of *Mesopolobus* (cf. ASKEW 1961). ver, so far this has not been definitely ed, and at least in the present material the es most commonly occurred as a parasite eromalids.

grus atomus (L.) (*Hym., Mymaridae*) has been reported as an egg-parasite of leaf- ers, but it has apparently not been mentioned as an enemy of *J. pellucida*. However, RVO et al. (1957) reported *Anagrus* sp. to parasite of *J. pellucida*, and the species was found to be *A. atomus*.

ondylus lindbergi Heikinh. (*Hym., Dryinidae*) been reported as an enemy of *J. pellucida* in Finland (HEIKINHEIMO 1957, KANERVO 1957, HEIKINHEIMO and RAATIKAINEN . KONTKANEN (1950 b) found three dry- d specimens of *J. pellucida*, but the species not identified. It may have been *D. lind-*

nchus tenuicornis (Kirby) (*Strepsiptera, Elen-*) has been established as a parasite of *llucida* in several countries. In Germany r (1914, p. 164, 1916, pp. 202, 279) reported der the name *E. walkeri* Curtis, and in certain publications evidently the same species is mentioned under the name *Strepsiptera* (HAUPT 1933, p. 255, 1935, p. 140, EMMRICH 1966 a). In many German papers it is mentioned by the name *E. tenuicornis* (ULRICH 1956, BAUMERT and BEHRISCH 1957, BAUMERT 1958, 1959, BAUMERT-BEHRISCH 1960 a and b). In Sweden it has been described under the name *Elenchinus delphacophilus* Ahlb. (AHLBERG 1925). In England (HASSAN 1939) and Finland (LINDBERG 1949, HEIKINHEIMO 1957, KANERVO et al. 1957, HEIKINHEIMO and RAATIKAINEN 1962) the name *E. tenuicornis* has mostly been used, but KONTKANEN (1950 b) reported what was probably the same species with the name *Strepsiptera*. In Hungary SZÉKESSY (1959 a) reported that he had found *J. pellucida* parasitized by *Strepsiptera*. In this case too, the species in question is evidently *E. tenuicornis*.

A species of *Pipunculidae* has been found to parasitize *J. pellucida* in Finland (KONTKANEN 1950 b).

Achorolophus gracilipes (Kramer) (*Acar., Erythraeidae*) has been mentioned in Finland as a parasite of *J. pellucida* (KARPPINEN 1958). In England one female *J. pellucida* was found to be parasitized by mites, evidently *Trombidium* sp. (HASSAN 1939, pp. 360, 361).

According to reports in the literature to date, at least 6 species of insects and 1—2 species of mites have been established to be enemies of *J. pellucida*.

HASSAN (1939, pp. 360, 361) has reported a female of *J. pellucida* in England infected with the fungi *Cephalosporium* sp. and *Acremonium* sp.

According to WATSON and SINHA (1959, pp. 155—157) and SINHA (1960), it is possible that EWSMV is pathogenic to *J. pellucida*. Later, however, KISIMOTO and WATSON (1965) did not confirm this.

A. Panstenon oxylus (Walk.)

According to v. ROSEN (1955 a and b, 1956 b, p. 20), synonyms of *Panstenon oxylus* are *Miscogaster oxylus* Walk., *P. assimilis* Thoms. and *P. omissus* Foerster but not *Pteromalus assimilis* Nees. HÅRDH (1950 b, 1953) the Review of

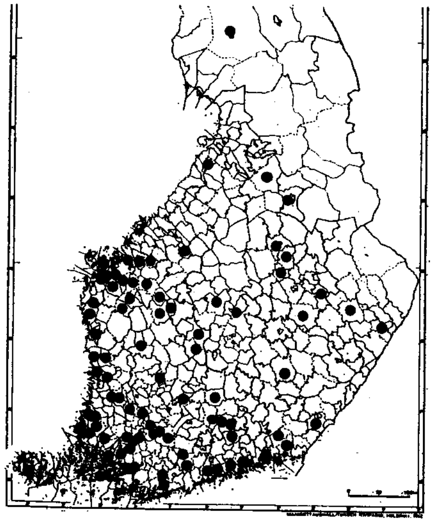


Fig. 37. Known localities of *P. oxylus* in Finland.

Applied Entomology (Vol. 53, A, p. 519) and possibly also Peck et al. (1964, p. 40) have employed the name *Panstenon assimilis* (Nees) for this species.

1. *Distribution*

The distribution of *P. oxylus* is poorly known. It has so far been encountered in England, Germany, Czechoslovakia, Sweden and Finland, as well as possibly in Austria (v. Rosen 1956 b, p. 23). Thomson (1878, p. 177) stated that it was scarce in the vicinity of Lund, but in the light of later finds it would appear to occur over a wide range in Sweden and in certain places, at least, it is apparently very abundant (v. Rosen 1956 b, pp. 22, 23, 60—64). In Czechoslovakia it has been reported by Peck et al. (loc. cit.) to be a common parasite of insects in grass stems. On the basis of the numerous specimens collected from spring wheat in Finland (Hårdh 1953, p. 91), the species is evidently rare, but locally abundant.

In the present studies the distribution of *P. oxylus* was investigated principally on the basis of stubble samples collected in differen parts of Finland. The samples were placed rearing boxes, and the adult pteromalids that emerged were collected daily. According to the results of these investigations *P. oxylus* is com mon at least from the south coast of Finland to the Arctic Circle (Fig. 37); samples were not taken north of this latitude. No accurate data are available on the geographical abundance of the species. According to samples taken from 43 communes in the autumn of 1961 and from 42 communes in the autumn of 1964, the density was lower south of the 62nd parallel than north of it. North of the 64th parallel, no samples were taken in either of the two years.

2. *Developmental stages*

E g g. The egg of *Panstenon oxylus* is ovate in shape and slightly curved (cf. v. Rosen 1956 b, p. 46, Fig. 27). The chorion is smooth, and the colour of the egg is greyish white. According to v. Rosen (1956 b, p. 27), the length of the egg in Sweden is quite variable, averaging 0.4 mm. In the present studies, 14 *P. oxylus* females were collected in South Ostrobothnia and were given honey-water as source of food. The females were allowed to oviposit on the egg groups of *J. pellucida* in the stems of spring wheat, and measurements were made of ten eggs, 0—2 days old, of each female. The mean diameter of the eggs was 0.12 mm (0.10—0.14 mm) and the mean length 0.34 mm (0.29—0.41). The length of the egg was correlated with the length of the left fore-wing of the female, which was taken as an indicator of the size of the female ($r = 0.85^{***}$, d.f. = 12). Furthermore, the diameter of the egg was also correlated with the length of the wing ($r = 0.54^{*}$, d.f. = 12).

L a r v a. Hårdh (1953, p. 92) has presented a photograph of the larva of *P. oxylus*, and v. Rosen (1956 b, pp. 28—30) has published a photograph of the larva and descriptions of the five larval instars.

P u p a. Descriptions of the pupa of *P. oxylus* have been presented by Hårdh (1953, p. 141) and v. Rosen (1956 b, pp. 31, 32). In the region

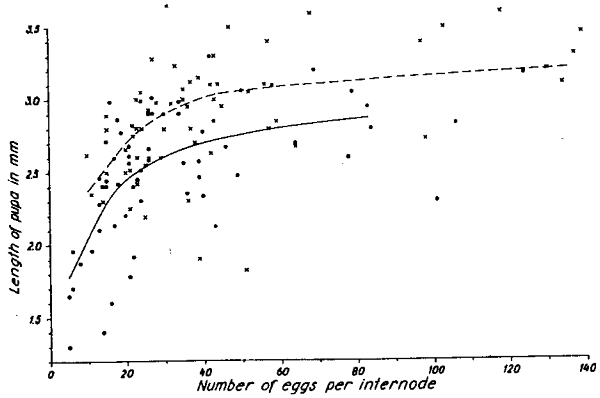


Fig. 38. Relationship between length of pupa of *P. oxylus* and number of delphacid eggs in internodes of spring cereals. Dots and solid line = males; Crosses and dashed line = females. Same material as in Fig. 39.

he present investigation, the length of the pupa varied from 1.3 to 3.3 mm (n = 68) that of the female from 1.8 to 3.7 mm 68). In order to determine the reasons for variations in pupal length, undamaged nodes of oats and spring wheat containing *xylus* larvae or sometimes pupae were cold in the autumn and spring of 1958, 1959 1961. The numbers of delphacid eggs available as food for pteromalids in the internodes counted, and the pteromalids found within taken and reared in glass tubes. After ation was completed, the length of the pupa measured. The results (Fig. 38) demonstrate the length of the pupa varied widely even n the number of delphacid eggs in the internode was the same. There were two main reasons uch variations: not all of the eggs in the rnode were counted; and the larva did not ume or was unable to consume all the eggs ent. The first source of error was a minor but the second factor was quite significant. here were few delphacid eggs in the internode, larva of *P. oxylus* usually ate all of them. if, as was generally the case, there were many present, say over 30, the larva destroyed t of them but ate only parts of them. Somees the eggs were embedded in the thick wall of the stem and the larva was unable to reach them.

The above errors were small, however, and there was a curvilinear relationship between the length of both male and female pupae and the number of delphacid eggs in the internode. Males could develop to the pupal stage on a smaller number of eggs than females. Furthermore, even when the same number of eggs were available, the male pupae were shorter than the female ones. The pupa apparently reached its maximum length when about 40—50 eggs were available as food supply for the larva.

A d u l t. Since the original species description, v. Rosen (1955 a and b, 1956 b) in particular has elucidated the characters of the species. Hårdh (1953, p. 91) has also published a picture of the species. In the present investigation, the size of both the male and the female varied considerably. In order to study the reasons for such size variations, the same material as was used in determining the pupal length was employed in the same way. As indicator of the size of the adult, the length of the left fore-wing was used. The results (Fig. 39) show that males developed to adults on a smaller quantity of eggs than females. The males achieved their maximum size when the number of delphacid

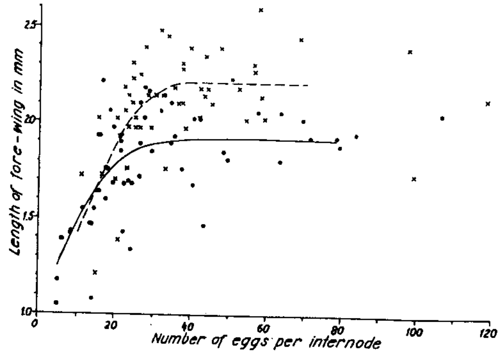


Fig. 39. Relationship between length of fore-wing of *P. oxylus* and number of delphacid eggs in internodes of spring cereals. Dots and solid line = males; Crosses and dashed line = females. Same material as in Fig. 38.

eggs available was about 30 and the females when the number was about 40. The length of the wing of the males was generally shorter than that of the females, even though the same amount of food was available.

3. *Life cycle*

The life cycle of *P. oxylus* was investigated in spring cereals and in first-year leys established under spring cereals. The insects were also reared in the insectary. In both Sweden (v. Rosen 1956 b) and Finland, *P. oxylus* usually has a single generation a year but also a partial second generation (Fig. 40). The female oviposits in the internodes of grass species con taining delphacid eggs, and according to HÅRD (1950 b) the species also occurs in the pupae o *Mayetiola* sp. in spring cereals. Hibernation o the species takes place, as far as is known, onl in the larval stage.

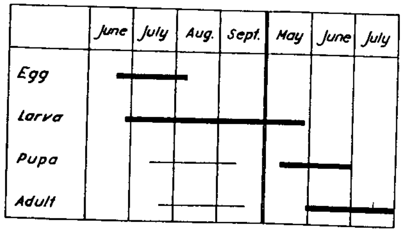
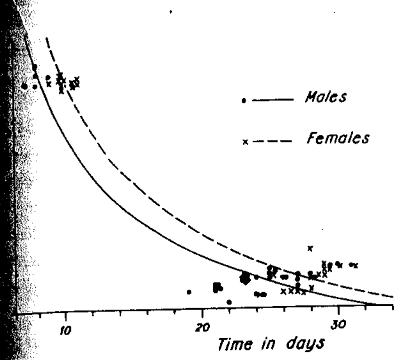


Fig. 40. Life cycle of *P. oxylus* in 1956—1964. The thin line denotes the occurrence of the incomplete second generation.

Egg stage. Eggs of *P. oxylus* were encoun tered from June 20. Since the first adults emerge as early as the latter part of May or early Ju and since the preoviposition time is short, egg would probably appear even earlier if there we delphacid eggs in the stems. The last egg deposited by the first generation were encoun tered in the trials on August 8. Later than thi hymenopterous eggs were found in cereals, bu they were probably deposited either by the partial second generation of *P. oxylus* or b some other species. In the insectary the duratio of the egg period at about 19°C was 48 hou According to v. Rosen (1956 b, p. 27), at temperature of about 20°C the eggs hatche after two days and at about 10—15°C afte 4—5 days.

Larval stage. The first larvae we observed in spring cereals at the end of Ju According to v. Rosen (1956 b, p. 34), the larv are full-grown after 8—14 days (at most 3 wee Usually, however, they overwinter in the regi



41. Relationship between temperature and the d of development of *P. oxylus* pupae in the insectary.

nvestigation and thus the duration of the l period is about 9 months. The larva inhabi the same internode during the whole of this provided that the wall of the internode ained whole.

upal stage. Pupation began during the od May 8—30. After being brought into a m room, the larvae that had overwintered in nsectary pupated, within the same period of in the light and in the dark. Pupation took at the same time at relative humidities of 4, 56, 67, 77, 87 and 100 %. In each of the ng containers there were 25 specimens. he pupation of males and females occurred pproximately the same time. For example, 958 22 males and 22 females in the insectary ated on an average date of May 28. The tion of the pupal stage of males and females ials carried out at different mean tempera is presented in Fig. 41, equations t(T—7.3)= nd t(T—6.9)=116 respectively. At 11°C the l period of 22 males was 24.2±0.38 days and of 22 females 28.4±0.35 days. The pupal period of males under these conditions was thus 4.2 shorter than that of the females (t=8.24***). either of the sexes was there any correlation ween the duration of the pupal period and the th of the fore wing (size of individual speci). The relative humidity had no effect on the l period, since it lasted approximately equally at all the previously mentioned humidities.

Table 33. Numbers of adult *P. oxylus* emerging at different hours of the day. Trial carried out in glass tubes in the insectary, June 2—7, 1960

Sex	Hours of day								Total
	20—6	6—8	8—10	10—12	12—14	14—16	16—18	18—20	
♂♂	8	3	1	6	4	3	2	3	30
♀♀	13	4	6	8	12	7	5	3	58
Total	21	7	7	14	16	10	7	6	88

Pupae of the first generation appeared between May 10 and June 30, and those of the second generation between July 14 and September 13. Some of the pupae overwintered, but they did not give rise to adults the following year.

Adult stage. The emergence of adult *P. oxylus* during the course of the day was studied in the insectary. According to the results (Table 33) and to observations made during one night, adults emerged at all times of the day and night, but emergence was maximal during the warm daylight hours and minimal during the cool hours of the night.

Most of the adults of *P. oxylus* were inside the stem at the time they emerged. They bored a hole in the stem wall and thus came out of the stem. A small proportion of the specimens were in internodes which had been broken, for instance during harvesting, and the adults could easily escape from such internodes without making holes. Nevertheless, in many such instances, they made holes in the stem. Sometimes pupae were encountered on the surface of the ground.

The first adults of the first generation appeared during the period May 27—June 11 approximately. The times of emergence of adults in the years 1958—1960 are shown in Fig. 42. It is seen that males of the first generation emerged slightly earlier than females. The dates by which half the males and females in the trials had been collected in the rearing boxes were as follows:

Year	Males	Females	Difference, days
1958	22. VI	26. VI	4
1959	10. VI	13. VI	3
1960	8. VI	13. VI	5

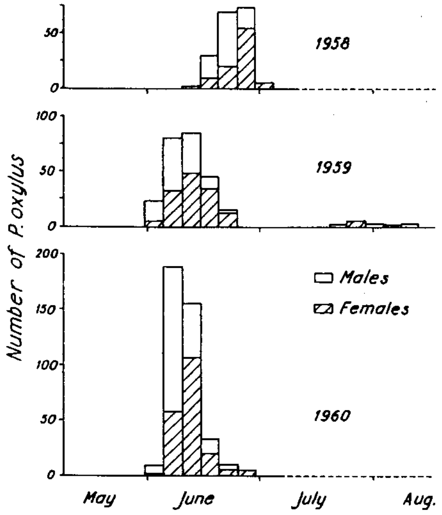


Fig. 42. Emergence of *P. oxylus* adults into glass tubes of rearing boxes or in Petri dishes in July—August, 1958—1960. The solid part of the abscissa axis shows the period during which observations were made, while the dashed part indicates that no observations were made. Same material as in Fig. 58.

The reason for the earlier emergence of the males, as seen in the above tabulation and as is well known for many insects, is the fact that, on the basis of the previously described trial, the pupal stage of the male *P. oxylus* lasts about 4 days less than that of the females (Fig. 41).

The life-span of adults was studied with the aid of rearing corks in the insectary. A male and a female were enclosed in the rearing cork, which was then attached to a stem of spring wheat containing eggs of *J. pellucida*. As nourishment, a dilute solution of honey-water was applied daily to the gauze of the rearing cork. At a temperature of about 16°C the average life-span of 11 males was found to be 26 days (4—35) and that of 13 females 37 days (14—55).

The life-span of the females was divided into the pre-oviposition, oviposition and post-oviposition periods. At a temperature of 16.5°C, the average pre-oviposition period of 17 females was 3 days (2—7). The oviposition period of 13 females at 15.5°C averaged 31 days (12—52), and the post-oviposition period of these same females averaged 3 days (0—11).

According to v. ROSEN (1956 b, p. 34), in ordinary years in Sweden *P. oxylus* pupates almost entirely the following spring. However, in certain extremely warm summers it has a tendency to produce a partial second generation. In the present investigations, a partial second generation was encountered every year, but only a few data were obtained on the emergence of its adults (Fig. 42). In the years 1958—1964 an average of about 4 % of the larvae of *P. oxylus* in the stems of spring cereals reached the adult stage during the same summer. These calculations were made by counting all the Hymenoptera found in the stems in August which had fed on delphacid eggs and which themselves had been in the egg stage in June or July, excluding those which could be regarded as *M. aequus*. All the larvae were reared, and when inspections were made in the autumn, the adults were confirmed to be *P. oxylus*. However, by no means all of the larvae reached the adult stage. The proportion of *P. oxylus* larvae that became adults in the autumn fluctuated from year to year, but there was not a significant correlation with temperature. In v. ROSEN's (loc. cit.) material 6 % of *P. oxylus* attained the adult stage in the same year. The method of calculation was different, however, and apparently gave a higher figure than that obtained from the above-mentioned experiments in the present investigation.

No detailed information is available on the fate of the second-generation adults emerging in the late summer. Some of them, however, apparently oviposited in cereal internodes containing delphacid eggs, since a second period of hymenopterous egg-laying took place in August. At this time the egg density was smaller than in July. The larvae arising from such late-appearing eggs remained quite small, however, and did not reach the adult stage when reared in the insectary.

Adults of *P. oxylus* occurred in the period between May 27 and September 20 (Fig. 40). First-generation adults appeared at least during the period May 27—July 30. They were m

ndant in mid-June in first-year leys established under cereals as well as in early July in als. Adults of the second generation appeared n at least July 21 to September 20. They eared to be most abundant around the middle August.

4. *Habitats and migration*

Habitats. *P. oxylus* occurred principally lace where grasses and cereals were growing. as not found in samples taken from forests, s, or fields of turnip rape and potatoes. The ies occurred in meadows and along the es of fields, but it appeared to be scanty on n sites. Netting samples taken in leys of erent ages (cf. Fig. 25) revealed the following nbers of specimens collected:

Age of ley, years	1	2	3	4 or more
of leys	26	26	26	17
of *P. oxylus*	16	5	1	1

relatively scanty material indicates that the ies was more prevalent in first-year leys blished under a cereal nurse crop than in r leys. The time of sampling was so early P. *oxylus* was in the process of emerging was just beginning to move to other sites. abundance in first-year leys thus gives quite od idea of the situation the previous autumn winter. There were many larvae in spring als under which grasses had been sown for blishing new leys. In hayfields, on the other d, the species was scanty. Similarly, *P. oxylus* considerably more abundant in cereal stubble ples examined in the spring than in the ble of timothy seed fields. From all the stigations and observations it appeared that population density of *P. oxylus* was considbly greater in cereals than in grass leys.

Migration. After emerging as adults, ales of *P. oxylus* usually remained stationary t of the time. On an average of a few times inute they walked for several seconds. The age rate of walking of one-day-old females = 5) on a glass surface in the laboratory at C was 6.0 mm/sec. (4.8—8.1). On growing ts they moved more slowly than on a glass

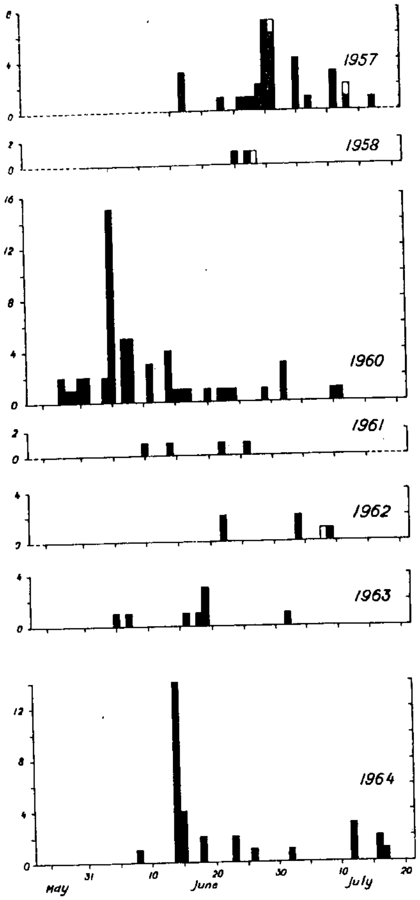


Fig. 43. Numbers of *P. oxylus* migrating in 1957—1964, according to material collected with netting apparatuses. Black part of columns = females, white part = males; other explanations in Fig. 24.

surface. Occasionally the females would fly for short distances.

Adults began to migrate during the days following their emergence from cereal stems. The period of migration was determined with the aid of the same netting apparatuses as were employed for studying the migration of *J. pellucida*. The results (Fig. 43) show that *P. oxylus* migrated at approximately the same period as *J. pellucida*. The course of migration of these two species can best be compared by examining the material having the largest numbers of *P. oxylus*. Half the specimens collected in the apparatuses were obtained by the dates given below:

Year	*P. oxylus*	*J. pellucida* All specimens	*J. pellucida* Healthy specimens
1957	1. VII	29. VI	23. VI
1960	7. VI	5. VI	5. VI
1964	15. VI	15. VI	15. VI

According to the above comparison, *P. oxylus* migrated at approximately the same time as its most important host species, *J. pellucida*, or possibly slightly later than it.

The sex ratio of *P. oxylus* in its hibernation sites in first-year leys was close to 1:1. The netting samples (Table 34) evidently do not give a true picture of the sex ratio, but instead demonstrate that the females are perhaps higher in the stand and are more easily collected by this method than the males. According to material collected with the netting apparatuses (4 males and 137 females; Fig. 43), it is mainly the females that migrate. The suction samples (Table 34) substantiate the view that virtually only the females move away from their sites of emergence. With this apparatus, Hymenoptera are evidently obtained with equal ease from all levels of the stand, so that when the females move away there should be more males than females remaining in the samples, as proved to be the case. According to all the previously mentioned samples, it is chiefly the females which migrate to spring cereals. Only along the edges of spring cereal fields were males obtained with the suction apparatus. Males always appeared in the samples

Table 34. Proportion of male *P. oxylus* in netting and suction samples taken from first-year timothy leys and spring cereals, May 31—July 20, 1957—1962

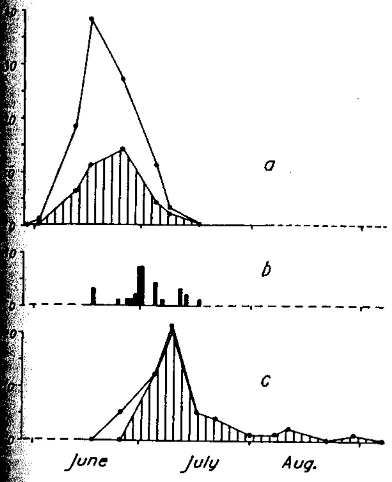
Sampling method	1st-year timothy				Spring cereals			
	No. of samples	No. of adults	Males No.	Males %	No. of samples	No. of adults	Males No.	Males %
Netting ..	17	31	11	35	22	35	0	0
Suction ..	55	118	73	62	49	72	6	8

obtained with the netting apparatus in the la
part of the migration period.

During migration *P. oxylus* moved chie
from first-year leys established under cereals an
from places consisting of dried grass of th
previous year — or the stubble of such places
principally to cereal fields, but perhaps also t
some extent to stands of other grasses, wher
there were sites suitable for oviposition. Figur
44 gives an example of the migration of *P. oxyl*
and its abundance during the summer in firs
year leys and oats. This figure was constructed
by combining data consisting of suction sample
taken at three localities at weekly intervals
well as the daily netting apparatus samples take
at three localities. According to similar suctio
samples taken in 1956, the seasonal variation
were quite similar, but during that year no male
at all were obtained from the oat fields. The dia
grams clearly show that the males remained i
the leys while the females migrated to oats, wher
there was initially a pronounced rise in popu
lation density followed by a slow decline. In th
samples taken in August there were evidentl
some second-generation specimens, but they di
not happen to include males, even though the
appeared in spring cereals after the emergen
of the second generation.

5. *Food supply and influence on J. pellucida*

Host species. HÅRDH (1950 b) showe
that in Finland *P. oxylus* is a parasite of th
pupae of *Mayetiola* sp. Later (HÅRDH 1953, p. 9
he mentioned that in England it was presume
to be an external parasite of *M. destructor* (Sa
Furthermore, Hårdh (1953, p. 92) reported th
in Finland *P. oxylus* feeds on larvae of *M. d*
tructor as well as on the eggs and larvae
Mesopolobus (*Amblymerus*) *graminum* (Hårdh
Moreover, his observations indicate that
oxylus also destroys the eggs and larvae
Harmolita hyalipenne Walk. in Finland. The m
tion made in this same connexion that the spec
apparently feeds on eggs of *Miris* is probably
correct, since the eggs concerned were evide



4. Occurrence of *P. oxylus* in first-year timothy leys
d in oats (c) as well as migration (b) in 1957. The
d area in a and c represent females and the unshaded
ales. The drawings a and c are based on suction
es taken from a total area of 0.9 m² on three fields.
Same material as in Fig. 24.

hose of *Miris* but of some delphacid, prob-
J. pellucida (cf. NUORTEVA 1959, p. 15,
KAINEN 1961 b, pp. 206, 207). Similarly,
port made by TÖLG and FAHRINGER (1911)
n Austria the species occurs as a parasite
lacosoma was, according to Ferriére, incor-
cf. HÅRDH 1953, p. 91).

Sweden, v. ROSEN (1956 b, pp. 28,49) states
P. oxylus feeds on the eggs of *J. pellucida*,
ccasionally it has also been observed to be
site of *Eurytoma suecica* v. Rosen. v. ROSEN
b, p. 33) has also shown that the larva may
on members of its own species. In his view,
ain source of food of the second generation
vae consists of larvae of the same or other
nopterous species (v. ROSEN 1956 b, p. 32).
ter investigations (KANERVO et al. 1957,
KAINEN 1961 b) have shown that in Fin-
too, *P. oxylus* feeds on eggs of *J. pellucida*.
s difficult in the field to determine what
es of leafhopper eggs were used as food.
ggs of only two species, *J. pellucida* and

Stiroma bicarinata (H.-S.), were found to serve as food under natural conditions in the field. As for other leafhoppers, it was not possible to identify their eggs, so that their suitability as a food source for *P. oxylus* had to be determined experimentally. Spring wheat containing eggs of *Megadelphax sordidulus* (Stål) was transferred outdoors. Later, hymenopterous larvae which had eaten the eggs were found in these plants. In the following summer these larvae produced *P. oxylus* adults. Adult females of *Javesella obscurella* (Boh.), *M. sordidulus*, *Xanthodelphax flaveolus* (Flor) and *Dicranotropis hamata* (Boh.) were allowed to oviposit in the internodes of oat plants. Subsequently, one *P. oxylus* female which had copulated was given access to such internodes for one or at most three days. After two weeks the internodes were opened, and it was discovered that the female had oviposited in the internodes containing egg groups of the above species and that the larvae had eaten eggs of all of the species and had reached medium sized on eggs of each leafhopper species proffered. It is very probable that under natural conditions, too, the polyphagous *P. oxylus* feeds on the eggs of the species tested in the above-described trials as well as on other species of leafhoppers which oviposit similarly in the stems of *Gramineae*. On the other hand, *P. oxylus* was not observed to consume the eggs located in the leaves.

In the field, *P. oxylus* larvae were found in the stem internodes of spring and winter wheat, oats, barley, rye, *Avena fatua*, *Phleum pratense*, *Festuca pratensis*, *Elytrigia repens* and in certain trials *Bromus inermis*. In England (HÅRDH 1953, p. 91) and Sweden (v. ROSEN 1956 b) the species has been encountered in spring cereals. It does not appear to be particularly selective about the kind of grass or cereal in which it oviposits. Sometimes it even deposits its eggs in internodes whose cavity is quite lacking in delphacid eggs. However, the larvae apparently do not survive in internodes if the ends of the delphacid eggs do not extend into the cavity. v. ROSEN (1956 b, p. 33) nevertheless mentions instances where larvae have been found in internodes without any delphacid eggs. Furthermore, he conducted experiments designed to determine the ability of *P. oxylus* to live on plant food alone. One *P. oxylus* egg was placed in the internode of spring wheat. Ten days later no living larva was found in this internode. In the same experiment, three *P. oxylus* eggs were put into one internode. After one month such internodes contained a very small larva. In this way he demonstrated that *P. oxylus* requires animal food, and that one or two immature stages of the same species may be sufficient. According to the experimenter, the trial also showed that the species could subsist on plant food.

In the present investigation, *P. oxylus* was only found in internodes containing delphacid eggs. Even in the experiments, it did not oviposit in internodes without delphacid eggs. The data obtained in studying the causes of the variations in size (Figs. 38, 39) likewise showed that the pupae and adults remained small if there were only a few delphacid eggs available, and in order to develop to the adult the larva required at least five delphacid eggs as food source. Consequently, the specimens of *P. oxylus* occurring in oats and spring wheat on the field apparently never developed into adults without feeding on insects of other species. Such animal food was their principal source of nourishment, and if there was only a little animal food available they did not grow to normal size, at least not on the plant food obtainable in the stems of oats or spring wheat. When scanty animal food was available, the development of small larvae to the adult stage was not always successful, and the females which subsequently developed produced only a small number of eggs.

Quantity of food. The quantity of animal food consumed by *P. oxylus* larvae in the field was determined from samples collected in oats and spring wheat in 1957 and 1958. At weekly intervals, internodes containing pteromalids were collected, and determinations were made of the number of delphacid eggs which had been damaged by the larvae; furthermore the larval instar was likewise reckoned according to the system of size classes proposed by v. Rosen (1956 b, Fig. 18, p. 29). The average larval

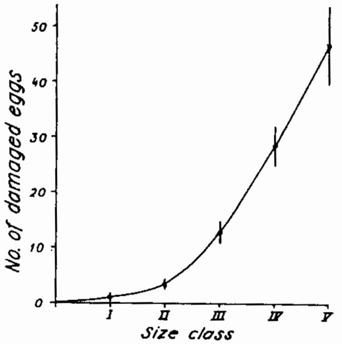


Fig. 45. Numbers of delphacid eggs damaged by different-sized larvae of *P. oxylus*. In the first size-class there were 7 larvae, in the second 18, third 55, fourth 84 and fifth 40. The vertical lines denote the 95 % confidence limits.

lengths of the different size classes were: first class 0.5 mm, second 1.0, third 1.8, fourth 2.[illegible] and fifth 3.8 mm. The larval instars estimated on the basis of size evidently agree with the actual instars better at the lower end of the scale than at the upper. The kind of cereal, whether oats or spring wheat, containing the delphacid eggs was not found to have any effect on the size of the larva. When the supply of leafhopper eggs was exhausted, the larvae generally made no further growth. The larvae ate the interior of the delphacid eggs but left the outer skin unconsumed. There were some internodes in the field containing less than five delphacid eggs. In such internodes the larvae had completely consumed all the eggs, but they died before reaching the pupal stage. Larvae which had eaten five delphacid eggs could develop into adult males, but to become adult, females had to obtain at least 10 eggs (Fig. 39). Larvae of the second and third size classes were able to develop into adult males and those of the third size class developed into females. Larvae of the fifth size class had destroyed an average of 47 eggs (Fig. 45). In most of the fields only a small proportion of the *P. oxylus* larvae attained the fifth size class, but in those fields where delphacid eggs

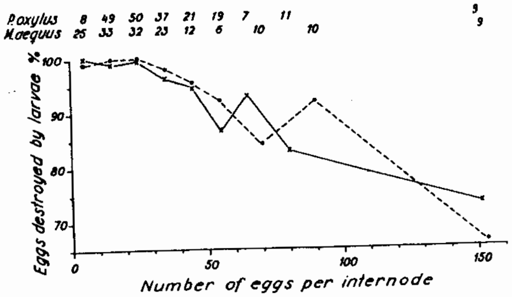


Fig. 46. Percentages of delphacid eggs in internodes destroyed by *P. oxylus* (solid line) or *M. aequus* (dashed line) in spring cereals, 1957—1962. The numbers at the top show the numbers of inhabited internodes examined for each point on the curves.

plentiful, a large proportion of the larvae hed the fifth size class and subsequently gave to large-sized adults.

the number of delphacid eggs in the nodes increased, the proportion of eggs ged by *P. oxylus* and also by *Mesopolobus* diminished (Fig. 46). However, by no s all of the damaged eggs were eaten by the . Only in those internodes containing few acid eggs were they completely consumed. e number of delphacid eggs increased, the tity of completely consumed eggs appeared ecline more sharply than the number of ged eggs. According to v. Rosen (1956 b,), the larva of *P. oxylus* normally eats 20—gs of *J. pellucida*. In the region of the present es, the number of eggs consumed was likeusually 20—30.

fluence on J. pellucida. *P. oxylus* ed to injure the eggs of *J. pellucida* by ovipos- in the egg groups of the latter species in of cereals. The female preferably deposited gs in thin-walled stems (cf. Table 37), and the generally destroyed 20—30, and sometimes than a hundred, eggs of *J. pellucida* (Fig. 46).

6. *Reproduction*

x ratio. The known sex ratios of pterospecies indicate a varying preponderance of females (Clausen 1940, p. 129). In the present investigation the sex ratio of *P. oxylus* was ascertained by collecting pteromalids from the stubble of oats and spring wheat in the springs of 1958—1960 and subsequently rearing the specimens in rearing boxes. No significant difference in the sex ratio was found between oats and wheat. Similarly, there were no significant differences in the sex ratio of *P. oxylus* in the different fields investigated. The data were combined for each year, and the results (Table 35) show a sex ratio of approximately 1:1. This method of determining the sex ratio can be considered to give a figure closer to that actually occurring in nature than the value obtained by netting or by suction samples (Table 34).

The effect of the food supply available during the larval stage on the sex ratio was studied, using material collected from fields of oats and spring wheat in 1958—1961. The material was

Table 35. Proportion of male *P. oxylus* obtained in rearing boxes, 1958—1960

Year	Total adults	Males No.	%
1958	179	91	51
1959	258	125	48
1960	400	204	51
Mean			50

Table 36. Relation between the supply of delphacid eggs and the sex ratio of *P. oxylus*. $\chi^2 = 11.50^*$, d.f. = 4

No. of delphacid eggs per internode	*P. oxylus* Total adults	Males No.	%
1— 10	13	12	92
11— 20	41	31	76
21— 30	53	25	47
31— 40	33	16	48
41—170	78	30	38

divided into categories on the basis of the numbers of delphacid eggs in the internodes. No significant sex ratio differences were found between oats and wheat, and thus the data for the two cereals were combined. The results (Table 36) demonstrate that there were more males than females of *P. oxylus* in internodes containing less than 21 delphacid eggs. The reason for this is not definitely known, but it is presumed that female larvae were unable to grow to the adult stage on as little food as males and thus died while still in the larval stage. Another possibility is that the female deposited more fertilized eggs in the internodes containing many delphacid eggs and fewer in those where there was only a scanty food supply.

In samples of spring wheat examined in 1962—1964, it was observed that 33 % of the internodes contained less than 21 eggs, while the figure for oat samples was 47 %. The proportions of such internodes among those inhabited by pteromalid larvae (*P. oxylus* and *M. aequus*) were 25 % for spring wheat and 28 % for oats. The scarcity of delphacid eggs in the spring cereals apparently increased the proportion of males of *P. oxylus* to some extent. If the population density of delphacid species in a certain locality is very low, the sex ratio of *P. oxylus* adults may shift to become male-dominated, while in areas with a high delphacid population density it may become female-dominated.

Parthenogenesis. Female pupae were reared in isolated conditions, and the adults emerging from them were allowed to oviposit in internodes containing eggs of *J. pellucida*. Each of the growing larvae had at its disposal a food supply consisting of at least 25 leafhopper eggs. It was demonstrated in these experiments that *P. oxylus* was able to reproduce parthenogenetically. All the progeny, of which 4 subsequently reached the adult stage, were males.

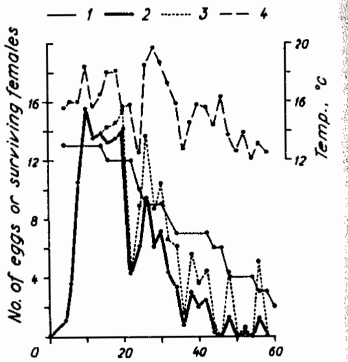


Fig. 47. Oviposition of 13 *P. oxylus* females in the insectary, July 1—Aug. 30, 1960. 1 = number of living females, 2 = average number of eggs per female per two-day period, 3 = average number of eggs per surviving female per two-day period, 4 = two-day mean temperature °C.

Copulation. Copulation appeared to take place in the first few after emergence. Under field conditions it presumably occurred before migration of the females, since males only seldom migrated and females collected from spring cereals laid fertilized eggs. Usually the females copulated, since on spring cereals, about half of the specimens which hatched were males. According to v. ROSEN (1956 b, p. 27), the male copulates with more than one female, but the female is fertilized only once.

Egg production. The fecundity of *P. oxylus* females was determined by counting the number of eggs laid in insectary experiments. A male and a female which had emerged on the same day were introduced into a rearing cage placed on an internode of spring wheat containing *J. pellucida* eggs. Every day water as well as honey-water were given through the gauze in the cork. At two-day intervals the cage

Table 37. Occurrence of *P. oxylus* in cereal internodes having walls of different thicknesses. In calculating χ^2 the figures marked by the vertical lines were combined

ness of all, mm	Oats: No. of internodes with delphacid eggs	Oats: Internodes with *P. oxylus* No.	%	Spring wheat: No. of internodes with delphacid eggs	Spring wheat: Internodes with *P. oxylus* No.	%	Barley: No. of internodes with delphacid eggs	Barley: Internodes with *P. oxylus* No.	%
......	6	4	67	0	0	—	0	0	—
......	401	238	59	264	158	60	22	14	64
......	239	99	41	178	98	55	41	20	48
......	128	43	34	85	43	51	23	4	17
......	125	27	22	45	21	47	13	2	14
......	65	16	25	17	4	24	1	0	0
......	36	2	6	11	4	36	1	0	0
......	30	2	7	1	0	0	0	0	—
......	46	0	0	1	0	0	0	0	—
	1 076	431		602	328		101	40	
......		91.65***			6.52			9.65*	
......		7			5			3	

its insects was transferred to another internode containing leafhopper eggs. Oviposition an average of 3 days after emergence and an average of 31 days. The fecundity curve 47) is typical of insects (cf. ANDREWARTHA BIRCH 1961, p. 37). The maximum phase of sition occurred about 8—20 days after gence, at which time each female laid about s per day. The small fluctuations in the were evidently correlated with variations daily temperature. According to v. ROSEN b, p. 27), egg production is probably y dependent on external factors, such as eather. According to him, under normal itions the total number of eggs per female rtainly over 30. In the above-described tes, the average number of eggs laid by 13 les was 149 (47—247) per female. The total ber of eggs was correlated with the length he fore wing, which has been used as an ator of the body size of the female (r = , y = —136.6 + 132.5x). Likewise, there positive correlation between the life-span he total number of eggs laid by the female 0.85***, y = 23.4 + 3.4x).

iposition through stem walls ifferent thicknesses. In 1959, of oats, spring wheat and barley were ted from fields. Measurements were made e stem wall thickness of internodes containing delphacid eggs, the measurement being made at the level of the centremost egg group, and the pteromalid larvae found within the internode were reared to the adult stage. In this material, at least in oats but possibly also in wheat and barley, the larvae of *P. oxylus* were found in the internodes with the thinnest stem walls (Table 37). The main reason for this was that the females of *P. oxylus* selected as oviposition sites the stems with the thinnest walls. They were unable to oviposit through the thickest walls, since the average length of their ovipositors was 0.84 mm (0.75—0.91) (n = 25), while occasionally the thickness of the stem wall exceeded 0.9 mm. Determining the location of eggs by means of larvae was made difficult by the higher mortality of pteromalid larvae in thick-walled than in thin-walled internodes. If the wall was thick, some or at times all of the delphacid eggs were inside the wall itself and the larvae were unable to get at them and consequently starved to death. Such cases, however, were quite rare.

Location of eggs in internodes. Observations showed that *P. oxylus* oviposited only in the vicinity of delphacid egg groups in the stem cavity. Usually the eggs were laid on the surface of the leafhopper eggs or freely on the inside of the stem walls. Occasionally they were within the innermost layer of the latter, and v. Rosen (1956 b, p. 27) even found eggs partly inside leafhopper eggs.

Experiments were carried out in order to ascertain where *P. oxylus* would deposit eggs. A rearing cork containing one *P. oxylus* female was placed on a spring wheat stem in which there were egg groups of *J. pellucida*. In this experiment it was found that the 14 females deposited their eggs at the following distances from the leafhopper egg groups:

Distance from egg group, mm	0	1—2	3—4	5—6
No. of *P. oxylus* eggs	28	76	38	44

7—8	9—10	11—12	13—14	15—16	17—18	21—22	0—22
28	28	12	9	3	4	2	272

The eggs were mostly deposited either under or above the leafhopper egg group. Occasionally they were also laid within the egg group or beside it. In cases where they occurred in the egg group, they were usually at the end of the group, and only 10 % were located near the centre of the group. The ovipositing females generally made their own hole through the stem wall and seldom used the hole made previously by the leafhopper. In the field it was not possible to distinguish eggs of *P. oxylus* from those of *M. aequus*. In certain years, however, there were so few *M. aequus* that the material collected from fields consisted almost entirely of *P. oxylus*. In this material, the eggs were located at the following distances from the delphacid egg groups:

Distance from egg group, mm	0	1—2	3—4	5—6	9—10
No. of pteromalid eggs	103	14	2	1	5

11—12	13—14	15—16	17—18	19—20	39—40	49—50	0—50
1	1	2	2	1	3	1	136

According to the above experiments, it is seen that the eggs of *P. oxylus* in cereal samples from the field were located closer to the leafhopper egg groups than was the case in the rearing cork experiments.

Vertical location of immature stages in the stand. Determinations of the vertical location of the immature stages of *P. oxylus* at different times of the summer were made by means of oat samples taken at weekly

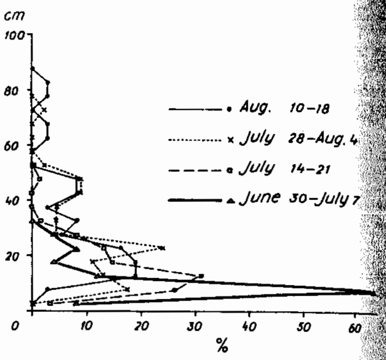


Fig. 48. Height above ground of upper end of internodes inhabited by immature stages of *P. oxylus* in oats during four different periods of the summer in 1959. The numbers of inhabited internodes varied from 25 to 61.

intervals. All the pteromalids were reared a most of them succeeded in reaching the adul stage. *P. oxylus* made up the bulk of them, bu *M. aequus* also occurred. In constructing the di gram shown in Fig. 48, all the definitely esta lished specimens of *M. aequus* were disregarde but it is possible that, especially in the fi samples of the season, a few specimens o *M. aequus* may have been included. It is see from the diagram that initially the immatu stages of *P. oxylus* were located in the lowe part of the stand but that later they also occurre in the upper parts. The best picture of the fin height occupied by the immature stages w obtained from the samples taken in August an September. According to the samples collected after July in the different years, it was found th the larvae of the generation of *P. oxylus* emergin towards the end of the summer were located i the lower part of both the oat and the whe stand and were at a distinctly lower level th the larvae of the spring generation (Fig. 49).

A considerable proportion of the larvae whi overwintered in the cultures died during th course of the winter, and it was not possible identify them as to species. All the larvae wh had fed on delphacid eggs and which succe in emerging proved to be *P. oxylus*, and

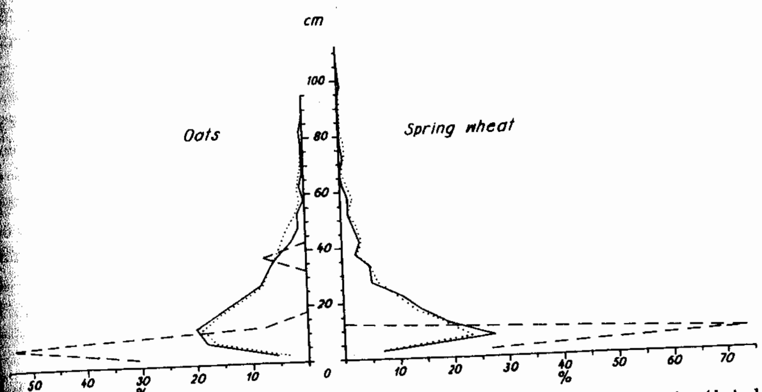


Fig. 49. Height above ground of upper end of internodes inhabited by autumn generation (dashed line) and spring generation (solid and dotted lines) of *P. oxylus* in 1958—1963. Numbers of inhabited internodes: autumn generation, 13 in oats, 15 in wheat; overwintered as larvae in cultures (dotted line), 1 577 in oats, 1 114 in wheat; emerged as adults in the spring (solid line), 805 in oats, 817 in wheat.

le that those which had died in the larval were of the same species. In the upper levels stand there were relatively more small than in the lower level, and the mortality small larvae during the winter was greater hat of the large-sized ones. Nearly all the which reached the adult stage in the spring progeny of the first generation, while an iable proportion of the small-sized larvae pparently progeny of the second gener-

7. *Fluctuations in abundance*

e internal factors affecting the abundance *oxylus* have been discussed in the previous n, and thus the following section is devoted y to external factors.

eather. Weather conditions appeared to the daily egg production of the females, en in exceptionally cool summers, such as oviposition was not badly hindered.

ctoclimatic factors affected the behaviour larvae in the internodes. In wet summers rvae were chiefly to be found in the upper f the internodes; for example, in plant les examined in August, 1960, 79 % of the teromalid larvae present were in the upper part. On the other hand, in dry summers they tended to move to the lower part of the internode; for instance, in 1959, examinations of similar plant samples revealed that only 46 % of the 589 pteromalid larvae were in the upper part. After dry summers most of the larvae were still in the lower part of the internode the following spring, while the year following wet summers they were mainly in the upper part. This was apparently of significance for the survival of the larvae. After dry summers the larvae occurred lower in the stubble than after wet summers, and the winter mortality was greater among the larvae situated high in the stubble than among those that were closer to the ground (cf. Table 38).

As regards the effect of humidity, an experiment showed that in the three most humid rearing containers (77—100 % humidity) 75 % of the overwintered *P. oxylus* larvae succeeded in reaching the adult stage, while in the three driest chambers (20—56 % humidity) only 60 % developed into adults (cf. p. 57). Even in the spring a reduction in air humidity did not, according to the results of this experiment and field observations, greatly increase the mortality of larvae and pupae. Moreover, submersion in flood waters did not appear to be harmful, since

Table 38. Mortality of pteromalid larvae at different heights in stubble of spring cereals. Examinations made May 5—11, 1964

Height above ground cm	No. of larvae	Dead larvae No.	%
1— 5	94	1	1
6—10	83	10	12
11—15	65	12	18
16—50	28	18	64
1—50	270	41	15
χ^2		58.70***	
d.f.		3	

in the spring of 1958 approximately as many *P. oxylus* emerged from stubble in a part of a field which had remained under water for one month as from stubble in the same field which had not been under water.

Winter losses were determined during the winters of 1957—1964. In plant samples collected in August there were a total of 1872 pteromalid larvae, of which only 32 (1.7 %) were dead. The mortality was not found to be higher in the upper parts of the stem. The following spring, during April and May, plant samples were collected from undamaged, erect stubble. Of the 898 pteromalid larvae encountered, 125 were dead. Among the dead larvae, some may have been *Mesopolobus*, but most were *P. oxylus*. According to these figures, the winter losses of *P. oxylus* were less than 14 %.

In the spring of 1964, determinations were made of the mortality of larvae at different heights in erect spring cereal stubble. It was found (Table 38) that the winter mortality was greatest in the upper part of the stubble. During the winter, the upper portion of the stubble was occasionally above the snow cover, and the hibernating larvae in this portion alternately froze and thawed. According to HÅRDH (1953, p. 84), repeated freezing is more destructive to *Mesopolobus graminum* larvae than constant freezing. It was obviously the freezing temperatures which caused the death of the *P. oxylus* larvae, particularly in the upper part of the stubble exposed to the winter air.

Food supply. The amount of food available had an effect on the abundance of *P. oxylus* in both wheat and oat fields. In the years 1958—1964, samples consisting of 100 plants were collected annually from 20 oat fields (cf. Table 43) and 17—20 spring wheat fields (cf. Table 44). Examinations were made of the numbers of internodes containing delphacid eggs as well as the numbers of internodes inhabited by pteromalids which fed on delphacid eggs. All the pteromalids were reared, and the number of *P. oxylus* (p) was calculated according to the equation

$$p = a + b + \frac{c}{d}\left(e + f\right) \text{ in which}$$

a = number of pteromalids as eggs + larvae at the time of inspection, but which did not pupate in the cultures,

b = number of *P. oxylus* pupae + adults,

c = number of *P. oxylus* pupae + adults in the stems at the time of inspection,

d = total number of pteromalid pupae + adults in the stems at the time of inspection,

e = number of adult pteromalids which had left the stems before the time of inspection, and

f = number of pteromalid larvae parasitizing *Mesopolobus graminum*.

The number of *P. oxylus* calculated by this method is approximate and may be somewhat greater than the actual number.

The results demonstrate that in all the years there was a distinct positive correlation between the numbers of *P. oxylus* and the numbers of internodes containing delphacid eggs. The correlation between years for oats was r = 0.90** (d.f. = 5, y = —41.8 + 0.549x) and for spring wheat r = 0.94** (d.f. = 5, y = —34.7 + 649x). It is thus obvious that the food supply in both oats and spring wheat was an important factor influencing the abundance of the species.

P. oxylus inhabited an average of 36 % (20—49 %) of the oat internodes containing delphacid eggs and 45 % (23—59 %) of the corresponding wheat internodes. In all the years internodes containing delphacid eggs considerably outnumbered those inhabited by pteromalids. There are apparently several reasons for this. One of them is that *P. oxylus* obviously did not find all the egg-containing internodes present in the fields and furthermore, may not have oviposited in all gg-containing internodes which it did find. ng other things, the wall of the internode ometimes so thick that the ovipositor could xtend into the cavity of the stem. In addiat times the amount of food in the interwas so small that the larva was unable to ye on it.

otic factors. Both in the experiments n the field *P. oxylus* deposited several eggs e same internode. In field samples, the wing numbers of pteromalid eggs were d in internodes of spring cereals:

f eggs per ernode ..	1	2	3	4	6	12
of tances ..	117	25	3	1	2	1

ost cases the eggs were of *P. oxylus*, but a l proportion may have belonged to *M.* r. After the larva had hatched from the it usually proceeded to destroy all the omalid eggs in the internode. Consequently, were only rarely two pteromalid larvae in ame internode, and only once were three d together. The larvae may even injure one her and some of them died owing to lack ourishment, so that very rarely did two omalids emerge from the same internode le 39). Assuming that one adult pteromalid out of each internode containing pterod eggs, a mortality figure of 27 % up to ime of emergence is obtained from the data d in Table 39. This figure gives an approxiindication of the part played by superparam in the mortality of the species. Even in internodes containing only one pteromalid egg, the egg did not always produce a larva.

39. Numbers of different stages of pteromalids ng on delphacid eggs in internodes of spring cereals. ata from the years 1957—1964 were combined

Stage	No. of internodes containing pteromalids	Pteromalids Total numbers	No./per internode
....	149	204	1.37
....	4 257	4 295	1.01
P. oxylus	696	697	1.00
M. aequus ...	655	655	1.00

Table 40. Numbers of internodes inhabited by *P. oxylus* and *M. aequus* in oats, 1961. Same material as in Table 23

Virus in oats	No. of internodes with delphacid egg	Internodes with pteromalids No.	%	χ^2 EWSMV	OSDV
EWSMV ...	16	3	19	—	—
OSDV	175	50	29	0.28	—
Not visibly infected ...	832	265	32	0.75	0.57

The most important of the competitive species was *Mesopolobus aequus*. In oat and spring wheat samples collected in the years 1958—1964 (cf. Tables 43, 44, 49 and 50), the correlation between these two species was investigated. In oats it was found to be r = —0.80* and in wheat r = —0.96***. Evidently the larvae of *M. aequus* destroyed the eggs of *P. oxylus* and perhaps even the larvae of the latter, in just the same way as *P. oxylus* killed immature stages of its own species. Every year the numbers of *M. aequus* in relation to the internodes containing pteromalids was smaller in oats than in spring wheat. Probably *M. aequus* restricted the numbers of *P. oxylus* more strongly in wheat than in oats. Differences were also found between the years. In warm summers and in years following warm summers, *M. aequus* was most abundant, and in such years it reduced the numbers of *P. oxylus* more than in cool summers and in years following cool summers.

Mesopolobus graminum (Hårdh) is a parasite of many Hymenoptera (GRAHAM 1957, p. 229, v. ROSEN 1960, p. 28, RAATIKAINEN 1961 b, p. 207). In the region of investigation *M. graminum* often occurred as a parasite of pteromalid larvae which fed on delphacid eggs in stems of cereals. In the larval stage it was not possible to distinguish the host species with certainty. It is obvious, however, that some of the hosts of *M. graminum* were larvae of *P. oxylus*. Assuming that *M. graminum* feeds on *M. aequus* and *P. oxylus* in the same ratio as the two latter species occur in cereal fields, *M. graminum* would have destroyed about 3 % of the immature stages of *P. oxylus* occurring in oats in the Augusts of the years investigated, and about 4 % of those in spring wheat. *M. graminum* reduced the numbers of pteromalids slightly more effectively in wheat than in oats.

In oats infected with EWSMV and OSDV, many of the delphacid eggs were in the leaves (cf. Table 23). Furthermore, virotic oat plants were stunted, and the walls of the internodes containing delphacid eggs were thick. The immature stages of *P. oxylus* occurred both in virotic and in healthy oats (Table 40). However, it is possible that virus diseases to some extent reduce the amount of space suitable for the immature stages of *P. oxylus*.

Effect of man. Since land clearing and the enlargement of the area devoted to cereals and hayfields, the numbers of *P. oxylus* must have increased greatly. This conclusion is based principally on observations made on the abundance of the species in different habitats. During the years of the present investigation, the density of immature stages of *P. oxylus* was highest in cereals, particularly spring cereals. The density of *P. oxylus* was approximately as great in oats as in spring wheat. However, with the exception of 1960, the ratio of *P. oxylus* to internodes containing delphacid eggs was greater in wheat than in oats (cf. Tables 43 and 44).

At harvest time of spring cereals, about 96 % of the specimens of *P. oxylus* were in the larval stage in the stems. The original method of cutting cereals long ago was by means of a sickle, later with a scythe, and still later with a mowing machine. At present, mowing machines are still used, but the commonest machine for harvesting cereals is the self-binder, while the use of combines is rapidly increasing. Now that the location of *P. oxylus* larvae at different levels in spring cereals is known (Fig. 49) and likewise the cutting height with the different methods (Raatikainen 1966 a), it is possible to calculate the proportions of larvae remaining in the stubble after different methods of cutting. According to these calculations (Table 41), when a scythe or mowing machine was used, only about 30—40 % of the larvae were left in the stubble, while with the combine harvester at least 60 % remained. A small fraction of the larvae were destroyed during the actual cutting process, for instance, under the wheels of the machines. The rest of the larvae in the cut stems were subjected either to drying on the field or to threshing. During the drying process, the larvae generally did not die, but instead remained and were subsequently threshed, during which process some of them succumbed. Some of the larvae ended up by being burned with the straw, others were buried in the soil during ploughing, while still others survived outside the field or sometimes remained on the ground until the following year. Most of the larvae remaining in the straw, often nearly all of them, were evidently killed during and after harvesting.

Table 41. Proportion of larvae of the spring-emerging generation of *P. oxylus* remaining in stubble cut by different methods

Method of cutting	% of larvae in stubble	
	Oats	Spring wheat
Mower	27	41
Scythe	30	—
Binder	50	63
Combine	60	73

Table 42. Emergence of *P. oxylus* adults to the surface after being buried as immature stages at different depths in the soil. The percentages are based on the assumption that there were equal numbers of insects in each treatment. Same trial in Table 54

Depth of soil cm	*P. oxylus* collected in cloth funnels			
	Total adults		Males	
	No.	%	No.	%
0	69	100	31	45
5	20	29	1	5
10	0	0	0	—

In the region of investigation, about half the stubble of cereal fields was ploughed in. During this process the larvae were buried in the soil. A study of the fate of such larvae was carried out in the spring of 1961. On May 20, 1½ kg of oat stubble was placed in each of 9 pits of area 0.5 m², comprising three different treatments of three replicates each. One was left uncovered as
ntrol. In the other two treatments the pit
covered with clay-containing surface soil,
to a depth of 5 cm and the other to a depth
0 cm. Above each of the pits a cloth funnel
placed. The results (Table 42) showed that
xylus was not able to rise to the surface after
ng buried under a 10-cm layer of soil, and
t of those under the 5-cm layer failed to
erge to the surface. Females appeared more
able of escaping from the soil cover than
les. The size of the females coming from the
trol plots and those covered with soil was
roximately the same (average wing lengths
0 and 2.12 mm respectively), so that the size
the insects obviously did not affect their
lity to escape from under a layer of soil.

n the region of investigation the cereal fields
e generally ploughed in the autumn, harrowed
following spring and resown with spring
eals, providing that a field of grass or some-
es clover had not been established under the
eal. In two different years, nine cloth funnels
e placed on fields of spring cereals which had
been under cereals the previous year. In nei-
year, however, were any *P. oxylus* adults
lected, even though counts showed that in the
vious years 25 and 50 larvae per square metre,
pectively, had remained in the field. It is thus
ious that larvae of *P. oxylus* were virtually
pletely destroyed in cereal fields after plough-
and harrowing.

Larvae of *P. oxylus* survived in those cereal
lds where seed of grasses or clover had been
dersown for the purpose of establishing leys.
cording to Raatikainen and Tinnilä (1959 a,
53), such fields made up about 47 % of the
al area devoted to cereals. The stubble almost
ways persisted after harvesting. Occasionally it
s burned, but the area of burned stubble was
s than one per cent. Calculations (cf. Table 41)
owed that on an average about half the larvae
P. oxylus remained in fields of cereals under-
wn with leys. This represents approximately
e-fourth of the *P. oxylus* larvae on cereal fields
harvest time.

A place in which to live (cf.
drewartha and Birch 1961). *P. oxylus* evidently did not suffer appreciably from a lack of places where it could live or as a result of the distribution of such places in an area. However, occasionally the stem walls of the cereals were so unfavourably constructed that the adult inside was incapable of escaping from the internode.

Overall mortality. Figure 50 gives a diagrammatic representation of the numbers of *P. oxylus* in the region of investigation at different times of the year. In the fields which were ploughed and tilled after the cereals were harvested, nearly all the specimens of *P. oxylus* died and the curve would have dropped close to the abscissa between segments e and f. For the fields where leys were established, the curve would have descended after segment d somewhat more steeply than the segments f, g and h and joined the abscissa at the right end of segment i. Thus, in all the cereal fields the mortality of *P. oxylus* was greatest during the egg and larval stages before the winter. Weather factors were apparently responsible for the death of less than 4 % of the progeny of *P. oxylus*, while the approximate figures for other factors were natural enemies about 35 %, man 50 %, place in which to live 2 %, and other factors 9 %.

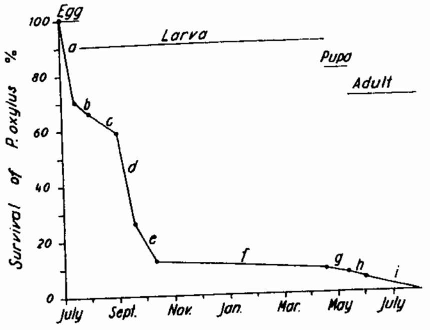


Fig. 50. Diagrammatic survival curve of *P. oxylus* in cereal fields and first-year leys established under them. Mortality factors: a = Superparasitism and *Mesopolobus aequus*, b = *M. graminum*, c = harvest and some other factors killing larvae, d = destruction of straw, e = ploughing, f = winter, g = factors destroying pupae, h = factors preventing emergence of adults from the straw, and i = other factors killing adults.

Table 43. Abundance of *P. oxylus* in oats in different years. Each year 100 plants from each of 20 fields (2 000 plants annually) were examined. Same material as in Tables 49, 55, 80, 83, 87 and 92

Year	Sampling period	Average sampling date	No. of internodes containing delphacid eggs	Internodes inhabited by *P. oxylus*	
				No.	%
1958	23. VIII—19. IX	8. IX	522	165	32
1959	28. VII—11. VIII	8. VIII	736	332	45
1960	1. VIII—16. IX	4. VIII	211	69	33
1961	2.—10. VIII	8. VIII	369	72	20
1962	12.—29. VIII	20. VIII	536	160	30
1963	5.—14. VIII	8. VIII	589	274	47
1964	11.—17. VIII	14. VIII	526	257	49

Fluctuations in abundance in 1958—1964. There were considerable fluctuations in the abundance of the immature stages of *P. oxylus* both in oats and in spring wheat. The figures varied according to whether they were calculated per ground surface area, per 100 plants or per number of food-containing internodes available (Tables 43 and 44). Similarly, there were marked variations in the numbers of specimens collected with the netting apparatuses (Table 45). Many factors, e.g. weather conditions and the location of the apparatuses, affected the numbers of pteromalids caught. The numbers of *P. oxylus* captured with such apparatuses give a poorer picture of the actual fluctuations of the species than the numbers obtained from samples of spring cereals. However, the catches with the netting apparatus reflect the numbers of immature stages the previous year.

The fluctuations in abundance of *P. oxylus* were probably caused chiefly by the availability of food (internodes containing delphacid eggs) but also by the abundance of the species *Mesopolobus aequus*, which competed for the same source of food. However, both the amount of food and the numbers of *M. aequus* were strongly influenced by weather conditions (mainly the temperature), so that food and competing species were probably primary factors, while weather was a secondary and partially primary factor regulating the abundance of *P. oxylus*.

Table 45. Abundance of *P. oxylus* obtained yearly with three netting apparatuses. Same material as in Fig. 24

Year	No. of adults	No. of males
1957	34	2
1958	3	1
1959	0	0
1960	55	0
1961	4	0
1962	6	1
1963	8	0
1964	31	0

Table 44. Abundance of *P. oxylus* in spring wheat in different years. Every year 100 plants were examined from each field. Same material as in Tables 50, 56, 80, 83, 88 and 92

Year	Sampling period	Average sampling date	Number of fields	No. of internodes containing delphacid eggs	Internodes inhabited by *P. oxylus*	
					No.	%
1958	18. VIII—2. IX	28. VIII	18	249	140	56
1959	3.—11. VIII	8. VIII	17	623	362	58
1960	1.—17. VIII	5. VIII	17	204	61	30
1961	2.—10. VIII	7. VIII	20	309	70	23
1962	12. VIII—1. IX	20. VIII	20	378	138	37
1963	5.—11. VIII	7. VIII	20	245	145	59
1964	11.—17. VIII	14. VIII	20	531	267	50

B. Mesopolobus aequus (Walk.)

ccording to v. ROSEN (1955 b, p. 89, 1961 a, 9) and GRAHAM (1957, p. 222) the following es are synonyms for this species: *Ablbergiella* (Walk.), *Amblymerus aequus* (Walk.), *Eutelus* Walk., *E.* (*Ptatytermus*) *decipiens* Thoms., *stenus purus* Walk., *Mormoniella oviphaga* bg, *Pteromalus aequus* Walk., *P. contractus* k., *P. leogoras* Walk., *P. odites* Walk., and *urpureus* Walk.

1. *Distribution*

aequus has been found in Madeira, Yugos- England, Germany, Czechoslovakia, Den- k, southern and eastern Sweden up to a ude of about 64°, and Finland (e.g. v. ROSEN 6 b, p. 26, 1961 a and b, 1966, PECK et al. 4). The species appears to be common in ope, and it has also been encountered in the (v. ROSEN 1961 a, p. 19).

Finland the species appears to be com- est in the southern part of the country. bviously also occurs in eastern Finland, as as further north than the actual locations e it has been observed (Fig. 51). In the on of the present investigation it was com- but not abundant.

2. *Developmental stages*

gg. According to v. ROSEN (1956 b, p. 27 Fig. 46), the average length of the egg is mm and it is less curved than the egg of *tenon oxylus*.

arva. v. ROSEN (1956 b, pp. 28—30) has lished descriptions of the five larval instars. e present studies the species, when occurring e field in its egg and larval stages, was not nguished from *P. oxylus*.

upa. v. ROSEN (1956 b, p. 31) has pub- d a picture of the pupa. In the region of resent investigation, the length of the male varied from 1.1 to 2.2 mm (n = 13) and of the female from 1.4 to 3.1 mm (n = 61). e was a curvilinear relationship between the lengths of both the male and female pupae and the numbers of delphacid eggs in the internode, as in the case of *Panstenon oxylus*. Males developed to the pupal stage on a smaller number of eggs than females, the situation again resembling that in *P. oxylus*.

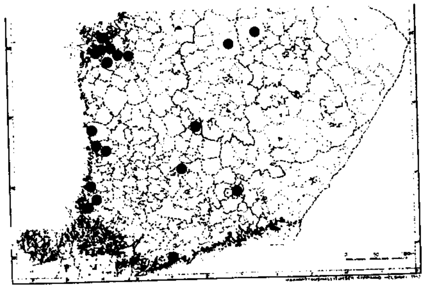


Fig. 51. Known localities of *M. aequus* in Finland.

Adult. Since the species was first described, v. ROSEN (1956 a, 1956 b, pp. 24—26, 1958, pp. 230, 231) and GRAHAM (1957, p. 223) in particular have studied the characters of the adult. In the present investigation, studies were made to find out the reasons for the variations in the size of the adults. Between July and September *M. aequus* specimens were collected from cereal fields, as was also the case with *Panstenon oxylus*. The results (Fig. 52) show that the males were able to develop into adults after consuming a smaller number of eggs than the females. The larva apparently needed over 30 delphacid eggs in order to develop into an adult of maximum size.

3. *Life cycle*

According to v. ROSEN (1955 a, p. 40), *M. aequus* has two generations per year in Sweden, although in later publications he mentioned only one (v. ROSEN 1956 b, p. 65). In Finland only one generation per year has been noted (Fig. 53) but in this case the female would appear to have a surprisingly long lifetime (about 11 months). The first eggs appeared in the stems of spring cereals after June 20; how-

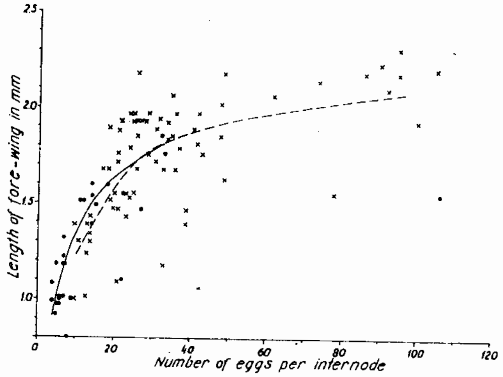


Fig. 52. Relationship between length of fore-wing of *M. aequus* and number of delphacid eggs in internodes. Dots and solid line = males, crosses and dashed line = females.

ever, it was not possible to distinguish them with certainty from the eggs of *Panstenon oxylus*. According to v. Rosen (1956 b, p. 27), at a temperature of about 10—15° the larvae hatched from the eggs after 4—5 days and at ca. 20°C after two days.

In mid-July large-sized larvae of *M. aequus* were found in cereals. The first males were found to emerge on July 26 and the first females on July 29. On an average, the males emerged a few days earlier than the females. The males died before the winter, and only the females hibernated. The following spring the females were active as early as April. In spring cereals they were encountered from June 7 onwards.

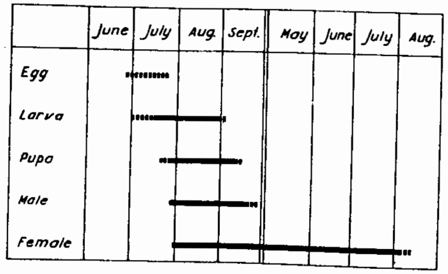


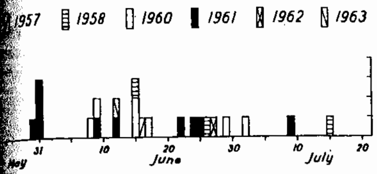
Fig. 53. Life cycle of *M. aequus* in 1956—1964. Explanations in Fig. 21.

4. *Habitats and migration*

In April and May *M. aequus* was found in leys, field edges and forest litter; it was not encountered in ploughed fields. According to v. Rosen (1961 a, p. 19), it is quite possible that the species overwinters in all parts of various plants. In Sweden, Denmark and England it has been found in conifer trees during the wintertime (v. Rosen 1961 b, 1962, 1966). However, v. Rosen (1961 b) is not sure whether the species concerned is actually *M. aequus* or perhaps some unknown sibling species.

Only a few females were collected in netting apparatuses as they migrated from their overwintering sites to places of reproduction (Fig. 54). The largest numbers were obtained in June. Evidently both *M. aequus* and *Panstenon oxylus* moved to spring cereals at approximately the same time in June and early July.

At the end of June and beginning of July *M. aequus* appeared to be most prevalent in cereal fields, but it also occurred in leys, as was the case with the data of v. Rosen (1956 b, pp. 60—64). There were no appreciable differences in the density of the adults between the margins and the central parts of the oat fields. There were about twice as many larvae per unit area of



g. 54. Migration of *M. aequus* in 1957—1964 cording to material collected with netting apparatuses. The times of collection are shown in Fig. On the ordinate are the numbers of *M. aequus*. All the specimens were females.

ound surface in spring wheat as in oats. Adults the new generation were found initially in eal fields and later, at the end of the summer in the autumn, in leys and in the ground getation of woods.

5. *Food supply and influence on J. pellucida*

ost species. According to v. Rosen 58, p. 231), larvae of *M. aequus* feed on all ds of eggs and larvae occurring in grasses. tikainen (1961 b, 1962) observed that they delphacid eggs in the internodes of cereals. r principal source of food, however, both weden and in Finland, appears to be eggs of *ella pellucida* (Ahlberg 1925, v. Rosen 1955 d b, 1956 b, 1961 a, Kanervo et al. 1957, isoo 1964, p. 37). According to v. Rosen 5 b, 1956 b, p. 33), the larvae are also capable ubsisting on a diet of plant food. In a later y, v. Rosen (1961 a, p. 19) mentions that ltative phytophages are an exception, and so it is not known whether *M. aequus* is able to oduce when the larva has fed exclusively on t food. In the present investigation, *M. aequus* only found in internodes containing the eggs other insects. From the field material it eared that *M. aequus* could not develop to adult stage without a source of animal food. was their main food supply, and if it was ty the larvae remained small and did not elop into adults in spring cereals.

uantity of food. The smallest num- of delphacid eggs on which the male larva ld develop into an adult was 5. The female, on the other hand, required 10 eggs (cf. Fig. 52). The female obviously required more food as a larva than the male. Without an adequate amount of food, the larva died. At least in oats and spring wheat the available plant food was not capable of replacing animal food.

If there were few delphacid eggs available, the larvae of *M. aequus* consumed them virtually completely, but if there were many [illegible] most of them were damaged rather than completely consumed. As the number of delphacid eggs per internode increased, the number damaged by *M. aequus* larvae likewise increased, but the percentage diminished (cf. Fig. 46). The number of eggs damaged was usually about 20—30 per larva, a figure which agrees with that found by v. Rosen (1956 b, p. 28) in Sweden.

Influence on J. pellucida. Larvae of *M. aequus* appeared to destroy the eggs of *J. pellucida* located in thin-walled internodes. On the average, the larvae probably destroyed 20—30 eggs, but sometimes over a hundred were consumed.

6. *Reproduction*

Sex ratio. In most years pteromalids were collected from spring cereals so late that some of them had already escaped from the plants. In the material collected at the times mentioned in Tables 43 and 44 a total of 328 adults of *M. aequus* were obtained in the years 1961—1963, 22 % of which were males. Since males were relatively more commion among the first emerging adults than among the last ones, the sex ratio found was actually too female-dominated. Since all the adults of *M. aequus* that emerged were assumed to be males, the proportion of males was found to be 34 %. The actual sex ratio was female-dominated and evidently between 1:2 and 1:4. Where there had been only a few delphacid eggs in the internodes (Tables 46), males principally emerged, while where there were many eggs the adults were mostly females. This can be interpreted as meaning that the normal sex ratio of *M. aequus* was female-dominated, but that if there was only a scanty food supply for

Table 46, Relation between the numbers of available delphacid eggs and the sex ratio of *M. aequus* in spring cereals, 1958—1961. $\chi^2 = 24.01$***, d.f. 4

No. of delphacid eggs in internode	*M. aequus*		
	Total adults	Males	
		No.	%
1— 10	18	16	89
11— 20	22	7	32
21— 30	25	4	16
31— 40	20	3	15
41—150	33	7	21
Total	118	37	31

the larvae, the females were more liable to succumb than the males, and consequently the sex ratio changed to become dominated by males. In the region of investigation, examinations of cereals in 1962—1964 showed that 10 % of the spring wheat internodes containing delphacid eggs had fewer than 11 eggs, while the corresponding figure for oats was 26 %. Correspondingly, 5 and 8 % of all the pteromalid larvae (*P. oxylus* + *M. aequus*) found in the internodes were located in those containing less than 11 eggs. A scarcity of food supply must thus have increased the proportion of males and evidently caused a decrease in the numbers of females.

Copulation and parthenogenesis. According to v. Rosen (1956 b, pp. 26, 27), adults are sexually mature immediately after emergence and copulate before the arrival of winter. The species may also reproduce parthenogenetically, in which case all the progeny are males.

Oviposition. Larvae of *M. aequus* have been encountered chiefly in graminaceous plants but also in *Achillea millefolium* and *Medicago sativa* (v. Rosen 1961 a, p. 19). In the region of investigation, larvae were found in the stems of spring wheat, oats, barley, rye and *Poa pratensis*. The species appeared to have a special predilection for wheat. In the years 1958—1964, an average of 16 % of the internodes of spring wheat containing delphacid eggs were inhabited by *M. aequus* larvae. In oats the corresponding figure was 7 %.

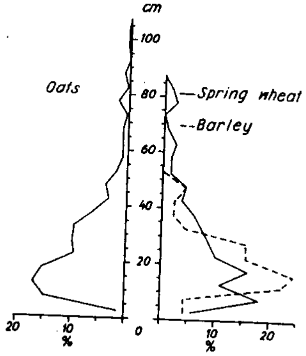


Fig. 55. Height above ground of upper end of internodes inhabited by *M. aequus* in 1958—1963. Numbers of inhabited internodes: oats 306, spring wheat 138, barley 45.

M. aequus apparently preferred to oviposit in thin-walled internodes than in those with thick walls. The material studied, however, was meagre, and the difference was not statistically significant.

The height in the cereal occupied by *M. aequus* was studied on the basis of plant samples taken after July. At this time some of the adults had already escaped from the interior of the plants, but the values obtained for the remaining specimens give a very good picture of the height occupied by all the adults (Fig. 55). These results show that in spring wheat and oats *M. aequus* occurred at approximately the same height as the spring generation of *Panstenon oxylus* (cf. Fig. 49).

7. *Fluctuations in abundance*

Weather factors. According to v. Rosen (1956 b, p. 27), weather factors probably have a marked effect on the total egg production. In Finland *M. aequus* appeared to be most abundant in the southern part of the country. In the region of investigation larvae were most prevalent in warm summers (1959, 1960) and in the summers following them (1960, 1961, 1964). They were less numerous in cool summers and

47. Emergence of *M. aequus* from spring cereal es in the insectary. The samples were collected in st at about the same phenological stage of the cereals

Year	No. of pupae	Emerged from pupae		χ^2	
		No.	%	1960	1961
....	128	119	93	—	—
....	236	213	90	0.49	—
....	153	96	63	33.88***	41.21***

ears following such cool summers. A good ure of the influence of weather factors on the ulation of this species can be obtained by paring the emergence of *M. aequus* in the years 1960—1962. The interval between the osition period and the emergence period was mer than average in 1960, slightly cooler average in 1961, and very cool in 1962 le 1). According to the results of this comon (Table 47), in the first two summers, the weather was warm or almost average, species succeeded in emerging, while in the cool summer of 1962 only 63 % of the mens managed to emerge, while the rest — perhaps in the field over 50 % — remained e pupal stage. Such pupae, when brought the insectary, died during the winter. Likein the fields in the spring of 1963 there larger numbers of dead specimens than , especially those in the pupal stage (Table Moreover, many of the dead insects had partially emerged, and some of the dead ts inside the stems had wings which had not lded.

od supply. During the years of these ies, both the absolute and the relative unts of food were generally adequate for species. Among the fields of spring cereal tigated, an average of at most 32 % (in) of the internodes of spring wheat conng delphacid eggs were inhabited by *M.* s, and in 1961 the corresponding figure oat fields was 23 %. In these same two , the proportions of delphacid egg-conng internodes inhabited by all species of malids were 62 and 42 % respectively. It is ous that the larvae of *M. aequus* alone could have occupied at least as many of the egg-containing internodes as the pteromalid larvae as a whole, if certain factors had not limited the abundance of the species. The relative food supply in certain places, however, was an important factor restricting the population of the species. Moreover, in some of the internodes there were too few delphacid eggs, and consequently the insects died while still immature, as was demonstrated by the sex ratio.

Table 48. Numbers of pteromalids (*P. oxylus, M. aequus, M. graminum*) which emerged and left the stems in autumn and *M. aequus* found dead in stubble the following spring

Inspection time	No. leaving stems in autumn	No. of dead *M. aequus*	
		Pupae	Adults
1961 2.—10. V ...	14	0	1
1962 13.—25. V ...	63	8	25
1963 2.—10. V ...	12	37	12

Biotic factors. According to v. Rosen (1956 b, p. 27), under experimental conditions the species deposits several eggs in the same internode. This may also occur in nature, but after competition between the offspring in the same internode, usually only one remains alive, as in the case of *Panstenon oxylus*.

The most important competitive species was *Panstenon oxylus*, whose requirements for living sites are about the same as those of *M. aequus*. In the region of investigation the presence of *P. oxylus* evidently restricted the numbers of *M. aequus*. However, in the warm summers of 1959 and 1960, *M. aequus* outstripped *P. oxylus* in occupying internodes containing delphacid eggs; even in 1961 it was still abundant (cf. Tables 43, 44, 49, 50). On the other hand, in cool summers and in years following cool summers, such as 1962, *P. oxylus* appeared to oust *M. aequus* from delphacid egg-containing internodes.

Mesopolobus graminum (Hårdh) deposited its eggs on the surface of, or near to, the pupae of *M. aequus* and probably also the larvae. The larva of the former developed into an adult after having consumed one pupa or nearly full-grown larva of *M. aequus*. *M. graminum* occurred as a parasite of *M. aequus* after about the end of July.

Table 49. Abundance of *M. aequus* and all pteromalids in oats in different years. Every year 100 plants from each of 20 fields (2 000 plants annually) were examined during the period July 28—Sept. 19. Same material as in Table 43

Year	No. of internodes containing delphacid eggs	Internodes inhabited by *M. aequus*		Internodes inhabited by pteromalids	
		No.	%	No.	%
1958	522	3	1	168	32.2
1959	736	13	2	345	46.9
1960	211	24	11	93	44.1
1961	369	84	23	156	42.3
1962	536	52	10	213	39.7
1963	589	17	3	291	49.4
1964	526	14	3	271	51.5

Table 50. Abundance of *M. aequus* and all pteromalids spring wheat in different years. Every year 100 plants were examined from each field, 18 in 1958, 17 in 195 and 1960, and 20 in 1961—1964. Examinations made Aug. 1—Sept. 2. Same material as in Table 44

Year	No. of internodes containing delphacid eggs	Internodes inhabited by *M. aequus*		Internodes inhabited by pteromalids	
		No.	%	No.	%
1958	249	6	2	149	59.[illegible]
1959	623	53	9	415	66.6
1960	204	65	32	126	61.[illegible]
1961	309	96	31	168	54.4
1962	378	71	19	209	55.3
1963	245	14	6	159	64.[illegible]
1964	531	76	14	343	64.6

In the years of this study, it probably destroyed at least 3—4 % of the immature stages of *M. aequus*. In the years following the warm late summer of 1959 and 1963, i.e. in 1960 and 1964, it was most abundant, and it then destroyed at least 7 % of the immature stages of *M. aequus* occurring in August.

The virus diseases EWSMV and OSDV may have reduced the availability of living sites suitable to the immature stages of *M. aequus* in the same way as the sites for *P. oxylus* were decreased.

Man. *M. aequus* appears to have become more prevalent subsequent to land clearing and the increase in the area devoted to cereals. At the time of cereal harvesting the species was already in the adult stage, so that destruction of the straw and ploughing of the field had no influence on the insects. In cases where the species occurred in delphacid eggs in hayfields some of the larvae succumbed when the hay was dried in July.

A place in which to live. In the region of investigation, the species evidently did not suffer appreciably from lack of or from unfavourable distribution of places where it could live. However, occasionally the stem walls of the cereals were so thick and hard that some of the adults were unable to escape and died inside the internode.

Fluctuations in abundance in 1958—1964. Whether calculated per unit area of ground, per 100 plants or per number of internodes containing delphacid eggs, the amounts of *M. aequus* were at a minimum at the beginning of the present study, reached a maximum around the year 1961, dropped to a second low point in 1963 and finally appeared to rise again in 1964 (Tables 49 and 50). Similar fluctuations were also seen in the material obtained with the netting apparatuses, although these variations naturally occurred one year later than those for the immature stages (cf. Fig. 54). Such fluctuations were apparently caused chiefly by weather conditions. The population density increased in 1959 and 1960, when the summers were warm, and consequently oviposition and development of the immature stages apparently succeeded well. In 1961, it was evident that there were many females in cereal fields, and moreover oviposition and larval development were successful. In contrast, in the cool summer of 1962 there was a relatively low density of immature stages, and a large proportion of the insects reached only the pupal stage before the arrival of winter. The pupae succumbed during the winter (cf. Tables 47, 48), and there were few adults the following year. In 1963, oviposition was apparently successful, but the density of immature stages was at a minimum because females were evidently scarce.

Although the food supply declined at the same time as the numbers of *M. aequus* increased, it had not yet become an important factor limiting the population density. *Panstenon oxylus* may somewhat retarded the increase in density *M. aequus*, but it was not able to prevent increase. *Mesopolobus graminum* showed an ase in numbers, but its effect in limiting opulation was slight during the entire period he investigation. The influence of man likeremained about the same throughout this od. There were some changes in the oat eties grown. In particular, the thick-stemmed ety Pendek became more widespread, but it ably had no great effect on the population ity of *M. aequus*.

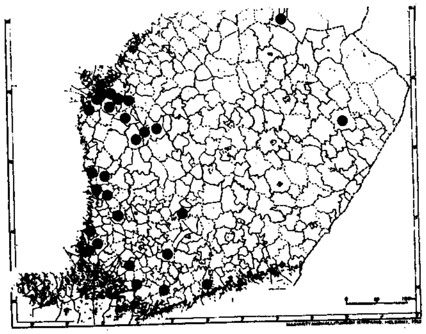


Fig. 56. Known localities of *A. atomus* in Finland.

C. Anagrus atomus (L.)

umerous species of the genus *Anagrus* have described. Enock and Waterhouse assumed in Europe there are about 25 of them YGER 1950, p. 39). In Belgium, DEBAUCHE 8) mentioned three species of *Anagrus*, one hich comprised two races. However, BAK- DORF (1934, p. 51) believed that there is only pecies in the genus, and he (BAKKENDORF pp. 268—270) regarded the other specific es as synonyms. According to KRYGER (1950, 9), there is apparently only one *Anagrus* es in Europe, and the name *A. incarnatus* will fit this species. WHALLEY (1956) is of pinion that the *A. atomus* and *A. incarnatus* ibed in Europe are ecological races of the species, and he uses for them the names *rus atomus* (L.) Hal. form *atomus* (L.) and *tomus* (L.) Hal. form *incarnatus* Hal. *Anagrus omus* has been found under natural condi- in *Tettigella viridis* (L.) but never in del- id species (WHALLEY, 1956). In the labora- it has oviposited and developed in the del- id species *Conomelus anceps* (Germar) also. the other hand, *Anagrus a. incarnatus* has rred in the field both in *T. viridis* and in hacid species.

the region of the present investigation, *tomus* occurred both in delphacid species in *Cicadoidea* species. All the specimens ied which were in the eggs of delphacids *A. atomus incarnatus*. *A. a. incarnatus* also ated in species of the *Cicadoidea* group.

1. Distribution

According to ANNECKE and DOUTT (1961, p. 7), the genus *Anagrus* is probably cosmopolitan. The information about *A. atomus* and the range of its races is incomplete, however, since it has not yet been possible precisely to delimit the species with absolute certainty, and there are only scanty data about the distribution of the taxon. According to KRYGER (1950, p. 38), the species occurs all over Europe, and *A. atomus incarnatus* has been recorded from France (MAILLET 1960), England (WHALLEY 1956), Belgium (DEBAUCHE 1948), Sweden (collected by O. Heikinheimo) and now from Finland.

In Finland, *A. atomus* is common (Fig. 56) and apparently occurs even north of latitude 64°.

2. Developmental stages

The different developmental stages of the species have been described in numerous publications. Among others, BAKKENDORF (1925) and MACGILL (1934) have described the egg, BAKKENDORF (1934), MACGILL (1934) and MAILLET (1960) the larva, and MACGILL (1934) the pupa. Descriptions of the adult are also to be found in DEBAUCHE (1948) and WHALLEY (1956). According to MAILLET (1960), the size of the adult varies in accordance with the number of individuals in the leafhopper egg.

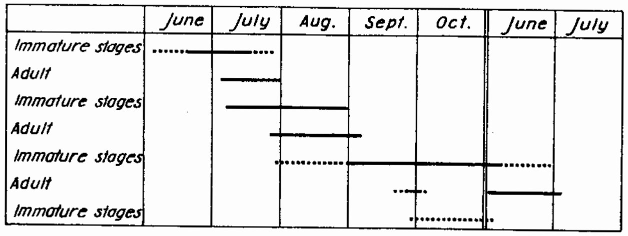


Fig. 57. Life cycle of *A. atomus* in 1958—1960. Explanations in Fig. 21.

3. *Life cycle*

A. atomus is multivoltine (cf. e.g. PIERRE 1906, MACGILL 1934, MAILLET 1960). In the region of investigation the species usually had three generations per year, but in warm summers, such as 1959, at least a part of the population had four generations (Fig. 57). According to BAKKENDORF (1925, pp. 254, 255), in Denmark the species has about 4—5 generations during the summer and it hibernates in the larval stage in the eggs of various leafhoppers, particularly those of *Conomelus anceps* (Germar). In the region of investigation *C. anceps* has not so far been found, and if it does occur, it is rare. As a result, *A. atomus* hibernated in the eggs of other species in that region. In the wintertime, immature stages of *A. atomus* were common and sometimes quite abundant in leys and in the stubble of cereals undersown with grass. In such places there were eggs of leafhoppers, among others *Macrosteles* spp., *Solenopyx sulphurellus* (Zett.) and *Philaenus spumarius* (L.). In isolation experiments made in the field *A. atomus* succeeded in overwintering in the eggs of *S. sulphurellus*, and quite probably it actually hibernates, as either a larva or an egg, in the eggs of this species and possibly of other leafhopper species as well.

Immature stages. No information is available on the duration of the egg stage and the different larval instars. According to MACGILL (1934), the egg and early larva are almost colourless, and consequently they cannot be observed with the naked eye in parasitized leafhopper eggs. The late larva, on the other hand, is red, so that at this stage it is easy to distinguish the parasitized egg through the tissue of the leaf blade. According to MACGILL (1934), a parasitized egg can be recognized when about 50 % of the total duration of the immature stages has elapsed. In the present studies, however, the larva of *A. atomus* was observed to become reddish when only about 30 % of the immature stage period had elapsed.

The total duration of the developmental period of the immature stages in *J. pellucida* eggs at 12.5°C averaged 35 days (31—39; n = 17). According to WHALLEY (1956), the developmental period of *A. a. atomus* and *A. a. incarnatus* are of approximately the same length, and at 25°C one generation in *Tettigella viridis* (L.) took 11 days and in *Conomelus anceps* (Germar) 13 days. MACGILL (1934) stated that *A. atomus* takes approximately 16 days to develop from the egg to the adult insect at 26—27°C.

Adult stage. Among the 324 pupae of *A. atomus* examined in the delphacid eggs in the leaves of spring cereals, 27 % had their head in the anterior end of the leafhopper egg. Among the 47 pupae in stems, 21 % had their head end in the anterior end of the egg. Such specimens, when they emerged as adults, made their way out of the anterior end of the egg and escaped directly to the surface of the plant. The remaining specimens, about three-fourths of the total, made their way out of the posterior end of the egg. If such individuals were in delphacid eggs located in the leaf sheath, they generally penetrated through the tissue of the sheath to the external surface. If the parasites were in eggs located in the

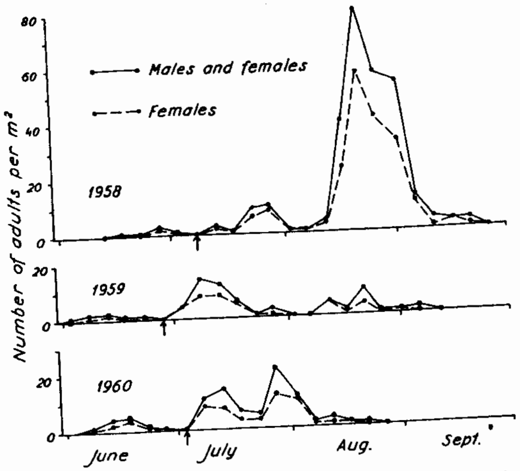


Fig. 58. Emergence of adult *A. atomus* per 5-day periods in the insectary from material taken from first-year timothy leys established under oats (left of arrow) and from oats (right of arrow) in 1958—1960. Same material as in Fig. 42.

, they emerged into the cavity, where they ined for some time before making their way ugh the stem wall and sometimes even ugh the leaf sheath in order to escape to surface.

he daily rhythm of adult emergence was ied in the insectary. The results (Table 51) w that emergence was definitely most active he morning and at mid-day, while no emerce was observed at night. Emergence during erent times of the season was investigated at localities in 1958—1960. In the spring all vascular plants on a total area of 2.5 m² on sites in first-year timothy leys established er cereals were collected and placed in rearing boxes. After the emergence of the oat seedlings, 100-plant samples were collected at weekly intervals. The plant parts containing delphacid eggs were separated and put into Petri dishes. All the specimens from both localities were combined and the quantities were calculated as numbers per square metre (Fig. 58). First-generation adults emerged at the end of June when the early summer had been cool and around the beginning of June in warm summer (Figs. 57 and 58). Thereafter they migrated, partly to fields of spring cereals, where they had not apparently previously been and where there were delphacid eggs to serve as a food supply for their larvae. The adults of the following generation in spring cereals emerged during the first half of July. The first adults of the third generation emerged at the end of July and beginning of August, although in cold summers this did not take place until the middle of August. Fourth-generation adults were not observed every year.

At a temperature of about 15°C the life-span of the adult varied from 2 to 6 days. The average

e 51. Numbers of adult *A. atomus* emerging at dift hours of the day. The insects were in Petri dishes in insectary July 9—30, 1960 and July 27—31, 1961

x	Hours of day								Total
	20—6	6—8	8—10	10—12	12—14	14—16	16—18	18—20	
♂	3	8	4	7	3	3	1	0	29
♀	5	12	14	10	12	3	3	0	59
otal	8	20	18	17	15	6	4	0	88

life-span of the female was 4 days and that of the male was possibly somewhat shorter. According to MacGill (1934, p. 60), the female appears to be fully mature as soon as it emerges from the pupal stage, and if suitable host eggs are available it begins to oviposit at once. The pre-oviposition period is thus very short. The oviposition period lasted a few days, while the post-oviposition period was likewise short and difficult to determine.

4. *Habitats and migration*

A. atomus occurs in many different kinds of habitat, as evidenced by the places inhabited by the species and the eggs of its hosts (cf. e.g. Haliday 1833, Pierre 1906, Ahlberg 1925, Bakkendorf 1925, 1934, MacGill 1934, Hassan 1939, Debauche 1948, Kryger 1950, Morcos 1953, Whalley 1956, Maillet 1960, Kanervo et al. 1957, Raatikainen 1962). It is apparently commonest in low, herbaceous vegetation in damp sites but also occurs in dryish places, trees and glasshouses. According to Debauche (1948), *A. atomus* (L.) inhabits many different habitats where grass grows, *A. incarnatus subfuscus* Förster occurs in forests, while the race *A. incarnatus incarnatus* Haliday is in damp, grassy sites. The latter race also occurs in trees (cf. Pierre 1906, Maillet 1960).

In the region of investigation *A. atomus incarnatus* seemed to be most abundant in oats, barley and timothy fields, but it was also common in wheat and rye fields as well as in many other sites where herbs and grasses grew. Perennial vegetation, especially ley, was evidently the chief overwintering site of the species. Adults emerging on such sites migrated to spring cereals. No detailed information is available on the distances travelled by the migrating specimens, but they evidently moved at least 50—100 metres, since large numbers of progeny of the first generation were found several score metres from the nearest overwintering sites. Some of the females may also have hibernated in host eggs buried in the surface soil during the ploughing of the cereal fields.

No data were obtained concerning the migration of the generations developing in spring cereals, but presumably the females did not move away from the field if there were adequate sites nearby suitable for oviposition. Both sexes were very active in the stand and were in movement for more than half the daytime. Laboratory tests showed that the average walking speed of five females at 20°C was 7.0 ± 0.24 mm/sec. and that of three males at 17°C was 5.5 ± 0.15 mm/sec. While walking they explored the surface with their antennae, often stopped for 1—4 seconds, and every half minute or so they took wing, often for periods of 1—3 seconds.

5. *Food supply and influence on J. pellucida*

Host species. *A. atomus* is a parasite of eggs, especially those of leafhoppers. According to reports in the literature, it has been encountered in the following species: *Megamelus notula* (Germar) (Whalley 1956), *Ditropis pteridis* (Spinola) (Morcos 1953), *Muellerianella fairmairei* (Perris) (Morcos 1953, Whalley 1956), *Javesella pellucida* (Kanervo et al. 1957), *Liburnia* sp. (Bakkendorf 1925, Hassan 1939), *Conomelus anceps* (Germar) (Bakkendorf 1925, Hassan 1939, Whalley 1956), *Tettigella viridis* (L.) (Pierre 1906, Bakkendorf 1925, Morcos 1953, Whalley 1956), *Typhlocyba rosae* (L.) (Tullgren 1916), ?*Typhlocyba* sp. (Bakkendorf 1934, Kryger 1950), *Erythroneura pallidifrons* (Edw.) (MacGill 1934) and *Macrosteles sexnotatus* (Fall.) (Bakkendorf 1925, Ahlberg 1925). In the region of the present investigation *A. atomus* occurred under natural conditions in the eggs of many leafhoppers of the delphacid and *Cicadoidea* groups. In trials carried out in the insectary *A. a. incarnatus* developed to the adult stage in eggs of the species *Stiroma bicarinata* (H.-S.), *Criomorphus albomarginatus* Curt., *Dicranotropis hamata* (Boh.), *Javesella pellucida*, *J. obscurella* (Boh.), *Megadelphax sordidulus* (Stål), *Xanthodelphax flaveolus* (Flor), *Macrosteles* sp., probably *M. cristatus* (Rib.) and *Solenopyx sulphurellus* (Zett.).

he species has also been found in the eggs Hemiptera (Bakkendorf 1934, Kryger 0) and agrionids (Bakkendorf 1925, 1934, bauche 1948, Kryger 1950).

uantity of food. According to cGill (1934), only one adult develops in egg of *Erythroneura pallidifrons* (Edw.), while rcos (1953) reports similarly that one adult erged from the egg of *Ditropis pteridis* (Spia) and *Muellerianella fairmairei* (Perris). In the sent studies, it was found, both experimeny and in the field, that only one adult of *atomus* was ever present in the egg of delcids. However, in large eggs, such as those *Tettigella viridis* (L.), several adults develop. rre (1906) found two parasites in one *T. idis* egg, while the numbers found by other rkers were 3—11 (Morcos 1953), 4 in the d and 9 in the laboratory (Whalley 1956) an average of 3.8, ranging from 1 to 8 aillet 1960).

nfluence on J. pellucida. One fele of *A. atomus* oviposits in many *J. pellucida* s, and those eggs in which a larva develops destroyed by the parasite.

6. *Reproduction*

ex ratio. The sex ratio of *A. atomus* ears to be either female-dominated or about In studies comprising the most extensive erial, the following results were obtained:

Investigator	Total specimens	Males No.	Males %
kendorf (1925)	875	177	20.2
kendorf (1934)	1 046	325	31.1
llet (1960)	266	132	50

ilarly, the material of MacGill (1934) wed a deficiency of males, and in the studies Whalley (1956) the sex ratio of the races *rnatus* and *atomus* was in both cases feminated, 1:3.

Table 52. Proportion of male *A. atomus* in different generations hatching from eggs collected in the field in different years

	1958			1959			1960		
	Tot.	Males		Tot.	Males		Tot.	Males	
		No.	%		No.	%		No.	%
1st generation	22	9	41	40	18	45	197	93	47
2nd »	25	6	24	37	11	30	70	26	37
3rd »	259	88	34	23	9	39	5	3	60
1—3rd »	306	103	34	100	38	38	272	122	45

n the present studies the sex ratio was ascered from material collected in 1958—1960 n timothy and oat fields (Table 52). The first eration probably developed in the eggs of the *Cicadoidea* group in timothy fields, while the second and third generations arose from the eggs of delphacids, principally *J. pellucida*, in oat stands. This material revealed that in all generations and in all years the sex ratio of *A. atomus* was female-dominated. Of the 678 specimens examined, 263 (38.8 %) were males.

Copulation and parthenogenesis. Immediately after emergence the adults were capable of copulating. Copulation was common in the insectary and apparently also under natural conditions, since most of the progeny were females. Parthenogenetic reproduction also occurred, and in this case all the progeny in the tests were males. MacGill (1934) and Whalley (1956) also found that parthenogenesis took place.

Egg production. According to the observations of Bakkendorf (1925) and MacGill (1934), the number of eggs produced by *A. atomus* is small, and Clausen (1940, p. 101) states that most mymarid species probably do not produce more than 100 eggs. In the present trials the number of eggs was not counted, but the numbers of progeny of three females which developed to the larval stage varied from 28 to 42. Oviposition was most active during the first and second days after emergence, and one female was able to deposit as many as 28 eggs in a 24-hour period.

Occurrence of immature stages in different plants. According to Bakkendorf (1925, 1934), MacGill (1934) and Kryger (1950), immature stages of *A. atomus* have been found in the following plant species: *Typha*, *Juncus effusus*, *Phragmites*, *Cyno-*

surus cristatus, *Salix pentandra*, *Alnus glutinosa*, *Mirabilis tubiflora*, *Nymphaea*, *Nuphar*, *Pelargonium*, *Angelica silvestris*, *Primula*, *Salvia*, *Plantago*. *Tussilago farfara* and *Cirsium oleraceum*. In the region of investigation, immature specimens were encountered in leafhopper eggs located in the leaves of oats, barley, wheat, rye, timothy, *Elytrigia repens*, *Deschampsia caespitosa*, *Calamagrostis purpurea* and *Trifolium pratense*. Furthermore, they occurred in eggs in the stems of all the above cereal species as well as those of *Festuca pratensis*. The species appeared to occur in a wide range of plants and in a great variety of sites, providing there was an adequate food supply. In spring cereals the species clearly preferred to oviposit in delphacid eggs in the leaves rather than in those in the stems (Table 53). In June and July, when there were many delphacid eggs in the leaves of oats and spring wheat (Fig. 29), there were more eggs parasitized by *A. atomus* in the leaves than in the stems. Toward the end of the summer, the proportion of delphacid eggs in the leaves declined and the population density of *A. atomus* increased. At this time an ever greater proportion of the parasitized eggs were located in the stems. In August, when the abundance of the species was determined in the different years (cf. Tables 55 and 56), it occurred only scantily in the leaves of spring wheat, but in oats it was mainly in the leaves. Even in early autumn, there were considerable numbers of leafhopper eggs and *A. atomus* in oat leaves.

In cereal leaves, *A. atomus* occurs in both the sheath and the blade. Since there were more leafhopper eggs in the sheath than in the blade, the parasite, too, was more abundant in the sheaths. When it occurred in the stems of oats, it was obviously more common in thin-walled than in thick-walled internodes, as seen in the following tabulation:

Thickness of stem wall, mm	0.2	0.3	0.4	0.5	0.6	0.7	0.8	>0.8
No. of *Anagrus*	55	9	3	5	3	1	3	3

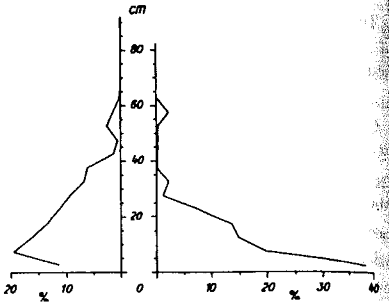


Fig. 59. Height above ground occupied by immature stages of *A. atomus* in delphacid eggs in oat leaves. Left curve: healthy or only slightly virus-infected plants (1 795 *A. atomus* specimens). Right curve: plants severaly infected with OSDV or/and EWSMV (908 *A. atomus* specimens).

Table 53. Proportions of delphacid eggs parasitized by *A. atomus* in stems and leaves of spring cereals. Same materials as in Tables 21 and 22

	Oats		Spring wheat	
	Stems	Leaves	Stems	Leaves
No. of delphacid eggs	36 579	1 377	17 189	5
Eggs parasitized by *A. atomus*, no. ...	1	727	0	5
» , %	0.0	52.8	0	100

Height occupied by immature stages in the stand. In all spring cereal species most specimens of the immature stages of *A. atomus* in the leaves and stems were located in the lower part of the stand. In oat fields, where the most extensive material was obtained, the immature stages were situated in the lowermost leaves in June, but as the plants grew taller the leafhoppers oviposited higher in the stand and consequently *A. atomus*, too, occurred at higher levels. In August they were at the heights shown in Figures 59 and 60. In the eggs of other leafhoppers laid in the leaves they were at approximately the same height, but less than 2 % of the total numbers of *Anagrus* in the leaves were in such eggs. In the stems, on the other hand, all were in delphacid eggs.

In oat stands which were severely infected with the virus diseases OSDV and EWMSV, *A. atomus* occurred at distinctly lower levels than in healthier stands (Fig. 59).

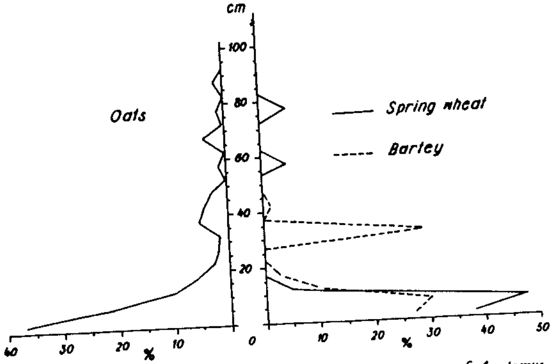


Fig. 60. Height above ground occupied by immature stages of *A. atomus* in delphacid eggs in stems of oats (592 *A. atomus* specimens), spring wheat (63) and barley (70).

7. *Fluctuations in abundance*

eather factors. The immature stages atomus readily succumbed when their envi- ment became too dry, notably when the plant in which their host eggs were located ered. This phenomenon was often observed he field, and in the cultures dry conditions the main cause of mortality.

he weather also had an indirect effect on the ndance of the species. In years when the ng and early summer were dry, the stems ereals emerged late, and consequently leafpers oviposited for long periods in the sheath blade of the leaves. In such summers there large numbers of the immature stages of *atomus*, especially in oats. For example, in the erial mentioned on p. 43, the following nbers of delphacid eggs parasitized by *A.* *mus* were found in the leaves of 700 Pendek

	Total delphacid eggs	Eggs parasitized by *A. atomus* No.	%
wet June (1957)	277	244	88
dry June (1958)	895	434	48

ood supply. According to MacGill 34, p. 61), Morcos (1953, pp. 414, 434) and Alley (1956), a small percentage of the host were parasitized by *A. atomus*. In the region of investigation, as shown by the data given in Table 53, only about 1.9 % of the delphacid eggs in oats and 0.02 % of those in spring wheat were parasitized by *A. atomus*. In more extensive material (e.g. Tables 55 and 56) the percentage of parasitism was about the same. These figures give the impression that the food supply was adequate; but actually it was scanty, since most of the delphacid eggs were located in the cereal stems, where they remained undiscovered.

In the years 1957—1960, oat samples were collected at weekly intervals, and the numbers of delphacid eggs and those parasitized by *A. atomus* in the leaves were counted. The results (Fig. 61) showed that wherever there were delphacid eggs, parasitized eggs were also present. The percentage of parasitized eggs was initially low, but in all years it rose to at least 90 towards the end of the summer (cf. Fig. 62). This, as well as numerous other counts and observations made in the field, clearly demonstrate that the food supply was a very important factor influencing the abundance of *A. atomus*, at least in oats and spring wheat. In June there were only a few delphacid eggs in the stands and the few parasites present evidently did not easily find them, but after the end of July there were larger numbers of parasites and then the numbers of leafhopper eggs in the leaves obvi-

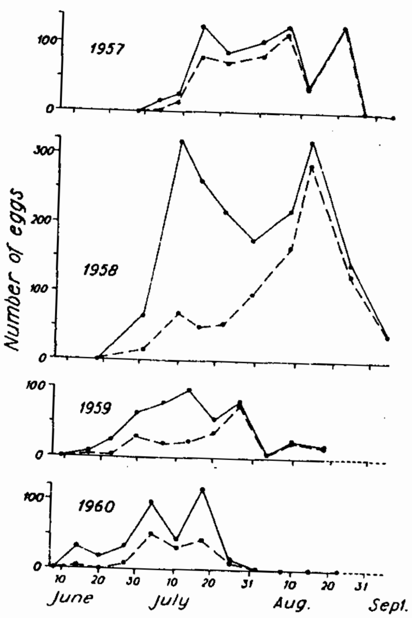


Fig. 61. Numbers of delphacid eggs in leaves of 200 (in 1957: 300) oat plants in 1957—1960. Solid line = eggs considered healthy + those parasitized by *A. atomus;* dashed line = eggs found to be parasitized by *A. atomus.* The solid part of the abscissa shows the period during which observations were made, while the broken part indicates, that no observations were made. Same material as in Fig. 16.

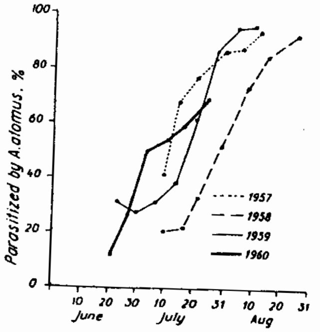


Fig. 62. Percentage of delphacid eggs in oat leaves parasitized by *A. atomus* in 1957—1960. The curves are 3-point moving averages. Same material as in Fig. 16.

Table 54. Emergence of *A. atomus* adults to surface after being buried as immature stages in soil at different depths. The percentages are based on the assumption that there were equal numbers of insects in each treatment. Same trial in Table 42

Depth of soil cm	*A. atomus* collected in cloth funnels			
	Total adults		Males	
	No.	%	No.	%
0	53	100	17	32
5	47	89	10	21
10	3	6	1	33

ously became the minimum factor limiting the abundance of the parasites.

According to MacGill (1934), *A. atomus* may deposit more than one egg in a leafhopper egg, but only one larva develops into an adult. In the region of the present investigation, nothing is known about competition with other individuals of the same species for the food source.

Biotic factors. Larvae of *Panstenon oxylus* and *Mesopolobus aequus* would feed on delphacid eggs parasitized by *A. atomus,* when these were located in the stems. However, there were only a few such parasitized eggs in the stems (cf. Tables 53, 55, 56) and usually they were undamaged, so that the above two pteromalids were obviously quite unimportant as enemies of *A. atomus.*

In the leaves of oats infected with OSDV and EWSMV there were more eggs and egg groups of delphacids than in healthy plants (cf. Table 23). Many plants in the region of investigation were infected with virus, and the density of the immature stages of *A. atomus* in virotic stands was greater than in uninfected oat stands. Furthermore, there appeared to be more *A. atomus* in stands damaged by the frit fly *(Oscinella frit* L., etc.) and by the barley yellow dwarf virus transmitted by aphids, than in healthy stands.

Effect of man. The population density of *A. atomus* appeared to be greater in cultivated areas than in the surrounding natural tracts. The density of the species was apparently greater in oats and barley than in wheat and rye. The species was also found in leys.

Table 55. Abundance of *A. atomus* in oats in different years. Each year 100 plants from 20 fields 00 plants annually) were examined during the period July 28—Sept. 19. Same material as in Table 43

Year	Delphacid eggs								Other leafhopper eggs
	Stems				Leaves				
	No. of internodes with delphacid eggs	Internodes inhabited by *A. atomus*		No. of *A. atomus*	No. of delphacid egg groups	Egg groups parasitized by *A. atomus*		No. of *A. atomus*	No. of *A. atomus* in leaves
		No.	%			No.	%		
....	522	4	0.8	4	62	60	97	163	0
....	736	11	1.5	59	449	25	6	124	0
....	211	2	0.9	3	5	2	40	4	0
....	369	18	4.9	49	10	0	0	0	1
....	536	13	2.4	47	104	65	63	167	1
....	589	11	1.9	63	124	92	74	269	0
....	526	22	4.2	80	627	356	57	792	0

When the cereal was cut so as to leave a tall bble, slightly larger numbers of specimens ained in the field than when cutting was ied out closer to the ground. However, the ing level did not greatly affect the abundance, e at this time there were only a few immature es still in the cereal.

he species survived to the following year in ds of cereal stubble undersown with ley, as as in leys which were not ploughed. In the on of investigation, about half the cereal ds were tilled, and in such fields the immature es, and evidently also some of the adults, buried in the soil. When the field was tilled he spring, the number of adults emerging he surface was evidently related to the depth which they had been buried, fewer escaping n greater depths than from shallow depths ble 54). Usually, however, the fields were ughed in the autumn, and in such fields arently even fewer adults succeeded in emerg to the surface than those which were not ied in the plough layer until the spring. The ds of cereals and herbage plants growing ely and abundantly in the region provided d sites for the reproduction of *A. atomus.* system of crop rotation, in which leys were blished under cereals and were maintained several years, further promoted the population increase of the species. Man thus affected abundance of *A. atomus* in many ways, both ctly and indirectly, usually tending to increase density but sometimes reducing it.

A place in which to live. There were numerous fields suitable for the species. They were small, usually only about 1 hectare in size, but were situated close to one another, and so could obviously easily be reached. The leafhopper eggs were generally laid in the leaves in the lower parts of the cereal stands, and only a small proportion of these eggs were destroyed as a result of drought or other causes, so that the eggs parasitized by *A. atomus* usually produced an adult parasite. From the latter part of July, *A. atomus* was also to be found in eggs in the stems, and most of the adult parasites arising from these eggs emerged into the stem cavity, from which some failed to escape. Morcos (1953, p. 414) observed the same kind of phenomenon when *A. atomus* attempted to make its way out of the eggs of *Ditropis pteridis* (Spinola) which

Table 56. Abundance of *A. atomus* in spring wheat in different years. Every year 100 plants from each field were examined during the period Aug. 1—Sept. 2, Numbers of fields: 18 in 1958, 17 in 1959 and 1960. and 20 in 1961—1964. Same material in Table 44

Year	Stems				Leaves			
	No. of internodes with delphacid eggs	Internodes inhabited by *A. atomus*		No. of *A. atomus*	No. of delphacid egg groups	Egg groups parasitized by *A. atomus*		No. of *A. atomus*
		No.	%			No.	%	
1958	249	3	1	31	0	0	0	0
1959	623	0	0	0	28	2	7	9
1960	204	0	0	0	0	0	0	0
1961	309	1	0	3	2	0	0	0
1962	378	3	1	19	0	0	0	0
1963	245	0	0	0	6	5	83	10
1964	531	7	1	26	17	13	76	44

were in *Pteridium aquilinum*. In the latter case, the mortality of the parasite was 77.3 %.

Fluctuations in abundance in 1958—1964. It was difficult exactly to determine the fluctuations in the abundance of the species from year to year, since the abundance varied considerably at different times of the summer (Figs. 61 and 62) and in different fields at any one time. In the material listed in Tables 55 and 56 *A. atomus* was relatively rare in 1960 and 1961, but otherwise abundant, especially in 1964. The most important factors affecting the variations in abundance appeared to be OSDV and drought. The early summer of 1958 was dry in the eastern parts of the region of investigation (cf. p. 43) and in 1959 this period was exceptionally dry throughout the whole region (cf. Tables 1 and 2). In these years the stems of cereals were late in emerging, and consequently the leafhoppers deposited a large proportion of their eggs in the leaves, with the result that there were moderate numbers of *A. atomus*. The summer of 1960 was warm and there were approximately normal amounts of *A. atomus*, although at the time of inspection of the samples the species was very scanty in cereals (cf. Fig. 61). The season of 1961 was moderately wet and few of the plants were virus-diseased. That year the leaves contained few delphacid eggs, and consequently there were small numbers of egg-parasites. In the years 1962—1964, on the contrary, virotic plants were numerous, there were many leafhopper eggs in the leaves, and consequently *A. atomus* occurred in moderate or large numbers.

D. Dicondylus lindbergi Heikinh.

Dicondylus lindbergi was described by HEIKINHEIMO (1957) from material collected in the region of investigation in 1956. HELLÉN (1953) had previously used the name *Gonatopus conjunctus* Kieff. for this species.

In the material of the present investigation, only those leafhoppers with an externally visible parasite were reckoned as parasitized by *D. lindbergi*. Consequently, some of the parasitized specimens must inevitably have been placed in the category of healthy leafhoppers.

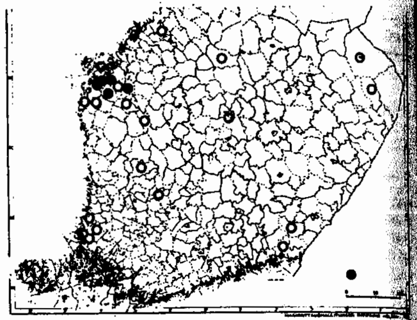


Fig. 63. Known localities of *D. lindbergi*. Solid circle = adult; open circle = larva in *J. pellucida*. The point at the lower right is Uusikirkko, now in the Soviet Union.

1. Distribution

The known occurrence of *D. lindbergi* is shown in Fig. 63. The actual distribution of the species, however, is probably much greater than that shown in the map.

2. Developmental stages

Egg. The egg of *D. lindbergi* taken from leafhopper nymphs was slightly curved (Fig. 64), 170 μ long, greyish white in colour and without sculpturing. In the ovaries the eggs were longer and narrower.

Larva. HEIKINHEIMO (1957) described the larval instars of the species, of which he observed four. However, there are apparently five instars, the first of which is inside the leafhopper nymph, the following three protrude from the host and are visible externally, while the fifth instar emerges from the host.

Cocoon and pupa. The pupa was about 3 mm long, and its length appeared to be posi-

Fig. 64. Egg of *D. lindbergi*.

Table 57. Size of *D. lindbergi* cocoon (mm) in relation to number of parasites in *J. pellucida* adult

sites	No. of cases	Outer cocoon		Inner cocoon	
		Length Mean ± S.E.	Width Mean ± S.E.	Length Mean ± S.E.	Width Mean ± S.E.
D. lind- *gi*	13	8.5±0.4	3.2±0.1	3.8±0.1	1.5±0.0
dbergi + *nuicornis*	9	7.9±0.6	3.0±0.2	3.4±0.1	1.3±0.0
D. lind- *gi*	5	6.7±0.6	2.9±0.3	3.5±0.2	1.3±0.1

correlated with the size of the cocoon. cocoon was usually symmetrically oblong, f disturbed when spinning, the larva might the outer cocoon as a kidney-shaped structure. The inner cocoon was symmetrically oblong was usually located in the centre of the outer on. The size of the cocoon seemed to be tively correlated with the number of parain the host (Table 57). If there was only one ite in the host, the cocoon appeared to be e, while if there were two or more parasites e same species in the host, it was small. In a lar way, the presence of *Elenchus tenuicornis* he same host leafhopper as *D. lindbergi* ared to cause a reduction in the size of the on of the latter.

dult. HEIKINHEIMO's (1957) original detion of the species has been supplemented AATIKAINEN (1961 a, pp. 129, 132). In the ent study it was noted that if there were two ites in one host, the larvae developed into ller adults than when only one parasite was ent.

3. Life cycle

In Finland *D. lindbergi* is univoltine. The times of occurrence of larval instars II, III and IV were determined from samples collected in the field, while those of instars I and V were established on the basis of cultures reared in the insectary. These periods of occurrence are depicted in Fig. 65, with the exception of the first larval instar, whose period of occurrence is so far uncertain.

Egg stage. According to HEIKINHEIMO (1957, p. 83), oviposition begins immediately after emergence of the female adults. No data are available on the duration of the egg period. *D. lindbergi* hibernates either as a first larval instar or as an egg in the abdomen of the leafhopper nymph.

Larval and pupal stages. The second larval instar generally began to protrude from its host in June, but in 1960 the first parasites were seen as early as the end of May. In most cases the larvae did not become visible until their host, *J. pellucida*, was in the adult stage,

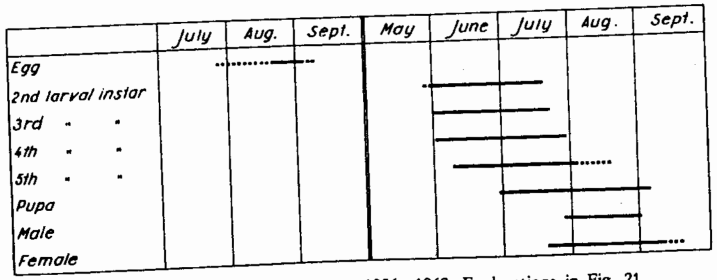


Fig. 65. Life cycle of *D. lindbergi* in 1956—1962. Explanations in Fig. 21.

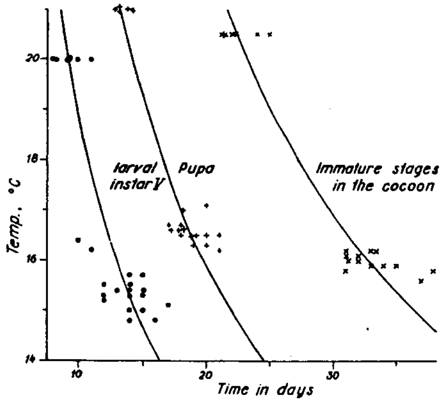


Fig. 66. Relationship between temperature and the speed of development of some *D. lindbergi* stages in the insectary.

but in about 5 % of the cases this occurred when the host was still a nymph. In leafhopper nymphs larval instars II—V became visible about one week earlier than in leafhopper adults. The same kind of phenomenon was also observed in the case of the related species *Dicondylus helleni* Raat. (Raatikainen 1961 a). In specimens parasitized by both *Elenchus tenuicornis* and *D. lindbergi*, or by two parasites of *D. lindbergi*, the parasite appeared about one week later than in adult specimens containing only one larva of *D. lindbergi*.

During emergence of larval instar V, it was generally the central portion of the larva that first became visible, followed by the head and finally by the posterior end. Emergence was most active around mid-day. The host was often still alive when the larva came into view, but died before it had completely emerged. Prior to dying, the leafhopper attached itself to the plant, where it remained after the parasite had left it. In tests carried out in the insectary at 21 °C the average walking speed of fifth-instar larvae (n = 5) was 2.8 ± 0.2 mm/min. The time between emergence from the host and beginning of cocoon-spinning averaged 16 min. 40 sec. ± 2 min. 30 sec. (n = 9). In the trials the larvae moved for an average distance of 5 cm before beginning to spin their cocoons. In the field, they evidently did not travel for such long distances.

In experiments conducted in large cages in the field, 54 % of the 137 cocoons examined were located on the lower surface of the leaves and 31 % on the upper surface. The remaining 15 % were on vertical surfaces in the leaf sheath or on the stem. The cocoons were often located on the basal part of the leaf blade and parallel to the direction of the blade. Observations were made on the spinning of the outer cocoon in the insectary. It was found that on average the larvae (n = 8) first spun one end for 11 minutes, turned 180° and spun the other end for 18 minutes. Then they returned to their original position, spinning for 24 minutes, and again turned to spin the second end for 17 minutes; and so the process continued. The outer cocoon was completed within about 12 hours, after which the larva spun the inner cocoon in about three days. The exact time required for spinning the inner cocoon was difficult to determine, since the spinning movements gradually decreased in frequency and finally the larva remained motionless for several days. It then pupated, with its head end upward in 68 % of the 79 pupae examined. The developmental period of the fifth-instar larva is described by the equation t (T—6.2) = 127, the developmental period of the pupa by the equation t (T—5.8) = 202, and the duration of the period spent within the cocoon by the equation t (T—6.2) = 321 (Fig. 66). At the time of cocoon-spinning around the end of June and beginning of July the cereal stands were short and the cocoons were located very low in the stands of full-grown oats (Table 58). The cocoons

usually in cereals, but they were also found
ther plants as well, for example, in the leaf
e and petioles of *Stellaria media*.

dult stage. When larvae emerged from
hopper nymphs, they subsequently reached
adult stage about one week earlier than
e which had come out of adult leafhoppers.
vae emerging from male and female leafpers reached the adult stage at he same time,
adults developing from leafhoppers parased simultaneously by *Elenchus tenuicornis* and
lindbergi appeared about a week later than
e which developed from adult leafhoppers
aining only one *D. lindbergi* parasite. The
od of adult emergence was thus very long
obviously not the same in different crops.
he leys, where almost all the nymphs with
ble *D. lindbergi* larvae remained, the adult
sites appeared somewhat earlier than in the
al fields. Furthermore, brachypterous *J. pellus-*
remained in the leys, and their progeny
rged earlier than those of the macropters in
cereals. Thus the developmental rhythm of
parasite and its host coincided well in the
rent fields.

warm summers the females emerged from
cocoons in late July or early August, while
ool summers they did so about a month
Only five males were observed, and they
ared at the same time as the females.
rgence was most active early in the morning
ble 59). No accurate information is available
the longevity of the females, but in the
ctary they lived for over 1½ months.

4. *Habitats and migration*

abitats. The density of *D. lindbergi* was
est in the same habitats as *J. pellucida*. In spring the larvae were most numerous in leys established under cereals, while after the migration of *J. pellucida* they were most abundant in spring cereal fields.

Migration. Larvae of *D. lindbergi* were transported along with the nymphs and adults of their leafhopper host. The distances travelled by the nymphs, were short, however, so in these cases the parasite larvae were carried only to the edge of the field or to the adjacent field. They were carried further by brachypterous adults and for the greatest distances by macropterous adults. The periods of migration of leafhoppers para-

Table 58. Height of *D. lindbergi* cocoons in oats, 1957—196

Height above ground cm	Cocoons No.	%
60—69	1	2
50—59	1	2
40—49	2	4
30—39	8	15
20—29	4	8
10—19	22	41
0— 9	15	28
Total	53	100

e 59. Numbers of *D. lindbergi* adults emerging at ent hours of the day from cocoons in the insectary. weather was partly cloudy and the mean daily temperature varied, 17—21°C

	Hours of day 20—6	6—8	8—10	10—12	12—14	14—16	16—18	18—20	Total
	1	0	0	0	0	0	0	0	1
	38	29	14	11	11	9	3	0	115

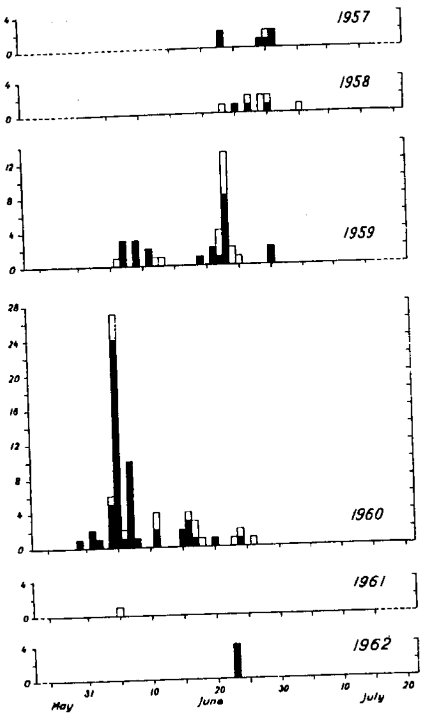


Fig. 67. Migration of *D. lindbergi*-parasitized leafhoppers in 1957—1964. The numbers of leafhoppers are shown on the left-hand ordinate. Black columns = *J. pellucida* parasitized by *D. lindbergi* alone; white columns *J. pellucida* parasitized by *D. lindbergi* + *E. tenuicornis*. Same material as in Fig. 24, where further explanations are given.

Table 60. Migration height of *J. pellucida* parasitized by *D. lindbergi* in 1958 and 1959. Same material as in Table 10

Year	Height of net m	Parasitized by *D. lindbergi*		Total	
		Alone	Together with *E. tenuicornis*	No.	% of *J. pellucida*
1958	10	0	0	0	0
»	6	2	0	2	1
»	2	2	1	3	2
1959	9	5	6	11	2.2
»	6	5	6	11	1.3
»	2	22	14	36	2.8

sitized by *D. lindbergi*, as determined from samples collected in the netting apparatuses, are shown in Fig. 67. When the samples were examined, only those leafhoppers where the parasite was seen on its surface were scored as parasitized by *D. lindbergi*, and consequently other leafhoppers as well may actually have contained a parasite which was not visible. In 1959 and 1960, when the greatest numbers of *J. pellucida* specimens were parasitized by *D. lindbergi*, half the parasitized leafhoppers had migrated by the same date as half the healthy ones. The period of migration of parasitized leafhoppers may be shorter, however, than that of healthy ones and appeared to be most intense during the middle of the migration period of *J. pellucida*. The density of migrating parasitized leafhoppers seemed to be greatest below the level of 6 metres. Parasitized specimens were collected, at a height of 9 metres, however, and apparently occurred even higher (Table 60). In neither of the two years of investigation were any statistical differences found in the migration height of parasitized and healthy *J. pellucida* leafhoppers.

In tests, the females usually moved slowly, exploring the surface, and occasionally ran at a speed of about 6—7 cm/sec. for a few decimetres. The males flew and thus were possibly able to travel further from their site of emergence than the females, which often remained in the same place for their entire life.

5. *Food supply, influence on J. pellucida and reproduction*

Host species. The female of *D. lindbergi* observes its prey by means of its visual sense, as mentioned by HEIKINHEIMO (1957, p. 83). When the point of a lead pencil was brought close to a female, it adopted a position of attack, and it did the same when shown a leafhopper nymph in a second closed Petri dish. Similarly, when the nymph of *Rhopalosiphum padi* (L.) was presented to the female at a distance of 1½ centimetres, it reacted as if it were a suitable prey, but after touching the nymph the female rejected it and in subsequent tests did not react to it. After examining the prey animal the female adopted a position of attack, but unless the prey moved the female did not attack it. When a leafhopper nymph was present, the female touched it with its antennae, and as soon as the nymph moved the female seized it. The female consumed some of the nymphs which it attacked and oviposited in others. Under experimental conditions, females captured and ate the nymphs of the following leafhopper species: *Javesella pellucida*, *J. obscurella* (Boh.), *Megadelphax sordidulus* (Stål), *Dicranotropis hamata* (Boh.), *Stiroma bicarinata* (H.-S.), and *Criomorphus albomarginatus* Curt. Females used their antennae to touch adults of *Javesella pellucida* and nymphs of *Macrosteles* sp. and *Psammotettix alienus* (Dahlb.) but did not seize them. In the laboratory the females also consumed water.

Under field conditions larvae of *D. lindbergi* were encountered only in the nymphs and adults of *J. pellucida*. Once (EP, Sulva, June 17, 1960) a 4th-instar larva, apparently of *D. lindbergi*, was found in a female of *Javesella obscurella* (Boh.), and evidently this species, too, is a host of the dryinid. In the field the adults and larvae of *D. lindbergi* feed, at least in part, on different prey animals, since the adult is more polyphagous than the larva.

Quantity of food. *D. lindbergi* females were reared for 18—38 days in rearing corks attached to oats (temp. ca. 13°C). The newly emerged female adult was placed in a rearing containing 20 *J. pellucida* of instars II to ymphs. The control corks contained the number of nymphs but no dryinid. The were opened when about half the nymphs e dryinid-containing corks had died. Subntly the dryinid was removed and placed new cork with 20 nymphs, and the control imilarly renewed. Four control corks and containing *D. lindbergi* females were used s experiment. It was found that the females d an average of at least 2.7 nymphs per day, a maximum of 3.8. Without food and water females in rearing corks attached to oats yed for 2—4 days.

fluence on J. pellucida. A leafer parasitized by *D. lindbergi* did not reach the t stage if the parasite already protruded to the ce when the host was in the nymphal stage. arasitized adult behaved differently from a hy one. For example, at the beginning of *llucida* oviposition, parasitized adults appeao be at a higher level in cereal stands than hy specimens. Furthermore, parasitized leafers died earlier than healthy ones and failed eproduce. *D. lindbergi* females killed and umed *J. pellucida* nymphs.

x ratio and copulation. In rearxperiments a total of 451 adults were ob- d from larvae of *D. lindbergi*; six of these were (1.3 %). One male under examination in nsectary copulated several times with different emales two days after emergence. Since the bers of males were extremely low, unfertilifemales probably produce female offspring, as do certain other dryinid species (cf. CLAU- 1940, p. 322). However, in certain closely ed species, such as *Dicondylus bicolor* (Hal.) *D. helleni* Raat., the sex ratio is approximately LINDBERG 1950, p. 2, STRÜBING 1956 a, p. RAATIKAINEN 1961 a, p. 135) and copulation ars to be common in these species.

ogeny number. To judge from the primordia found in the ovary, the females sit at least 30—50 eggs. The eggs were sited in the abdomen of the leafhopper ph. Generally there appeared to be only egg per nymph, but at times two or even three parasite larvae were found in one host. This phenomenon, however, was probably not polyembryony, which occurs in some other species of the family (cf. CLAUSEN 1940, p. 322).

6. *Fluctuations in abundance*

Weather factors. No data are available on the total number of eggs laid at different temperatures, but it may be greater in warm oviposition periods than in cool periods.

The larva of instar V appeared to tolerate the humidity conditions existing in the fields, and no differences in the mortality of the other instars were observed from year to year. Obviously, variations in humidity had little direct effect on the mortality of the immature stages of the species, but indirectly, through the host, drought appeared to influence the abundance of the species.

Food supply. *J. pellucida* was the main host of *D. lindbergi*; it rarely occurred in other species. Since at most only 11 % of the adults of *J. pellucida* were parasitized by *D. lindbergi*, a scarcity of host animals was never a factor limiting the absolute numbers of the parasite in any of the years studied. However, the distribution of the hosts may have meant that the female dryinid was unable to find more than a fraction of them. The proportions of *D. lindbergi* in nymphal populations of *J. pellucida* of different density are not known, but in adult populations in oat and spring wheat fields of varying leafhopper density, the proportion of parasitized insects was about the same in all the populations. There were fluctuations, however, from year to year.

In sweep-net samples taken in 1958—1964 from oats and spring wheat, *D. lindbergi* occurred more often in female than in male leafhoppers ($\chi^2 = 205.52^{***}$; Table 61). When the host and parasite are of different sexes, it is possible that they affect one another's survival in a different way than when they are of the same sex. However, no such difference was noted in the material obtained with the netting apparatuses in this investigation, and likewise there was no differ-

Table 61. Occurrence of *D. lindbergi* larvae in *J. pellucida* in material from spring cereals (cf. Tables 64 and the sex ratio of some healthy leafhoppers was not determined) and netting apparatuses (cf. Table 18) in 1958—19

	Spring cereals			Netting apparatuses		
	Total	Males		Total	Males	
		No.	%		No.	%
Healthy leafhoppers	17 082	10 388	60.8	5 738	3 207	55.9
Parasitized by *D. lindbergi*	628	202	32.2	84	49	58.3
» » *D. lindbergi* + *E. tenuicornis*	305	170	55.7	35	24	68.6

ence in either material when *D. lindbergi* and *Elenchus tenuicornis* were in the same host leafhopper. When *J. pellucida* was parasitized by *E. tenuicornis* no difference in effect was found, whether the host and parasite were of the same sex or of different sexes (Raatikainen 1966 b).

Biotic factors. The female of *D. lindbergi* evidently avoids depositing more than one egg in each host, but occasionally there were two or even three larvae of *D. lindbergi* in one *J. pellucida* specimen. In material collected with a net at the end of June and beginning of July from oats and spring wheat, 623 specimens of *J. pellucida* had one *D. lindbergi* parasite and only five had two parasites (cf. Tables 64 and 65). When there was more than one parasitic larva in the same host, the host appeared — at least in the cultures — to succumb more readily than if it contained only one parasite. In the cultures, it happened seven times that only one 5th-instar *D. lindbergi* larva emerged from an adult leafhopper containing two parasites, while only once did two larvae emerge from such a host. This experiment indicates that the host generally died as the first larva emerged, and the second larva succumbed before it succeeded in emerging from the dead host.

Singular parasitism was the most frequent form, but multiple parasitism was also common. The latter form of parasitism was investigated in two years: in 1958, when a high proportion of leafhoppers were parasitized by *Elenchus tenuicornis*, and in 1960, when a high proportion were parasitized by *D. lindbergi* (cf. Table 62). In both years there were so many specimens containing parasites of both species that the possibly greater mortality of leafhoppers parasitized by both species simultaneously could not be established.

In the leafhoppers parasitized by both *E. tenuicornis* and *D. lindbergi*, usually only one larva of the latter species was visible (304 such cases), but in one specimen taken from spring cereals two such larvae were seen (data in Tables 64 and 65). When the adult leafhopper contained one *D. lindbergi* larva and one male pupa of *E. tenuicornis*, in 24 cases (75 %) *E. tenuicornis* emerged from the host, in 3 cases (9 %) *D. lindbergi* emerged, and in 5 cases (16 %) both parasites succeeded in emerging. When the adult leafhopper contained a *D. lindbergi* larva and a female of *E. tenuicornis*, in nine cases *D. lindbergi* emerged before *E. tenuicornis* became visible, while in four cases the *E. tenuicornis* female became visible on the surface of the host before the 5th-instar larva of *D. lindbergi* emerged. Even though the female became visible, it was unable to produce offspring, since the host as well as the female itself succumbed. These trials, as well as many other observations, clearly show that the *D. lindbergi* larva usually died if the same leafhopper also contained a male *E. tenuico* reas it often stayed alive if the host contained male *E. tenuicornis*.

Table 62. Frequency of *J. pellucida* parasitized by *D. lindbergi* and *E. tenuicornis* in samples collected by net from spring cereals during the periods July 1—17, 1958 and June 14—18, 1960. At the end of the sampling periods the first final-instar larvae of *D. lindbergi* appeared

	1958		1960	
	No.	%	No.	%
Parasitized by *D. lindbergi*	57	2.5	250	6.8
» » *E. tenuicornis*	889	39.2	466	12.7
» » both species	75	3.3	49	1.3
Non-parasitized	1 250	55.0	2 908	79.2
	2 271	100.0	3 673	100.0

63. Annual abundance of *J. pellucida* parasitized by *ndbergi* according to samples taken with 3 netting ratuses. Only those leafhoppers with an externally visible parasite were reckoned as parasitized. Same material as in Fig. 24

Total no. of *J. pellucida*	Parasitized by *D. lindbergi*			
	Alone	With *E. tenuicornis*	Total	
			No.	%
691	3	6	9	1.3
2 680	22	14	36	1.3
1 177	55	14	69	5.9
152	0	1	1	0.7
135	4	0	4	3.0
106	0	0	0	0
1 778	0	0	0	0

the spring and early summer prior to the rgence of *D. lindbergi*, *Achorolophus gracilipes* rred in nymphs and adults of *J. pellucida* often killed its host. If both *A. gracilipes* *D. lindbergi* were in the same host, the latter rally died. *A. gracilipes* could possibly also sitize the larva of *D. lindbergi*, since it parasitized *Dicondylus helleni* Raat., which in turn parasitized *Megadelphax sordidulus* (Stål) (cf. Raatikainen 1961 a). Such cases, however, if they rred at all, were extremely rare.

e immature stages in *D. lindbergi* cocoons sometimes seen to be infested with parasitic menoptera, but so far these have not been rmined. In cultures reared in large cages on field in 1961, 13 cocoons out of 137 (9 %) had such parasites, with only one parasite per cocoon.

The numbers of *D. lindbergi* were influenced by many other biotic factors besides those mentioned here. Among other things, pteromalids and *Anagrus atomus* destroyed *J. pellucida* eggs, and consequently less food and fewer oviposition sites remained for *D. lindbergi* than if such Hymenoptera had not been present.

Effect of man. The population density of *D. lindbergi* was greatest on cultivated land; the species occurred sparsely in wild and half-wild areas. The effect of man on the population was generally indirect; i.e. the numbers of *J. pellucida* changed first, after which *D. lindbergi* was correspondingly changed. The harvesting of cereals had virtually no effect on the mortality, since at harvest time the population consisted of immature stages in the leafhopper nymphs and to some extent as adults. Only a few individuals were destroyed, for instance, by the wheels of the machine. In the region of investigation about half the cereal stubble area was ploughed, and about 90 % of the *J. pellucida* nymphs died during this process in the ploughed fields (Raatikainen and Tinnilä 1959 a, p. 55). *D. lindbergi* in the dead nymphs likewise succumbed. During ploughing, a few *D. lindbergi* adults were evidently also killed.

Fluctuations in abundance in 1958—1964. The density of *D. lindbergi*, as well as the proportion of *J. pellucida* parasitized by *D. lindbergi*, varied considerably during the

64. Annual abundance of *J. pellucida* parasitized by *D. lindbergi* in netting samples from oat fields. In 1959 and 200 net sweeps were made from each field; in the other years 60 sweeps. Only those leafhoppers with an externally visible parasite were counted as parasitized. Same material as in Tables 75, 82—85 and 93

Sampling period	Average sampling date	No. of samples	No. of sweeps	Total no. of *J. pellucida*	Parasitized by *D. lindbergi*						
					Alone		With *E. tenuicornis*		Total		
					No.	%	No.	%	No.	%	No. per 60 net sweeps
28. VI—10. VII	4. VII	7	420	1 256	35	2.8	36	2.9	71	5.7	10
25. VI—11. VII	3. VII	10	2 000	5 210	7	0.1	86	1.7	93	1.8	3
17. VI— 1. VII	23. VI	13	2 600	3 954	152	3.8	62	1.6	214	5.4	5
19.—30. VI	23. VI	20	1 200	684	68	9.9	8	1.2	76	11.1	4
5.— 7. VII	7. VII	20	1 200	1 800	121	6.7	12	0.7	133	7.4	7
26.—27. VI	26. VI	20	1 200	1 951	2	0.1	2	0.1	4	0.2	0
29.—30. VI	30. VI	20	1 200	1 023	1	0.1	1	0.1	2	0.2	0

Table 65. Annual abundance of *J. pellucida* parasitized by *D. lindbergi* in netting samples from spring wheat. In 19 200 net sweeps were made from each field; in the other years 60 sweeps. Only those leafhoppers with an externally visible parasite were counted as parasitized. Same material as in Tables 76, 82—84, 86 and 93

Year	Sampling period	Average sampling date	No. of samples	No. of sweeps	Total no. of *J. pellucida*	Parasitized by *D. lindbergi*						
						Alone		With *E. tenuicornis*		Total		
						No.	%	No.	%	No.	%	No. pe net swe
1958	1.—10. VII	7. VII	5	300	1 357	29	2.1	29	2.1	58	4.3	12
1960	17. VI—1. VII	27. VI	8	1 600	1 329	27	2.0	10	0.7	37	2.8	1
1961	19.—30. VI	24. VI	20	1 200	829	65	7.8	17	2.1	82	9.9	4
1962	5.— 7. VII	6. VII	20	1 200	1 616	117	7.2	40	2.5	157	9.7	8
1963	26.—27. VI	26. VI	20	1 200	1 661	1	0.1	1	0.1	2	0.1	0
1964	29.—30. VI	30. VI	20	1 200	1 420	3	0.2	1	0.1	4	0.3	0

years of these studies (Tables 63—65). In 1958 there were moderate numbers of *D. lindbergi*. The proportion of *J. pellucida* parasitized by the species gives a better picture of the actual numbers of *D. lindbergi* in 1958 than the numbers calculated per 60 net sweeps, since in that year samples were taken from fields where there were many specimens of *J. pellucida*. In the warm summers of 1959 and 1960, the proportion of parasitized leafhoppers increased. Since in these years the numbers of hosts were small, the values calculated per unit area of ground surface or per 60 sweeps did not rise so much as the relative amounts. In the summer of 1962 there were still abundant adult leafhoppers parasitized by *D. lindbergi*, but oviposition was probably poor owing to the cool, wet weather. In the following year the population density was at a minimum, and it did not even appear to rise during the following summer, i.e. 1964.

There was sufficient food in all the years, and the natural enemies of the species evidently had no important influence on the variations in abundance. In the autumn of 1959 and spring of 1960 relatively the largest areas of newly established leys were ploughed, because they had grown poorly in the dry summer of 1959. Such measures probably had a pronounced effect in reducing the absolute numbers of the species. However, the species increased substantially, showing that cultural practices in this case did not cause the previously mentioned change in abundance. The most important factor affecting the fluctuations in population evidently consisted of weather influences.

E. Elenchus tenuicornis (Kirby)

Many species and genera belonging to the family *Elenchidae* have been described. According to Bohart (1941), however, the family *Elenchidae*, as reconstituted, contains only the single genus *Elenchus*. According to Hassan (1939, p. 364), nearly all the stylopid parasites that have been bred out of delphacids belong to one species, *Elenchus tenuicornis* (Kirby). According to Lindberg (1949, p. 32), the species described from Europe actually belong to one and the same species, and Baumert (1959, p. 401) states that all the elenchids known at present belong to *E. tenuicornis*. Thus, *E. tenuicornis* has many synonyms (cf. Bohart 1941, Hofeneder and Fulmek 1942, 1943, Hofeneder 1952, Székessy 1954). If all the elenchids belong to one species, then this species has an extremely wide range and presumably consists of several races. Not all investigators agree, however, that all the elenchids should be combined into one species. For example, Bohart (cf. Hinckley 1963, p. 473) distinguished several *Elenchus* species in 1952, and according to Pierce (1961, p. 468) the family *Elenchidae* comprises at least 7 genera and over 11 species. He is of the opinion that in Europe there are two species, *Elenchus walkeri* Curtis in England and Ireland, and *E. tenuicornis* Kirby in England. The species proposed by Pierce (1961), however, are probably not species but taxa of a few or one polytypic species.

In the present studies, the leafhoppers considered to be parasitized by *E. tenuicornis* were those in which the parasite had visibly protruded the host or whose morphology had been ed so much that they were unquestionably sitized (cf. Lindberg 1949, Raatikainen b). In identifying the specimens it was not ible to dissect all the leafhoppers to verify ther they contained a parasite or not. Para- d males of *J. pellucida* were satisfactorily rmined by the method used, but some the parasitized females were unavoidably uded among the healthy leafhoppers.

1. Distribution

Baumert's (1959) opinion of the delimi- n of the species is correct, *E. tenuicornis* is opolitan. According to reports in the litera- in Europe *Elenchus* occurs at least in Ireland, land, France, Germany, Austria, Czecho- kia, Hungary, the Soviet Union (Carpa- s), Denmark, Sweden and Finland. Outside pe, the localities where it has been found de the Canary Islands, Cape Verde, Mauri- Turkistan, Japan, Queensland, the Fiji ds, Hawaii, Mexico, California, 'Dakota', and Maryland (Hofeneder and Fulmek , 1943, Hofeneder 1952, Williams 1957, essy 1959 b, 1965, Lindberg 1960, Pierce Hinckley 1963, Emmrich 1966 a). At all ts, *E. tenuicornis* evidently occurs throug- most of Europe and the islands off the hwest coast of Africa, and in this entire there is only one species. According to ent knowledge, the general distribution of species is suboceanic.

onsiderable information is available on the rrence of *E. tenuicornis* in Finland. Current prove that it is common is southern and ral Finland, but its northern boundary is rtain (Fig. 68).

2. Developmental stages

g g. According to Hassan (1939, p. 365), egg is oval in shape and its long diameter .068 mm.

a r v a. The first-instar larva is called a gulinid after the name given by Chobaut

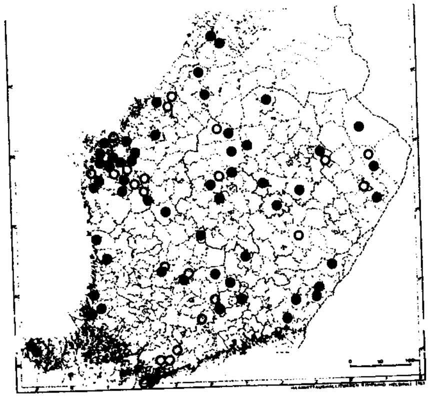


Fig. 68. Known localities of *E. tenuicornis* in Finland. Solid circle = parasite in *J. pellucida*; open circle = parasite in other delphacid.

(cf. Hassan 1939). This campodeoid type of larva has been described by several investigators (e.g. Hassan 1939, p. 366, Lindberg 1939, pp. 71—75, Baumert 1958, pp. 367—375). The other larval instars are of the apodous type. According to Baumert (1958, pp. 395—419), *E. tenuicornis* have five larval instars, while Williams (1957, pp. 82—84) gives the figure as six for *E. templetoni* Westw.

Pupa. Hassan (1939, pp. 367, 368) described the prepupa and pupa of the male, while Lindberg (1939, pp. 98—101) and Baumert (1958, pp. 420, 421) gave descriptions of the pupa. According to Williams (1957), the female of *E. templetoni* does not have a pupal stage but instead a pseudopupuparium. Lindberg (1939) stated that the female larvae of *E. tenuicornis* pupates inside its larval skin, and Baumert (1958) also mentioned that the female pupates.

Adult. In Sweden, Ahlberg (1925, pp. 81, 82) described *E. tenuicornis* parasitizing *J. pellucida* and gave it the name *Elenchinus delphacophilus* Ahlb., while in Germany Baumert (1959, pp. 343—365) gave a full description of *E. tenuicornis* which he reared from *J. pellucida* Lindberg (1939, pp. 93—96, 103—107) described *E. tenuicornis* parasitizing species of

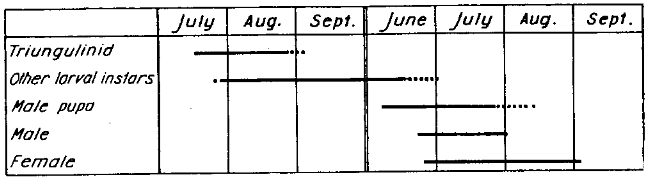


Fig. 69. Life cycle of *E. tenuicornis* in *J. pellucida* in 1956—1962. Explanations in Fig. 21.

Chloriona in Finland and mentioned it as a new species *Elenchinus chlorionae* Lindb., while Hassan (1939, pp. 369—371) presented a rather lengthy description of *E. tenuicornis* occurring in England. In the literature reviews by Hofeneder and Fulmek (1942, 1943), Hofeneder (1952) and Székessy (1959 b), information is available on other descriptions published up to 1959.

3. Life cycle

In the region of investigation *E. tenuicornis* was found to have one generation annually (Fig. 69), just as in southern Finland (cf. Lindberg 1939). In Germany it has two generations a year, the summer generation living about 3 months and the winter generation 9 months (cf. Baumert 1959, p. 380, Emmrich 1966 a). In the laboratory it is apparently possible to rear 4 generations annually of the *Elenchus* studied there (Baumert and Behrisch 1957, p. 435). In England, too, *E. tenuicornis* has two generations each year; the life-span of the first is slightly more than three months and that of the second nearly nine months (cf. Hassan 1939, p. 348).

Egg. The eggs remain within the female all the time. The period during which eggs were present was apparently at least a month, as in the case studied by Hassan (loc. cit.).

Triungulinid. In the field, triungulinids were discharged about one month after the extrusion of the cephalothorax of the female, and in the laboratory they were discharged about 2—3 weeks after copulation. The timing of the discharge was studied in the insectary during the period July 29—Aug. 14, 1959. The times of day when the discharge of triungulinids from 27 females began were as follows:

Hours	20—6	6—8	8—10	10—12	12—14	14—16	16—18	18—20
Cases	3	5	5	5	4	2	2	1

It is seen that the triungulinids generally began to be discharged in the morning and around mid-day. At first there was an abundant discharge from the female, but later it declined and finally only a few triungulinids appeared within a given unit of time. They were also discharged at night, but less profusely than in the daytime. In 21 cases examined, the period of triungulinid discharge lasted an average of 44 hours. When it began in the morning, its average duration was 40 hours (n = 14), and when it began in the afternoon it lasted 53 hours (n = 7). The duration of the discharge period was negatively correlated with the surrounding temperature (r = —0.43*). The correlation was not necessarily linear, even though it has been calculated here as if it were.

In the warm summer of 1960 the discharge of triungulinids began in mid-July, while in the summer of 1958, which was slightly cooler than average, it began in August (Table 66). During the warm season, triungulinids were produced during a period of only about two and a half weeks, while in the normal season the period lasted three and a half weeks. The triungulinids were discharged from both male and female leafhoppers at approximately the same time. The material was also grouped according to different types of parasitism (cf. Raatikainen 1966 b), but no differences in time of discharge were found between the various types.

66. Emergence of *E. tenuicornis* triungulinids in the insectary and proportions of unhatched healthy delphacid eggs in 1958—1960. The numbers of delphacid eggs were obtained from the material shown in Fig. 16

ar	No. of *E. tenuicornis* females	Triungulinid emergence			Percentage of unhatched delphacid eggs at	
		began	ended	duration days	start of emergence	end of emergence
58	29	4. VIII	27. VIII	24	79	29
59	56	26. VII	13. VIII	19	44	12
60	41	16. VII	31. VII	16	32	2

n 1960, most of the *J. pellucida* eggs had tched before the beginning of triungulinid charge, but in the cool summer only a small portion had hatched (Table 66). The develop- ntal rhythms of *J. pellucida* and *E. tenuicornis* s differed from one another in the different rs. *J. pellucida* nymphs were always present ing the time of triungulinid occurrence, but 958, the numbers present at that time amoun- to only a small proportion of the eventual al, and the nymphs available were young tars I and II), while in 1960 the proportion high and the nymphs were in more advanced ges (instars I to III).

The life-time of triungulinids was investigated open glass containers in the laboratory, using erent temperature and humidity conditions. ere were 40 specimens in each treatment, and y were examined at half-hour intervals. The rtality of the triungulinids was as follows:

Temp. °C	Approx. humidity %	50 % mortality
14	90	4 hours 30 min.
23	60	3 » 18 »
25	57	2 » 36 »

he life-time of the triungulinids was extremely ort, as had been reported by Baumert (1959, 376). According to Baumert (op. cit.), external nditions, especially air humidity, have a pro- und influence on the longevity of triungulinids, d this seems also to be valid in the region of present investigation.

The triungulinids were in movement during ost of their period of life. The average rate of ovement of one-hour-old specimens (counted m the time of discharge) on a glass surface 20°C was 0.304 ± 0.014 mm/sec. (n = 15). Thus, at temperatures of 20—23°C, the total distances travelled would be about 3—4 metres. The actual distance, however, was evidently less, since the triungulinids stopped from time to time and their speed of movement decreased as they became older. According to Baumert (1959, p. 379), the average rate of movement was approximately 70 cm per hour, which seems to agree well with that found in the present studies. Since the host leafhopper moves somewhat during the period of triungulinid discharge, the triungulinids from one female are obviously spread to one or several plants and to the ground nearly. The area of movement of a triungulinid is often restricted to a single cereal plant and the ground surface adjacent to it, evidently considerably less than one cubic metre. Similarly, Baumert (1958, p. 377) reported that the radius of action of the triungulinids was small.

When a triungulinid was confronted with a *J. pellucida* nymph, it did not always seize it. In some cases, however, it attacked the legs, abdomen or thorax of the prey, and sometimes even its head. It preferred the abdomen and penetrated into this part. Triungulinids did not attack nymphs or adults of *Macrosteles* and *Rhopalosiphum padi* (L.). In tests conducted by Lindberg (1939, p. 85) and Baumert (1958, p. 381), the triungulinids penetrated into delphacid leafhoppers but not into other species. It is apparent that even under natural conditions the triungulinids select delphacid nymphs as hosts, but they are able to parasitize a different delphacid species from the one in which they have originally grown. Under experimental conditions, many triungulinids often attacked one leafhopper (cf. Lindberg 1939, Baumert 1959,

Table 67. Emergence of *E. tenuicornis* males parasitizing *J. pellucida* in the insectary, 1959 and 1960

Host	1959				1960			
	No.	First	Half	Last	No.	First	Half	Last
Nymphs	40	27. VI	3. VII	21. VII	0	—	—	—
Adult males with one visible *Elenchus*	164	27. VI	6. VII	19. VII	84	22. VI	28. VI	5. VII
Adult females with one visible *Elenchus*	123	26. VI	6. VII	16. VII				
Adults with two visible *Elenchus*	65	30. VI	7. VII	14. VII	6	25. VI	26. VI	4. VII
Adults with both *Dicondylus* and *Elenchus* visible	10	30. VI	1. VII	8. VII	21	23. VI	29. VI	5. VII

BAUMERT-BEHRISCH 1960 b). Similarly, in the field many of them entered one host. According to BAUMERT (1958, p. 385), the triungulinids migrate within their host, and shed skins of triungulinids are to be found most abundantly in the thorax and abdomen of *J. pellucida* and least frequently in the head.

Apodous-type larval instars. The endoparasitic larval instars are usually in the abdomen of the host, but sometimes extend in part into the thorax (BAUMERT 1958). According to WILLIAMS (1957, p. 87), the feeding to *E. templetoni* is apparently by abstraction of nutrients from the blood of the host, while BAUMERT (1958, p. 393) states that the larva of *E. tenuicornis* probably obtains peroral liquid nutrition. The species hibernates as larvae of the apodous type in leafhopper nymphs both in Finland (Fig. 69) (LINDBERG 1939, p. 116) and in Germany (BAUMERT 1959, p. 380).

According to BAUMERT (1958, p. 410), the final-instar larva protrudes to the outer surface of the host. In the region of investigation, the male larvae visibly protruded in June or at the latest in early July. The females became visible slightly later, toward the end of June and in July.

Pupa. A few hours after protruding to the surface of the host, the male larva pupates, while the female pupates even earlier (BAUMERT 1958, p. 420). The pupae were within the living host and were visible on either side of the abdomen or sometimes on the ventral surface, usually between the segments. If there was only one parasite, it was generally seen between the 6th and 8th segments; but if there were two parasites, one was usually visible between the 4th and 6th and the other between the 6th and 8th segments. In exceptional cases the larva did not become visible on the surface and pupated in the interior of the host's body. According to BAUMERT (1958, p. 421), the pupal stage of the female is very short, and that of the male in the studies made by LINDBERG (1939, p. 100) lasted 6—10 days. Male pupae were encountered in June and July (Fig. 69).

In the region under investigation the females were visible only in adult leafhoppers, while some of the males could already be seen in the nymphs. Among more than 200 specimens of *Chloriona* parasitized by *E. tenuicornis*, there was only one in which the male parasite did not become visible until the host was adult (LINDBERG 1939, p. 96). When the host was *Dicranotropis hamata* (Boh.), the male *E. tenuicornis* protruded in about 8 % of the adults, for *Xanthodelphax flaveola* (Flor) the figure was 93 % and for *J. pellucida* 100 % (LINDBERG 1949, p. 27). In the region under investigation, the *E. tenuicornis* male became visible in both the nymph and the adult of *J. pellucida*. As regards the material collected from the field, however, it was not possible to determine the frequency with which the male already protruded at the nymph stage. A rough estimate of tbis is perhaps 10 %. There were differences from year to year. For instance, in the years 1957 and 1958 almost none of the males became visible until their *J. pellucida* ho

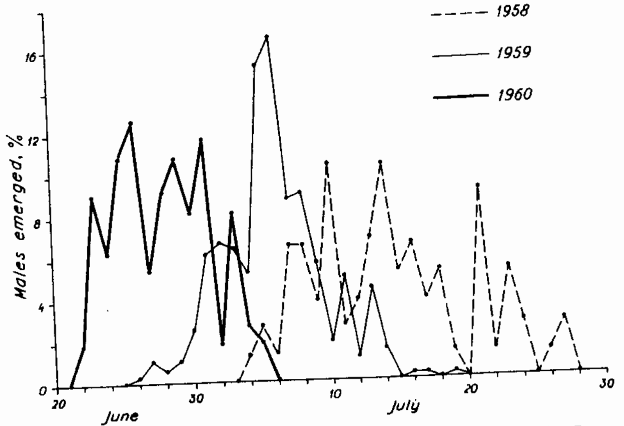


Fig. 70. Emergence of *E. tenuicornis* males per day in 1958—1960. Parasitized *J. pellucida* adults were collected from the field about a week before the emergence of the first males and reared in Petri dishes in the insectary.

in the adult stage, while in 1959 many of were already visible in the nymph.

ale. The emergence of the male of enuicornis from its pupa at different times he day was ascertained in the insectary ng the period June 27—July 8, 1959. During daytime of the above period the sky was tly cloudless or about 5—10 % covered with ds. On three days the entire sky was overcast short time. The numbers of *E. tenuicornis* s emerging from adult *J. pellucida* were as ows:

ours	4—6	6—8	8—10	10—12	12—14	14—16	16—18	18—20	20—22	22—4
mbers	2	41	71	51	53	50	37	10	2	0

ording to this test, the males did not emerge ight. When the maximum temperature was w 25°C, emergence appeared to take place nly at mid-day, but when on certain days the perature rose higher than this, emergence med to be retarded during the warm hours increased again in the afternoon when the perature dropped. The material is small, wever, and there were no statistically significant differences in it. According to HASSAN 39, p. 374), the males usually emerge early he morning, before 9 a.m.

When the pupa had protruded already in the nymph of *J. pellucida*, the males seemed to emerge slightly earlier than when the pupa had protruded in the adult (Table 67). Since nymphs parasitized by male pupae of *E. tenuicornis* remained almost without exception in perennial grass stands, such as leys and edges of fields, it is possible that *E. tenuicornis* males appeared slightly earlier in such places than in cereal fields. Males emerged simultaneously from both male and female leafhoppers adults. Similarly, emergence of males took place at about the same time in adults parasitized by one and by two *Elenchus* parasites. Furthermore, when *J. pellucida* adults were parasitized by both *Dicondylus* and *Elenchus*, the *E. tenuicornis* males emerged more or less concurrently with those from hosts containing only the one *Elenchus* parasite (Table 67).

In years when the temperature in spring and early summer was normal, emergence of males began at the end of June and beginning of July. In warm years, such as 1960, this process began as early as around June 20, while in cool summers it did not begin until the early part of July (Fig. 70). The period during which males emerged in the insectary varied from about two to four weeks.

Table 68. Longevity of *E. tenuicornis* males emerging at different times in the insectary

Emergence time	No. of males	Longevity		
		Mean	Minimum	Maximum
6—8	26	6 hrs 48 min.	3 hrs 30 min.	26 hrs
8—10	47	6 » 06 »	2 »	9 » 30 min.
10—12	30	5 » 18 »	2 »	24 »
12—14	21	5 » 18 »	2 »	19 » 30 »
14—16	19	6 » 00 »	3 »	21 »
16—18	3	10 » 30 »	1 »	15 » 30 »
18—22	2	13 » 00 »	12 »	14 »

The longevity of males in Petri dishes in the insectary was studied during the period June 27—July 8, 1959. The daily mean temperature ranged from 12 to 20°C, with a maximum of 30° and minimum of 3°. The average longevity of 148 males was found to be 6 hours 12 minutes, but it varied widely, as seen from the following figures:

Longevity, hours	1	2	3	4	5	6	7	8	9	10
No. of males	2	7	13	36	24	29	9	7	6	4

	12	14	15	16	18	20	21	24	26
No. of males	1	1	1	1	1	2	2	1	1

According to this test, as well as to the results of Hassan (1939, p. 374), Lindberg (1939, p. 115) and Baumert (1959, p. 377), males live for only a few hours. According to Baumert (1959, p. 379), the life-span of males is longer under cool than under warm conditions. He succeeded in keeping males alive for as long as three days (temp. ca. —4° — +2°C). In the region under investigation, males which emerged on cool mornings (max. temp. 18°C) lived for about 24 hours, while those which emerged on hot mornings (max. temp. 30°C) lived for not more than 6 hours. The males with the longest life-span appeared to be those which emerged in the evening, while those with the shortest life-span had emerged around mid-day (Table 68). Since the life-span of the male was usually less than 24 hours, the period of emergence denotes at the same time the flight period of the males (Fig. 70). In the Petri dish cultures, the males flew during the daytime. According to investigations in England, males likewise fly during the daytime hours under natural conditions (Levis and Taylor 1965, p. 426).

Table 69. Extrusion of *E. tenuicornis* females and emergence of males in *J. pellucida* adults in the insectary, 1959. The figures are percentages

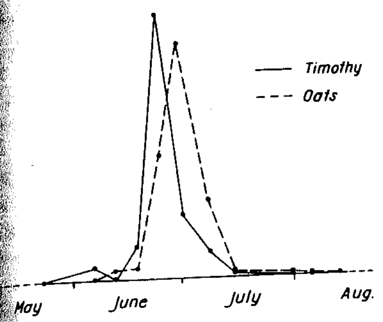
	No. of observations	20.-24. VI	25.-29. VI	30.VI 4. VII	5.-9. VII	10.-14. VII	15.-19. VII	20.-24. VII
Female extrusion	88	2	9	24	43	18	4	0
Male emergence ..	362	0	3	27	55	14	1	0

Female. The female of *E. tenuicornis* remains inside the host leafhopper during its entire life, and its cephalothorax is the only part visible on the surface of the host. In years with a warm spring and early summer, females started to become visible towards the end of June. The first females became visible just before the emergence of the males, but not all of them were visible during the flight period of the first males, as shown by the examples in Table 69. The flight period of the males in the leys was probably earlier in relation to the time of appearance of the females than was the case in spring cereals.

The male travels both by flying and by moving along the surface of the ground. After copulation, triungulinids are produced inside the female and are subsequently discharged through the opening in the cephalothorax.

4. Habitats and migration

Habitats. According to reports in the literature, *E. tenuicornis* generally appears in adows and fields on moist or wet sites. In dry ces and forests it seems to be less frequent. the region of investigation, leafhoppers parasitized by *E. tenuicornis* were found in all cereals, kinds of leys, field edges, meadows, wasteland forests. In autumn and spring its immature ges were most numerous in cereal stubble ere young ley was growing. They were also ly abundant in leys as well as to a certain ent in other stands of perennial grasses.



ig. 71. Numbers of *J. pellucida* parasitized by *E. nuicornis* in netting samples (200 sweeps each) taken a first-year timothy ley and an oat field at Laihia in 1959. Same material as in Figs. 19 and 20.

The seasonal changes in abundance of *E. tenui- nis* were investigated in the years 1958—1962 means of netting samples taken at weekly ervals in first-year timothy leys established der cereals and also in oat fields (same samples in Figs. 19 and 20). In 1959, the largest mbers of leafhoppers parasitized by *E. tenui- rnis* were found, and in both sampling series .9 % of them occurred in *J. pellucida* (Fig. 71). rasitized adult leafhoppers were most abundant timothy in the middle and latter part of the igration period of *J. pellucida* (cf. Fig. 24). ost of the parasitized hosts migrated to cereals, d consequently *E. tenuicornis* was also carried ere (Fig. 71). Some of the parasites, for example ose inside leafhopper nymphs, remained in the ys or were brought to them by migrating adult sts. However, after the migration period, there ere only low densities of *E. tenuicornis* in grass- nds; even though leys and pastures made up about 55 % of the cultivated area in this region (Official statistics of Finland III, 54), they contained fewer *E. tenuicornis* than cereals, which comprised about 35 % of the cultivated land. In other places the total numbers of *E. tenuicornis* after leafhopper migration were probably even smaller than in leys.

Table 70. Proportions of *J. pellucida* parasitized by *E. tenuicornis* in timothy leys during three consecutive periods of the summer (cf. text). Same material as in Fig.19

Period	No. of *J. pellucida*	Parasitized by *E. tenuicornis*		χ^2	
		No.	%	I	II
First	1 187	196	16.5	—	—
Second ..	2 195	1 197	54.5	458.15***	—
Third ...	995	514	51.7	302.87***	2.17

Every year the numbers of parasitized specimens of *J. pellucida* obtained by netting were divided into three approximately equally-sized groups according to their time of occurrence during the season, and the corresponding groups from each year were then combined (Tables 70 and 71). The results demonstrate that in both timothy and oats the proportion of leafhoppers parasitized by *Elenchus* was smallest at the time when the adult leafhoppers first appeared and increased throughout the summer. Since fewer leafhoppers apparently moved to spring wheat than to oats at the beginning of *J. pellucida* migration and since there were larger numbers of parasitized leafhoppers towards the end of migration than at the beginning, the proportion of parasitized leafhoppers was usually greater in spring wheat than in oats (cf. Tables 75 and 76).

Table 71. Proportions of *J. pellucida* parasitized by *E. tenuicornis* in oats during three consecutive periods of the summer (cf. text). Same material as in Fig. 20

Period	No. of *J. pellucida*	Parasitized by *E. tenuicornis*		χ^2	
		No.	%	I	II
First	1 972	131	6.6	—	—
Second ..	1 805	634	35.1	471.50***	—
Third ...	2 551	1 246	48.8	933.53***	80.52***

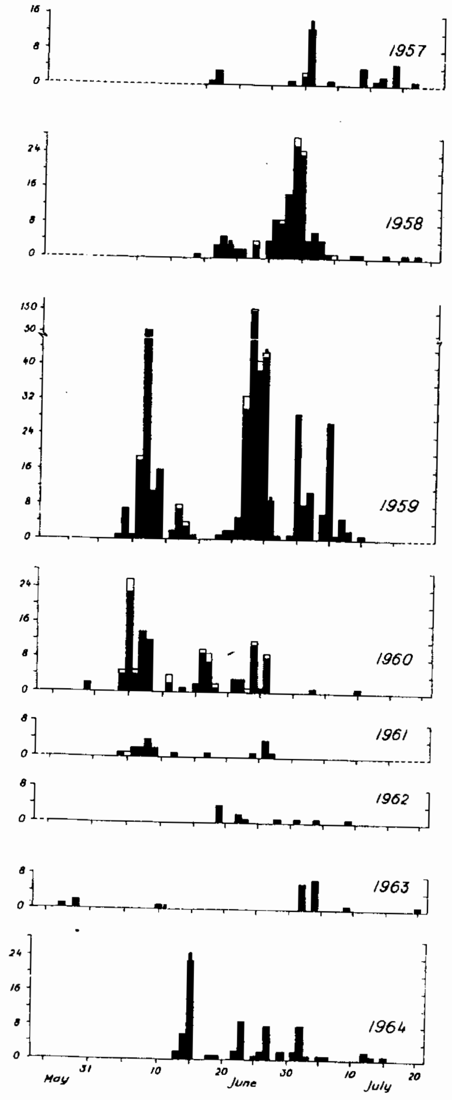


Fig. 72. Migration of *E. tenuicornis*-parasitized leafhoppers in 1957—1964. The numbers of leafhoppers are shown on the left-hand ordinate. Black column = *J. pellucida* parasitized by *E. tenuicornis* alone; white column = *J. pellucida* parasitized by *E. tenuicornis* + *D. lindbergi*; narrow black column = other leafhoppers parasitized by *E. tenuicornis*. Same material as in Fig. 24, where further explanations are given.

Movement. The movement of triungulinids has already been discussed earlier. The other larval instars do not move outside their host. The adult female remains throughout its entire life within the host. The males move either by flying or by walking along the surface. The average speed of movement of males at 20°C along a glass surface was 4.1 ± 0.08 mm/sec. ($n = 6$). The flights covered at least 5 metres, and under experimental conditions, males flew a number of times during their life-time.

Transport with host. After *E. tenuicornis* became visible in the host nymph, the host evidently rarely moved to another field. However, since the *Elenchus* parasites which became visible in nymphs were always males, it is evident that a larger number of males remained in the overwintering sites than females.

According to Lindberg (1939, pp. 140, 141, 1949, pp. 34, 35, 1960, p. 5), *Elenchus* causes brachyptery in certain delphacids but presumably not in all species. It may produce brachyptery in *J. pellucida* (Lindberg 1949, p. 35), but this was not found in the region under investigation. Brachypterous leafhoppers travelled for considerably shorter distances than macropterous individuals, but because at the most only small numbers of brachypters were caused by *E. tenuicornis*, the parasite did not appreciably decrease its own chances of dispersal by its host. Parasitized brachypterous leafhoppers appeared to travel only to the adjacent fields, just as did the unparasitized brachypters. But the material studied was small, so that a reliable comparison could not be made.

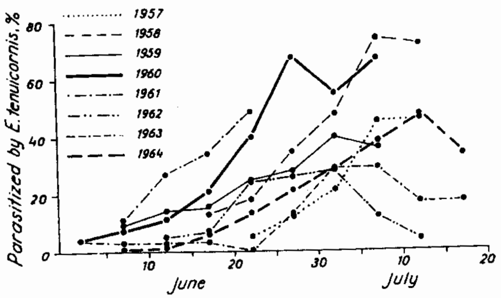


Fig. 73. Percentages of migrating *J. pellucida* parasitized by *E. tenuicornis* according to material collected with netting apparatuses in 1957—1964. The material from each year was grouped into 5-day periods. The curves are 3-point moving averages. Same material as in Fig. 24.

E. tenuicornis was transported for the longest distances by macropterous hosts. Fig. 72 shows the migration periods of macropterous delphacids parasitized by *Elenchus*. The material consisted of 932 *J. pellucida* specimens (99.1 %) and 8 of *J. obscurella* (Boh.) (0.9 %) which were parasitized by *Elenchus*. The species was not observed in other leafhoppers. According to the samples obtained with the netting apparatuses, *J. pellucida* was definitely the most important means of dispersal of *E. tenuicornis*, and the great majority of *Elenchus* occurring on cultivated land re carried from field to field by macropterous *pellucida*. The parasite was obviously some- es carried for distances of several kilometres the host.

n the years 1958—1964 the first leafhoppers asitized by *E. tenuicornis*, all of which were *pellucida*, migrated on June 7 on the average, ich was 5 days later than the leafhoppers sidered to be healthy. The proportion of asitized *J. pellucida* increased during the sum- r in all years, although at the end of the mig- on period there was occasionally a small line (Fig. 73). The dates by which the netting paratuses had collected half of the *J. pellucida* ecimens parasitized by *Elenchus* alone as well half the healthy specimens were as follows:

Year	Parasitized	Healthy	Differences, days
58	29. VI	19. VI	10
59	23. VI	22. VI	1
60	8. VI	5. VI	3
61	9. VI	7. VI	2
62	22. VI	22. VI	0
63	2. VII	10. VI	22
64	23. VI	15. VI	8

ccording to these data, *J. pellucida* parasitized *Elenchus* migrated an average of 7 days later an specimens which were apparently non-parasitized.

The height of migration of *J. pellucida* parasitized by *E. tenuicornis* was studied in 1958 and 1959. The results, presented in Table 72, show that the density of the parasitized *J. pellucida* was greatest below 6 metres, although it was considerable even at 10 metres. The height of migration of healthy *J. pellucida* was compared with that of specimens parasitized by *Elenchus* alone. In this comparison, only male specimens considered to be healthy were used, since among apparently healthy females there may have been parasitized individuals. According to Tables 10 and 72, it is seen that in 1959 the height of migration of parasitized leafhoppers was significantly greater than that of healthy specimens ($\chi^2 = 7.20^*$, d.f. = 2), and that in 1958, too, the parasitized leafhoppers appeared to migrate at higher levels than the healthy ones, but this time the difference was not statistically significant

Table 72. Migration height of *J. pellucida* parasitized by *E. tenuicornis* in 1958 and 1959. Same material as in Table 10

Year	Height of net, m	Parasitized by *E. tennicornis*			
		Alone	With *D. lindbergi*	Total No.	Total % of *J. pellucida*
1958	10	32	0	32	33
»	6	60	0	60	25
»	2	43	1	44	28
1959	9	94	6	100	20
»	6	194	6	200	23
»	2	225	14	239	19

($\chi^2 = 2.73$, d.f. = 2). These results, as well as the data in Table 72 on the proportion of parasitized individuals among all the specimens, demonstrate that at all the heights studied the proportion of leafhoppers parasitized by *E. tenuicornis* was about the same, or slightly greater at the higher than at the lower levels. Thus the parasite is evidently capable of being easily transported to new sites by its host.

5. *Hosts and influence on J. pellucida*

Host species. If *E. tenuicornis* is delimited in the way proposed by BAUMERT (1959), the species has thus far been found to parasitize about 55 leafhopper species, (cf. HOFENEDER and FULMEK 1942, 1943, HOFENEDER 1952, WILLIAMS 1957, SZÉKESSY 1959 b, 1965, LINDBERG 1960, RAATIKAINEN 1960 a, PIERCE 1961, HINCKLEY 1963). The hosts belong to the family *Delphacidae* with the exception of *Platybrachus* which is a member of the family *Issidae* (cf. PIERCE 1961). Even in Europe, *E. tenuicornis* is known to parasitize scores of delphacid species, and in Finland it is a parasite of at least 16 leafhopper species, when the host *Javesella obscurella* (Boh.), not previously recorded, is included (cf. LINDBERG 1939, 1943, 1949, KONTKANEN 1950 b, RAATIKAINEN 1960 a).

In cultivated fields in the region of investigation *E. tenuicornis* was encountered in the leafhopper species *J. pellucida*, *J. obscurella* (Boh.), *Stiroma bicarinata* (H.-S.), *Megadelphax sordidulus* (Stål), *Xanthodelphax flaveolus* (Flor) and *Dicranotropis hamata* (Boh.). Usually it occurred in *J. pellucida*, but a few percent of the individuals were in other species (cf. Tables 75, 76). It was shown experimentally that a triungulinid which had come out of a parasitized *S. bicarinata* specimen was able to grow to the adult stage in *J. pellucida*. Similarly, in England (HASSAN 1939) and Germany (BAUMERT 1959) *E. tenuicornis* has been transferred from one host species to another, and individuals from different hosts have been found to copulate with one another.

Influence on J. pellucida. Many studies have been made on the effect of *E. tenuicornis* on its host. The species causes changes the host, which are morphological (e.g. HAU 1935, p. 140, HASSAN 1939, LINDBERG 1949 ULRICH 1956, BAUMERT-BEHRISCH 1960 a and RAATIKAINEN 1966 b), anatomical (e.g. BAUMERT-BEHRISCH 1960 a and b) and ethological (e.g. HEIKINHEIMO and RAATIKAINEN 1962, p. 16). In addition, the development of the parasitized leafhopper is retarded (BAUMERT-BEHRISCH 1960 a). In the region under investigation, parasitized specimens of *J. pellucida* emerged (cf. Table 70), migrated (cf. Fig. 73) and appeared in spring cereals (Table 71) slightly later than healthy leafhoppers. The level of migration of parasitized *J. pellucida* may have been slightly higher than that of non-parasitized specimens, as previously discussed. At the time of leafhopper oviposition, parasitized individuals appeared, on average, higher in the spring cereal stand than healthy specimens, as has been demonstrated by HEIKINHEIMO and RAATIKAINEN (loc. cit.). Furthermore, parasitized leafhoppers were incapable of reproduction.

After the emergence of a male *Elenchus*, the host continued to survive for a short while, but soon a fungal mycelium grew on the exposed part of the pupa inside the host; owing possibly partly to harmful fungi and micro-organisms and partly to other causes, the leafhopper died after a few days. If a male *Elenchus* became visible in the nymphs of a leafhopper, the host lived for a much shorter time than a healthy leafhopper. Even if the male did not become visible until the host had become adult, the life-time of the host was shorter than that of a non-parasitized leafhopper.

Leafhoppers parasitized by female *Elenchus* lived longer than those which were parasitized by males. However, the mortality of female-parasitized leafhoppers increased greatly after the discharge of triungulinids. The mortality of adult *J. pellucida* after the beginning of discharge of triungulinids in the experiments was as follows:

Days after discharge	1	2	3	4	5	6	7	8	9	10	11
No. of adults died	0	5	3	5	2	1	1	1	1	0	1

nder natural conditions the life-span of leafpers parasitized by *Elenchus* females was prob- longer than in the trials (mean life-span days).

6. *Reproduction*

ex ratio. In the material of HASSAN (1939, 376, 378) and LINDBERG (1939, pp. 95, 101), sex ratio of *Elenchus* was about 1:1 or slightly e-dominated. In the studies of BAUMERT 59, p. 392), the ratio of males to females in interior of the host was approximately 5:4, le the ratio of males to females among the asites visible on the surface of the host was ut 7:1.

he sex ratio in the field was difficult to dete e in the present investigation, since some of males emerged before the protrusion of ales, and by the time all the protruded ales had become visible, some of the maleasitized leafhoppers had already died. In 1959, ing the period July 1—8, which was the time most active emergence of *Elenchus* males (cf. ble 69), specimens of *J. pellucida* parasitized by nchus were collected by net in spring cereals. ere were 858 specimens in which a male nchus was visible and 144 with a visible ale, i.e. a percentage of 86 % in favour of males. The corresponding numbers of speciens taken at the same time in timothy were 319 les (95 %) and 18 females. It is obvious that sex ratio during this year, as well as in many her years, was male-dominated. In the cultures reared in the insectary, there were even higher proportions of males, since more female-parasitized leafhoppers died than male-parasitized ones prior to the protrusion of the parasites.

Copulation. The male is capable of copulation immediately after emergence. In Petri dishes the male copulated several times either with the same female or with various females. The male was able to fertilize at least two different females. BAUMERT (1959, p. 375) also found that males fertilized several females. The species did not reproduce parthenogenetically.

Progeny number. The number of triungulinids was determined in the following way. Before emergence of the triungulinids the parasitized leafhopper and a piece of living oat leaf were placed in a glass tube 1½ cm in diameter, which was closed with a rubber stopper. After the triungulinids had been discharged, the leafhopper in all cases lived for a few days longer. The triungulinids died in the tube and usually remained attached to the walls of the tube, where they could easily be counted under a microscope.

According to BAUMERT (1958, p. 381), triungulinids penetrate into the original host leafhopper. In the present studies the numbers of triungulinids that penetrated into the hosts were not ascertained, so that the figures obtained were evidently slightly smaller than the actual numbers. However, the number of emerging triungulinids found in these studies, averaging 1620 ± 110.5 per female, was higher than those reported by HASSAN (1939), LINDBERG (1939) and BAUMERT (1959) (Table 73). The numbers

Table 73. Number of progeny of *E. tenuicornis* according to studies made in Europe.
E = identified from egg, L = identified from triungulinid

Host	No. of females	Stage	Progeny number			Investigator
			Mean	Min.	Max.	
loriona	5	L	1 360	1 200	1 500	LINDBERG 1939
nomelus anceps (Germar)	4	E	1 465	1 450	1 480	HASSAN 1939
icranotropis hamata (Boh.) .	1	E	1 480			HASSAN 1939
iomorphus williamsi China	3	E	1 480	1 480	1 480	HASSAN 1939
esella pellucida	1	E	1 493			HASSAN 1939
» »	1	L	965			BAUMERT 1959
» »	10	L	1 620	1 095	2 165	Present study
roma bicarinata (H.-S.) ..	2	L	2 058	1 899	2 217	» »

of emerging triungulinids found by LINDBERG (1939) were likewise smaller than the actual numbers, since some specimens were overlooked. The number of triungulinids per female in his study was evidently about 1 500 or slightly less. So far, only a few determinations have been made on the number of progeny of *E. tenuicornis*. The results obtained, however, suggest that there are differences in this number in different regions and also in different hosts.

7. *Fluctuations in abundance*

Weather factors. Triungulinids readily succumbed when the air humidity decreased. In the dry summer of 1959 the humidity was so low that many more triungulinids must have died in the field than in other summers. In this same year the drought also appeared indirectly to affect the mortality of *E. tenuicornis* females. Some crops, for instance leys, suffered from the drought before the emergence of triungulinids, and some of the parasitized leafhoppers in them died indirectly — and probably also directly — as a result of the drought. That summer, parasitized leafhoppers survived best in patches of *Elytrigia repens* in the fields, since such patches remained alive even during dry periods.

The temperature apparently caused the life cycles of *E. tenuicornis* and *J. pellucida* to differ from one another. After the dry early summer of 1959, most of the male pupae already became visible in nymph hosts, while in the cool years of 1957 and 1958 they did not appear until their host had reached the adult stage. When they became visible in nymphs, they remained in stands of perennial plants, where the density of *Elenchus* females was small. Every year, leafhoppers parasitized by females migrated principally to cereals, where in 1959 the proportion of *Elenchus* males was evidently smaller than usual. However, this cannot have greatly affected the fertilization of the females, since males can successfully copulate with many females.

Food supply. If the parasitic larva did not find a delphacid nymph within a few hours, it died. Even if it did find a nymph, it did not always attack it. Every year, the bulk of the larvae obviously died before they were able to locate a leafhopper nymph. Evidently a scarcity of hosts was a very important factor limiting the abundance of the parasite.

In some years many of the *J. pellucida* leafhoppers had not yet reached the nymphal stage before the time when the triungulinids appeared, while in other years nearly all of them had attained the nymphal stage (Table 66). This factor probably had an influence on the abundance of *Elenchus*.

Biotic factors. It often happens that several triungulinids penetrate into the same leafhopper nymph. Under experimental conditions, *Chloriona* and *J. pellucida* have been found to be parasitized by as many as 34 triungulinids (LINDBERG 1939, p. 84, BAUMERT 1958, p. 385). According to LINDBERG (1939, p. 83), among nymphs of *Chloriona unicolor* (H.-S.) collected from the field, 83.5 % contained one triungulinid, 11 % contained two, 4.5 % three and 1 % four. There was seldom more than one pupa, however, so that evidently leafhoppers parasitized by several *Elenchus* died at an early stage of development.

The numbers of *J. pellucida* containing visible *E. tenuicornis* parasites according to netting samples taken in oats and spring wheat (same material as in Tables 75 and 76) were as follows:

Period	Numbers of *Elenchus* per host		
	1	2	3
1958, 28. VI—10. VII	468	31	2
1959, 25. VI—15. VII	1 093	136	6
1960, 17. VI— 1. VII	198	10	—

Once an adult *J. pellucida* containing 5 visible *E. tenuicornis* parasites was found in a timothy ley.

In all the years the proportion of leafhoppers parasitized by more than one *Elenchus* was considerable, and there were differences from year to year. In 1958 7 % of the *J. pellucida* specimens parasitized by *Elenchus* contained more than one parasite, while in 1959 the figure was 11 % and in 1960 5 %. The material from 1959 differed statistically from that of both 1958 and

(χ² = 8.95** and 7.75**). These differences be partially explained by the fact that the ples were taken at different phenological s, but another reason was probably that proportion of *J. pellucida* leafhoppers that parasitized by *Elenchus* was positively cor-ed with the percentage of specimens para-d by more than one *Elenchus*.

cultures, leafhoppers parasitized by more one *Elenchus* appeared to succumb more ily than those containing only one parasite. *J. pellucida* parasitized by several *Elenchus* s, often only one male—or sometimes two—eeded in emerging, and the rest died. If the leafhopper contained both a female and a *Elenchus*, the male usually emerged and the died shortly afterwards, the female succumb-n the host. If there were several *Elenchus* in same host, some of them became visible r the wings. If such parasites were females, could not copulate.

equently both *E. tenuicornis* and *Dicondylus rgi* were present in the same *J. pellucida* imen. Usually in a leafhopper parasitized *Dicondylus* only one *Elenchus* was visible, but e collection from spring wheat, 9 out of pecimens parasitized by both *Dicondylus* and *chus* had two male *Elenchus* visible. As pre-sly discussed in the chapter on *Dicondylus*, ome cases *Elenchus* died and only *Dicondylus* ived. In some instances both parasites died. largest numbers of *J. pellucida* parasitized oth species occurred in the years 1958—1962 the smallest numbers in 1963 and 1964 bles 64 and 65).

the cultures the wings of an *Elenchus* male sometimes attached to one another, so that male was unable to go in search of a female. ften occurred that the movements of the hopper host of the female parasite prevented ulation between the latter and a male. LIND-G (1939, p. 109) and BAUMERT (1959, p. 376) e also observed this phenomenon. Usually male remained close to the leafhopper with female parasite and at a later attempt copu-on finally succeeded. At times, however, the abandoned any further attempt and moved away. BAUMERT (1959, p. 377) found experimentally that about two-fifths of the males copulated with females in macropterous *J. pellucida* and half copulated with females in brachypterous leafhoppers.

A few percent of the *Elenchus* females collected on the field after the flight period of *Elenchus* males contained eggs which did not develop. There may be several reasons for this. According to BAUMERT (1959, p. 376), the female occasionally remains unfertilized even though it has copulated several times with males. Some of the females appeared so late that only a few males were any longer present, and these remaining males did not always succeed in locating the females (cf. Table 69). A further reason may be that the female was too old, for in that case the male no longer copulates with it, as was assumed by PERKINS (1918, p. 129) in the case of *Stylops* females.

Occasionally *Elenchus* did not visibly protrude at all from the leafhopper but died inside its host. Such cases are not rare, according to BAUMERT (1958, p. 410).

Effect of man. The direct effect of cultural practices on *E. tenuicornis* was small. However, in 1959 in the region under investigation and in the surrounding areas, various insecticides against *Rhopalosiphum padi* (L.) were used on about 20 % of the area devoted to oats, 15 % of the barley area and 5 % of spring wheat (RAATIKAINEN and TINNILÄ 1961, p. 16). The insecticides were applied during the flight period of *Elenchus* males, and they killed both *J. pellucida* and probably also *Elenchus* males. In other years, virtually no insecticides were used.

Indirectly, man has had a considerable influence on the abundance of *Elenchus*. The main host of the species, *J. pellucida*, as well as many other hosts, have become more numerous since land has been taken into use, especially for cultivation, and the parasite has likewise become more abundant. Every year, ploughing of fields and burning of stubble in the region are estimated to have destroyed from one-fourth to a half of the nymphs in cereals, and *Elenchus* was naturally killed at the same time (cf. Fig. 76).

Table 74. Annual abundance of delphacids parasitized by *E. tenuicornis* according to samples taken with 3 netting apparatuses. Same material as in Fig. 24

Year	Total no. of *J. pellucida*	No. of *J. pellucida* parasitized by *E. tenuicornis*				No. of *J. obscurella* parasitized by *E. tenuicornis*
		Alone	With *D. lindbergi*	Total		
				No.	%	
1958	691	125	6	131	19	1
1959	2 680	505	14	519	19	2
1960	1 177	109	14	123	10	0
1961	152	19	1	20	13	0
1962	135	11	0	11	8	0
1963	106	19	0	19	18	1
1964	1 778	74	0	74	4	2

Fluctuations in abundance in 1958—1964. The variations in abundance of *E. tenuicornis* from year to year were studied with the same material as had been used for *Dicondylus lindbergi* (Tables 74—76). Similarly in this material, the proportion of parasitized *J. pellucida* out of the total gives a better indication of the numbers of *E. tenuicornis* in 1958 than the numbers calculated per 60 net sweeps. After the warm dry summer of 1959, the numbers per unit surface area, per 60 sweeps and the proportion of parasitized *J. pellucida* specimens dropped sharply, and the decrease continued even the following summer. Thereafter came a slight increase, and finally after the summer of 1962 another decline occurred. The fluctuations in *E. tenuicornis* were thus different from those of *Dicondylus lindbergi* (cf. Tables 63—65).

Biotic factors apparently had only a negligible effect on the fluctuatious in abundance. In the years 1958 and 1959, when there were many leafhoppers parasitized by more than one *Elenchus*, it is probable that a higher percentage of the hosts died before the emergence of the parasites than in other years, when the proportion of parasitized specimens was small. This, however, can only have depressed the numbers of parasitized leafhoppers by a small amount. *Dicondylus lindbergi* was most abundant during the period when the numbers of *Elenchus* decreased for the first time. The former species likewise could not have had much influence, since there were few leafhoppers parasitized by it (cf. Tables 63—65). Other biotic factors were observed to have an even smaller effect on the fluctuations in *Elenchus* abundance than the above-described factors.

The total numbers of host animals declined in the summer of 1959, and this evidently had some influence on the decrease in *Elenchus*. The absolute supply of food, however, was not such a strong limiting factor as the relative amount. Even the effect of food scarcity was apparently not a main factor in depressing the abundance of the species, but rather a side factor.

Insecticides were used mostly in 1959, and they obviously destroyed some of the leafhoppers parasitized by *Elenchus*, as well as some of the *Elenchus* males and also healthy delphacids, whose progeny might have been used as hosts by the triungulinids. In the autumn of 1959 and spring of 1960 considerable areas of newly established leys were ploughed, and these leys contained

Table 75. Annual abundance of delphacids parasitized by *E. tenuicornis* in netting samples from oat fields. In 1959 and 1960, 200 net sweeps in each field, in the other years 60 sweeps. Same material as in Table 64

Year	No. of samples	*J. pellucida*								No. of other hosts parasitized by *E. tenuicornis*		
		Total no.	Parasitized by *E. tenuicornis*									
			Alone		With *D. lindbergi*		Total					
			No.	%	No.	%	No.	%	No. per 60 net sweeps	*J. obscurella*	*M. sordidulus*	*S. bicarinata*
1958	7	1 256	516	41.1	36	2.9	552	43.9	79	1	—	—
1959	10	5 210	2 614	50.2	86	1.7	2 700	51.8	81	1	—	1
1960	13	3 954	517	13.1	62	1.6	579	14.6	13	1	1	—
1961	20	684	48	7.0	8	1.2	56	8.2	3	—	—	—
1962	20	1 800	389	21.6	12	0.7	401	22.3	20	—	—	—
1963	20	1 951	310	15.9	2	0.1	312	16.0	16	—	—	—
1964	20	1 023	77	7.5	1	0.1	78	7.6	4	—	—	—

76. Annual abundance of *J. pellucida* parasitized by *E. tenuicornis* in netting samples from spring wheat. 960, 200 net sweeps were made in each field, in the other years 60 sweeps. Same material as in Table 65

Year	No. of samples	*J. pellucida*								No. of other host parasitized by *E. tenuicornis*		
		Total no.	Parasitized by *E. tenuicornis*									
			Alone		With *D. lindbergi*		Total					
			No.	%	No.	%	No.	%	No. per 60 net sweeps	*J. obscurella*	*M. sordidulus*	*S. bicarinata*
......	5	1 357	435	32.1	29	2.1	464	34.2	93	1	—	—
......	8	1 329	244	18.4	10	0.7	254	19.1	10	—	1	—
......	20	829	96	11.6	17	2.1	113	13.6	6	—	—	—
......	20	1 616	445	27.5	40	2.5	485	30.0	24	—	—	1
......	20	1 661	292	17.5	1	0.1	293	17.6	15	1	—	—
......	20	1 420	90	6.3	1	0.1	91	6.4	5	—	—	—

phacids parasitized by *Elenchus*, which were rally killed. Although cultural practices had e effect on the decrease in numbers of *chbus* occurring after the summer of 1959, e effects were nevertheless small and evily had no great influence in reducing the bers of the parasites.

he chief factor limiting numbers in *Elenchus* nsidered to have been drought. During the od of triungulinid appearance in 1959 and the weather was very dry (cf. Table 2) and ously many of the triungulinids died before had succeeded in entering a host. Furthere, some of the parasitized hosts died as a equence of the drought at the end of the mer of 1959. The decrease in abundance was hered by biotic and nutritional factors as well y man. In the summers of 1960 and 1961 e was a rise in the numbers of *E. tenuicornis*, the decrease in abundance beginning during cool summer of 1962 was further enhanced the drought occurring in 1963, and the bers of parasites reached a second minimum 964.

F. Achorolophus gracilipes (Kramer)

ccording to OUDEMANS (1912, p. 156) and/ KARPPINEN (1958, p. 43), synonyms for this ies are *Achorolophus ignotus* Oudms, *Erythraeus landicus* Trägårdh, *E. ignotus* Oudms, *E. phaoides* (de Geer) var. *gracilipes* (Kramer), *Rhyncholophus gracilipes* Kramer and *R. intermedius* Trägårdh. The Review of Applied Entomology (Vol. 53, A, p. 519) uses the name *Erythraeus gracilipes* (Kramer) for this species.

KARPPINEN (1958) identified the mite occurring in the present material as *A. gracilipes* (Kramer), and most of the specimens examined by the author were of this species. Not all the mites, however, were morphologically identical, since there were at least two different types. In the present investigation the name *A. gracilipes* is employed for the mite encountered.

1. Distribution

According to OUDEMANS (1912, p. 208) and KARPPINEN (1958), *A. gracilipes* occurs in Italy, France, Switzerland, Germany, the Netherlands, Sweden, Finland, Greenland and the USA. In Finland, leafhoppers of the genus *Javesella* infested with mites were found in all the communes where examinations were performed (cf. Fig. 74). At the end of May and beginning of June 1957, when two-thirds of the data on distribution were obtained, the frequency of mites in nymphs of *Javesella* leafhoppers inhabiting first-year leys was ascertained. A total of 4 541 nymphs were examined. The average percentage of mite-infested nymphs in the main region of investigation, in different inland areas of the country and along the south coast was 6.7 %, and the variation, ranging from 5.3 to 7.6 % was not significant.

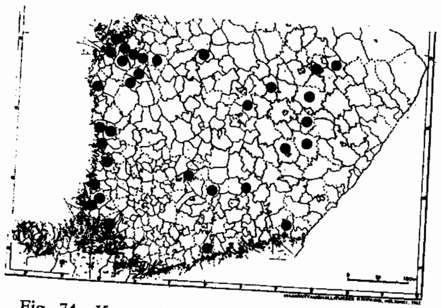


Fig. 74. Known localities of red mites in *Javesella* leafhoppers.

2. *Developmental stages and life cycle*

Apparently only the nymph of *A. gracilipes* has been described in the literature (cf. e.g. Oudemans 1912, Karppinen 1958), and in the present investigation no adults were discovered. According to Oudemans (1912, p. 208), nymphs occur from May to September. In the region of the present study, mites were found in *J. pellucida* as early as May 12 in 1959 and as late as July 11 in 1958. They appeared in leafhopper nymphs in mid-May, usually during periods of warm weather. The frequency of mite-infested leafhopper nymphs was greatest at the beginning of the season and thereafter slowly declined. At the time of emergence of *J. pellucida*, there were still moderate numbers of mites on the nymphs, and they were even found on a few adults, too. In cultures, mites remained for several days on their hosts, and in some instances for even more than 14 days.

3. *Habitats and migration*

A. gracilipes were found in leys, on the ed of fields and on waste land. During the per May 18—27, 1961, the numbers of mites leafhoppers at Laihia was studied in leys different ages. The specimens were collec with a sweep net. During this process, some the mites became detached from their hos but the numbers ultimately found can be reliab compared between the different samples and ley In each field 20 × 20 net sweeps were mad and the numbers of mite-parasitized leafhopp in the subsamples were immediately counte The results (Table 77) show that mites occurr on four species of leafhoppers and that they we least frequent in first-year leys.

The mites readily became detached from the hosts and moved among plants and on the ground for several days at least. They were no seen to attach themselves to a new host. Som of the mites were carried from place to place b their hosts, i.e. by nymphs or adults of del phacids.

4. *Hosts and influence on J. pellucida*

Hosts. According to Oudemans (1912, p. 207), *A. gracilipes* has been found in the following genera: *Phalangium* (*Phalangiidae*), *Belaustiu* (*Erythraeidae*), *Erythraeus* (*Erythraeidae*), *For cula* (*Forficulidae*), *Melanoplus* (*Acridiidae*), *Dry obius* (*Aphidae*), *Centrotus* (*Membracidae*), *Asilu* (*Asilidae*), *Haematopota* (*Tabanidae*), *Athou* (*Elateridae*), *Lagria* (*Lagriidae*), *Phyllodecta* (*Chrysomelidae*) and *Orchestes* (*Curculionidae*).

Table 77. Abundance of mite-parasitized leafhopper nymphs and numbers of mites in them in samples taken from leys of different ages. All the *Javesella* nymphs were apparently *J. pellucida*

Age of ley, years	No. of leys	*Javesella*			*Megadelphax sordidulus*			*Stiroma bicarinata*			*Doliotettix pallens*			Leafhoppers		
		Total	Parasitized by mites No.	%	Total	Parasitized by mites No.	%	Total	Parasitized by mites No.	%	Total	Parasitized by mites No.	%	Total	Parasitized by mites No.	Tota[illegible] of mi[illegible]
1	4	845	4	0.5	658	1	0.2	25	0	0	217	0	0	1 760	7	[illegible]
2	4	36	10	28	404	56	14	9	1	11	315	8	3	850	75	[illegible]
3—5	4	70	5	7	1 041	42	4.0	16	3	19	757	11	1	1 969	62	[illegible]

the region of the present investigation, the ies has been encountered on the following ies of leafhoppers: *J. pellucida*, *Stiroma bicari-* (H.-S.) (Karppinen 1958), *Megadelphax dulus* (Stål) (Raatikainen 1960 a), *Dicrano- is hamata* (Boh.) (Raatikainen and Vasa- nen 1964), *Javesella obscurella* (Boh.), *J. dubia* m) (St. Rauma commune), *Criomorphus albo- inatus* Curtis, *Doliotettix pallens* (Zett.), *Diplo- us abdominalis* (F.) and *Solenopyx sulphurellus* t.). Once it was found on a larva of *Dicon- belleni* Raat., which was parasitizing *Mega- hax sordidulus* (Raatikainen 1961 a). It is ible that the species also occurred on other ropods as well.

the region of investigation the mites were lly present on the nymphs of leafhoppers and rarely on adults. Examinations of *Javesella* phs collected in first-year leys in 1957—1964 prising nearly all the nymphs in Table 78) wed the following numbers to be infested mites:

per nymph	1	2	3	4	5
bers of nymphs	421	45	15	3	1

erally, only one mite occurred per parasitized , but in one case an adult had two mites. first-year leys the mites apparently occurred uniformly among nymphs of all delphacids. *J. pellucida* was the most abundant species, bulk of the mites were on it. There were also phs of *Doliotettix pallens* (Zett.) in first-year but a much smaller percentage were mite- sted than on *J. pellucida*. In leys more than year old, *J. pellucida* was less numerous than other delphacid species together, and in such most of the mites occurred in other species, icularly *Megadelphax sordidulus* (Stål), *Stiroma rinata* (H.-S.) and *Doliotettix pallens* (Zett.) also Table 77).

nfluence on J. pellucida. *A. gracilipes* ched itself to all parts of the body of *J. pellu-* as mentioned by Karppinen (1958). At the of May 1960 an experiment was carried out scertain the effect of mites on the mortality *J. pellucida* nymphs. Timothy and oats were ced in six plastic cylinders as food source for the leafhoppers. Nymphs of *J. pellucida* parasitized by mites were collected from the field, of which 6 were in instar IV and the rest in instar V. The nymphs were placed in cylinders, two containing 20 nymphs and a third 16. The control cylinders contained the same numbers of nymphs at the same developmental stages but not infested with mites. The experiment was examined three times, and it was found that the numbers of living *J. pellucida* after different periods of time were as follows:

Days after start	Non-parasitized	Mite-parasitized	χ^2
9	51	24	9.02**
21	37	8	17.42***
29	28	4	16.53***

This experiment demonstrates that the mortality of *J. pellucida* was greater for the parasitized specimens than for the healthy ones. The first parasitized nymphs were found in the field 7 days before the start of the experiment, so that the mortality caused by the mites became manifested quite soon.

This experiment was continued until all the nymphs had become adults, and the material was supplemented with further material from two other replicates. The entire material consisted initially of 80 healthy and 80 mite-parasitized nymphs of *J. pellucida*. 52 of the healthy specimens ultimately emerged, but only 2 of those that were parasitized ($\chi^2 = 67.11$***). This test demonstrates that nearly all the mite-parasitized nymphs of *J. pellucida* died before reaching the adult stage.

The proportion of *Javesella* nymphs parasitized with mites was determined during the period May 18—27, 1961, on eight first-year and eight older leys which had been established under a cereal nurse crop. This is the same material as in Table 77 but with the addition of 4 more first-year leys. On the basis of the untransformed figures, 0.6 % of the *Javesella* nymphs in first-year leys were infested, while in the older leys the figure was 14 %. According to analysis of variance, which was made with arc sin-transformed values, the proportion of mite-parasitized leafhoppers was greater in the older leys than in

Table 78. Frequency of leafhoppers parasitized by mites in first-year leys

Year	Date	No. of fields	Nymphs				Adults		
			Javesella			*M. sordidulus*	*J. pellucida*		*J. obscurell*
			Total	Parasitized by mites		Parasitized by mites	Total	Parasitized by mites	Parasitized by
				No.	%	No.		No.	No.
1958	27. V—3. VI ..	6	2 191	13	0.6	—	9	—	—
1959	1.—2. VI ..	6	1 725	10	0.6	—	—	—	—
1960	20. V—2. VI ..	8	1 590	178	11.2	1	358	5	1
1961	30. V—4. VI ..	11	1 346	21	1.6	10	—	—	—
1962	1.—5. VI ..	13	919	15	1.6	1	109	—	—
1963	21.—24. V ..	7	1 312	0	0.0	—	41	—	—
1964	25.—26. V ..	18	2 275	49	2.2	—	4	—	—

those only one year old (F = 4.98*, d.f. = 1 and 14). Numerous visual observations support this result, so that possibly a higher proportion of the *Javesella* nymphs in old leys were infested with mites than in first-year leys.

5. *Fluctuations in abundance*

In the years 1958—1964, the proportions of leafhoppers parasitized with mites were determined in first-year leys. Counts were usually begun about one week after the first mites had appeared, but in 1959 this was done, on the average, considerably later. The results (Table 78) show that most of the mites observed were on nymphs of the genus *Javesella*. They apparently occurred with equal relative frequency in the different species, and since *J. pellucida* made up by far the bulk of this genus, as many as about 95 % or even more of the mites occurred on *J. pellucida*, except in the years 1961 and 1962, when they were abundant on other species as well. The proportions of leafhoppers parasitized with mites were generally small and evidently even smaller than the percentages in Table 78 suggest. The counts were made with the unaided-eye, and leafhoppers parasitized with the conspicuous red mite are more liable to be included in the material than the less conspicuous non-parasitized leafhoppers. The relative abundance of mites was greatest in 1960. This was also supported by other observations made in the field. Another year showing a relative rise in mite infestation was apparently 1964. The fluctuations in abundance of *Dicondylus lindbergi* (Tables 64 and 65) and *Dicranotropis hamata* (Raatikainen and Vasarainen 1964) were quite similar, while those of *Elenchus tenuicornis* (Tables 75 and 76) were almost the opposite. However, the numbers of these different species were probably not to any great extent dependent on one another, but rather the weather conditions evidently affected each species separately. The mites were relatively more abundant after warm summers, while after the cool summer of 1962 they were at a minimum. Since the numbers of leafhoppers examined in 1963 were small and since the time of counting may have been too early, additional counts of the proportion of *Javesella* nymphs parasitized by mites were made on June 11 and 17 of this same summer. At the former count, about 1 000 nymphs and 3 000 adults of *J. pellucida* were examined, and at the latter count the numbers amounted to about 1 000 nymphs and 4 000 adults. Not a single mite was found on any of these leafhoppers, which clearly demonstrates that the extent of mite infestation was indeed at a minimum that year.

G. Other animals

I n s e c t s. Kontkanen (1950 b) reported a species of *Pipunculidae* parasitizing *J. pellucida*. In the region of investigation, a pipunculid was found only once in *J. pellucida* (at Laihia, June 25, 1959) and it was obviously of no significance as regards the abundance of the leafhoppers.

ome bugs may be very important natural mies of certain leafhoppers (cf. e.g. Hinckley). In the region of investigation, leafhopper were often found which may have been ly eaten by bugs. Many species of bugs rred in the fields, but none of them were nd to feed on leafhopper eggs. However, it is sible that bugs were predators of *J. pellucida* his region.

pi d e r s. Spiders were common in the rnating sites of *J. pellucida*. In suction sam- taken at the beginning of June in first-year as many as 20—30 spiders per square metre often collected. The numbers appeared to ven higher in older leys. Suction samples n in spring cereals in June and July contained a few spiders per square metre, and their bers appeared to increase towards the end the summer. In first-year leys the spider ies *Dicymbium nigrum* (Blackw.), *Meioneta tris* (C. L. Koch) and *Linyphia pusilla* dew. were found to kill nymphs of *J. pellu-* Evidently many other species of spiders leafhopper nymphs, but no information was ined about them.

iders were of very little significance as ators of *J. pellucida*. Leafhopper nymphs lly travel by walking and are seldom caught piders' webs. Moreover, nymphs and adults ch may have become caught in the web often eeded in escaping before the spider could them. Furthermore, the amount of food sumed by spiders is generally very small e.g. Kanervo 1946). When a female of *yphia pusilla* was reared in the insectary, it sumed at most two *J. pellucida* nymphs of tars IV and two of instar V within a period 35 days.

i t e s. According to Hassan (1939) and ntze (1937), *Trombidiidae* mites occur on hoppers. The mite species parasitizing leaf- ppers are so poorly known, however, that red mites observed in the present studies those mentioned by Hassan and Kuntze may ually be of the same species, or at least some them may be identical. Kuntze (1937) also orted that some mite species, perhaps of the genus *Pediculoides*, occurred on an *Idiocerus* leafhopper.

V e r t e b r a t e s. According to Kuntze (1937, p. 381), frogs and lizards may eat leafhoppers. In the region of investigation, however, these animals were not significant as predators of *J. pellucida*. There were only a few frogs and lizards in the fields, and in an experiment *Lacerta vivipara* Jacq. made several attempts to catch nymphs of *J. pellucida* but never succeeded.

Many species of insectivorous birds inhabited the region investigated, but they were not important in affecting the mortality rate of *J. pellucida*. It is possible that certain of these birds may have captured *J. pellucida*.

The vole species *Microtus agrestis* (L.), *M. arvalis* (Pall.) and *Arvicola terrestris* (L.) inhabited the cereal fields and broke cereal straws into fragments a few centimetres long. Such damage occurred every year and was at a maximum in 1962. That year voles, probably mainly *A. terrestris*, caused considerable destruction to oats, particularly in Satakunta, South and North Savo and South Ostrobothnia. The voles usually caused such damage in July and August, a period when there were many *J. pellucida* eggs in the straw. Some of the eggs were destroyed when the voles cut plants to pieces and others succumbed in the fragments on the ground. However, it was estimated that voles did not destroy even as much as 0.1 percent of *J. pellucida* eggs on the average.

Lepus timidus L. and possibly also *L. europaeus* Pall. ate oats in the field, and destroyed the *J. pellucida* eggs in the stems at the same time. However, these species were quite insignificant in affecting the population dynamics of *J. pellucida*. Similarly, other wild mammals may have had a negligible influence on the numbers of leafhoppers.

On pastures, eggs of *J. pellucida* in grasses entered the digestive canal of grazing cattle, horses and sheep. Pastures made up about 11 % of the cultivated land in the region and the density of *J. pellucida* in them was very low, so that domestic animals could not have destroyed more than an extremely low proportion of leafhopper eggs. As far as is known, there are no mammalian predators of *J. pellucida.*

H. Viruses and fungi

Viruses. *J. pellucida* is a vector of at least EWSMV, OSDV, maize rough dwarf virus and Aster yellows virus, as mentioned in the introduction. According to Lindsten (1959, 1961 a and b), it is a vector of two viruses which cause oat striate and red disease (OSRD) and oat dwarf tillering disease (ODTD). However, the viruses involved are probably EWSMV, which causes OSRD, and OSDV, which causes ODTD.

In the region of investigation *J. pellucida* is a vector of EWSMV and OSDV (Ikäheimo 1960, 1961). Both viruses are transmitted transovarially, although this rarely occurs with OSDV (e.g. Vacke 1966). According to Watson and Sinha (1959) and Sinha (1960), EWSMV is probably pathogenic to *J. pellucida*. Later, however, Kisimoto and Watson (1965) demonstrated that abnormalities were rare in eggs of *J. pellucida* females mated to males of another family, but they increased with sibling matings. Furthermore, they did not find that EWSMV caused mortality in the immature stages. In the region of investigation *J. pellucida* eggs were found which were similar to the dead eggs described by Watson and Sinha (1959, pp. 158, 159), but the egg mortality of EWSMV-infected females was not greater in the experiments than that of healthy females. Moreover, the mortality of eggs of OSDV vectors was not greater than that of non-infected leafhoppers; in the trial there were 3 826 eggs of non-infected leafhoppers, of which 81 (2.1 %) had been destroyed. All the leafhoppers in the trial had been collected as nymphs from an area of about 10 ares in a first-year timothy ley.

The numbers of eggs of OSDV vectors and healthy leafhoppers were determined in 1965. At the end of April *J. pellucida* nymphs were collected from first-year leys established under oats. The capacity of the nymphs to transmit virus to oats was tested on two consecutive occasions. There were four specimens which transmitted OSDV and also four which were found to transmit it and which were thus sidered to be healthy. During the period oviposition the leafhoppers were reared on and every four days they were transferred to plants. The average number of eggs depos by the OSDV females was 178 and that of healthy females 385. The difference was statistically significant (t = 2.16), but it is po sible that virus-infected leafhoppers lay few eggs than non-infected.

The influence of OSDV and EWSMV on reproduction and mortality of *J. pellucida* is far 'uncertain. However, these viruses are prob ably not severely pathogenic to *J. pelluci* Nevertheless, they do have an indirect effect the mortality of the species, since in viro stands the leafhopper often oviposited in the leaves rather than in the stems, and consequently the proportion of eggs destroyed by pteromalid perhaps decreased, while that destroyed by *Anagr atomus* rose (cf. pp. 43, 70, 78 and 86).

In a similar fashion, the barley yellow dwa virus transmitted by aphids appeared indirectly to influence the numbers of *J. pellucida*. In field infected with this virus the leafhopper apparently often oviposited in the leaves and as a result the number of eggs destroyed by *A. atomus* in creased.

Fungi. In all the years some of the delphacid eggs in the stems and leaves were black. Such eggs were also found in the *J. pellucida* cultures. The first black eggs were observed about two weeks after the beginning of oviposition and the numbers appeared to increase slightly as the summer progressed. However, the numbers of black eggs were very small in all years; at the end of August 1957, for instance, only 21 out of 4 879 eggs were black, or a figure of 0.4 %. The cause of the blackening was not ascertained. Such eggs were found to be infected with *Botrytis* sp. and *Cephalosporium* sp.

J. pellucida nymphs killed by parasitic fungi were discovered several times in the field, and nearly every year some of the nymphs in the cultures likewise died as a result of fungal di ease. In material collected at Laihia (EP) in Ju nd at Pälkäne (EH) on June 7, 1957, the species *Entomophthora major* (Thaxter) M. fs. was identified in diseased *J. pellucida* hs. In the cultures, *J. pellucida* nymphs sometimes infected with *Penicillium* sp., however, did not appear to be patho- to the host.

fhopper adults killed by parasitic fungi found nearly every year both in the field n the cultures. The fungus species *Ento- hora major* (Thaxter) M. Gustafs. was identi- n *J. pellucida* material collected at Laihia ne 1957, while *E. sphaerosperma* Fres. was mined in material collected at Sulva and on July 31, 1957. Occasionally *Ento- hora* fungi killed specimens of *J. pellucida* in the field, but only once (at Sulva around the beginning of August, 1957) were they seen to destroy a considerable proportion (perhaps ten per cent) of the *J. pellucida* adults in an oat field. The species was identified as *E. sphaerosperma.*

According to Gustafsson (1965, p. 144), *Entomophthora sphaerosperma* is one of the commonest *Entomophthora* species in large areas of the world. It has been reported as infecting psyllids, aphids, *Thysanoptera, Lepidoptera, Diptera, Coleoptera* and *Hymenoptera. E. major* has been found on aphids, *Diptera* and *Coleoptera* (Gustafsson 1965, p. 134). According to Hinckley (1963, p. 473), a species closely related to *E. major* is an important cause of mortality of *Nilaparvata lugens* (Stål) populations in Fiji.

VI VARIATIONS IN ABUNDANCE OF JAVESELLA PELLUCIDA

A. Oscillation

variation in abundance occurring within eriod of one generation — in this case within one year — is called oscillation erdtfeger 1956).

he summers of 1957—1960, the numbers *pellucida* were determined at intervals of one week in first-year leys established cereals, in oats, and in 1958 also in spring at 1—3 places in Laihia, Ylistaro and Sulva igs. 16—20, 28).

the years 1961—1964, determinations of pper abundance were made five times lly in oats and the leys established under as well as twice annually in spring wheat; ese years there were 20 sampling localities ig. 1). At the same time studies were made many factors as possible which affected bundance of *J. pellucida* and their significance ding the mortality of the species.

1. Spring cereals

dults. During the course of the migration d (Fig. 24) the density of *J. pellucida* adults ts and other cereals rose rapidly (Fig. 20). In oats the average number of adults at the end of the migration period in the years 1961—1964 was about 56 per m^2, of which 8 were parasitized. This figure was obtained from the material in Table 85, using the method of calculation proposed by Heikinheimo and Raatikainen (1962, p. 19). Since there were many sources of error, the calculated number is only approximate.

Leafhoppers parasitized by *Dicondylus lindbergi* and males of *Elenchus tenuicornis* died considerably earlier than healthy leafhoppers, and furthermore a small proportion were killed by parasitic fungi. In 1959, some of the leafhoppers in stands which were severely infested with aphids and barley yellow dwarf virus and were exceptionally dry, died owing to lack of food. In most years the density of adults declined appreciably in July, and the last adults were obtained in August or September.

Eggs in stems. The numbers of ovipositing females and the numbers of eggs deposited by them determined the abundance of eggs. If there was an average of 15 healthy *J. pellucida* females per square metre in oats in 1961—1964, as found by the netting surveys, and if each female deposited an average of 402 eggs (cf. p. 41), there should have been about 6 000 eggs per

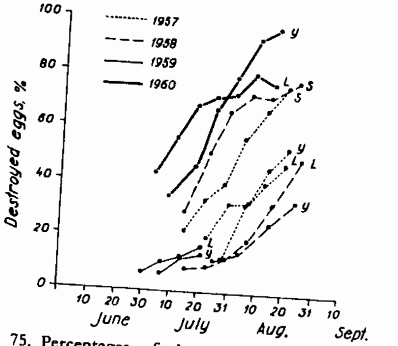


Fig. 75. Percentages of destroyed delphacid eggs in cereal stems in 1957—1960. Localities: L = Laihia, S = Sulva and Y = Ylistaro. The samples from Sulva in 1958 were from spring wheat, while all the others were from oats. The curves are 3-point moving averages. Same material as in Fig. 16.

square metre. However, after making appropriate calculations, it was found that the number of *J. pellucida* eggs in oats (Table 87) was approximately 4 500 per m². This number was thus about 75 % of that calculated in the manner described above. The number of eggs per female probably varied from year to year. For example, in 1959 the number of eggs in the field appeared to be substantially larger than in 1957, even though in the cultures it was smaller in the former year (cf. Table. 19).

The numbers of eggs in the stems increased rapidly (cf. Figs. 16 and 28), but immediately after the first eggs had appeared, mortality factors began to bring about their destruction. In 1957—1960 investigations were made at about weekly intervals on the proportion of delphacid eggs destroyed — chiefly those of *J. pellucida* — in a total of eight oat fields and one wheat field. The results (Fig. 75) show that the percentage of eggs destroyed increased during the course of the summer, and in seven out of ten instances at least half the eggs in the last samples were destroyed. In samples taken from fields other than those of oats and wheat described above, an average of more than half the delphacid eggs were destroyed. It can thus be concluded that probably over half the eggs of *J. pellucida* in oat and wheat stems were destroyed.

The pteromalid species *Panstenon oxylus* *Mesopolobus aequus* were responsible for the dest tion of most of the eggs in Fig. 75. In all ca the proportions of eggs destroyed by these pte malids appeared to be greater in spring wh than in oats. In oats, larvae of *Panstenon ox* apparently caused the highest relative mortali in the years 1957—1960 and 1962—1964, whi *Mesopolobus aequus* was perhaps the chief cause 1961. In all the years *M. aequus* was relatively more abundant in spring wheat than in oats, and in the former crop *M. aequus* caused the highest relative mortality in 1960 and 1961, while *P. oxylus* was more damaging in 1957—1959 and 1962—1964

The larvae of both species began to destro *J. pellucida* eggs in the stems about 3—4 da after oviposition, and the numbers of egg destroyed per internode rose rapidly (cf. Fig. 45

Adult pteromalid females may also have been able to destroy *J. pellucida* eggs during the pro cess of oviposition.

Anagrus atomus females oviposited in the egg of leafhoppers in stems. Particularly at the end of July and later there were small numbers of immature stages of this species, and in all the years investigated the species was not importan as an egg predator of *J. pellucida* (cf. also Tables 55 and 56).

Even in internodes containing no pteromalid larvae, the *J. pellucida* eggs were often dead The proportions of dead eggs were highest in thick-walled internodes (Table 79). Such internodes containing dead delphacid eggs were to be found in the lower part of the stand, and their proportion was greatest at the beginning of the oviposition period of *J. pellucida*. In both the pteromalid-containing internodes and those without these predators, *J. pellucida* eggs were destroyed in a similar manner.

Of the dead eggs in the stems, it was easiest to ascertain the numbers destroyed by Hymenoptera; and for example in 1963 they comprised about 84 % of the total number of eggs destroyed in oats and about 92 % of those in spring wheat. The death of the other eggs was due to several different factors. Among other things, the female occasionally damaged the eggs during and after

79. Frequency of destroyed delphacid eggs in oats weeks after the appearance of the first eggs in the The data include only those internodes in which pteromalids were found. $\chi^2 = 93.01^{***}$, d.f. = 6

ickness of stem wall, mm	Total eggs	Destroyed eggs No.	 %
—0.2	51	2	4
—0.4	201	16	8
—0.6	344	7	2
—0.8	560	20	4
—1.0	470	61	13
—1.2	453	68	15
and no cavity	99	25	25

process of oviposition. Some of the eggs crowded into dense groups, and particularly se at the ends of the groups appeared to be troyed more readily than the others, possibly being crushed by the plant tissue. According Kisimoto and Watson (1965), lethal genes prevent the development of *J. pellucida* eggs; the region of investigation, too, this may happened, as is evident from the material cribed on p. 116. However, the effect of sible lethal factors on mortality seems to be ll. A small proportion of the eggs were bably infertile and consequently failed to elop. Bugs, certain other enemies and pathos may have killed some of the eggs. Furmore, nonpredators were responsible for troying a small fraction of the eggs.

the region of investigation, the cereals were ally harvested by binder, but mowers were widely used, and combines were becoming mmon, especially in the later years of the estigation. When cutting was performed with binder, about 5 % of the delphacid eggs had yet hatched (Raatikainen 1966 a), and in case of combine harvesting the figure was bably 1—2 %. Cereals cut with a binder or wer were dried in the field, and probably bulk of the eggs hatched before threshing. cording to Jürisoo (1964, p. 55), eggs in reals are destroyed during the process of eshing. However, threshing was evidently ponsible for the destruction of at most one cent of the *J. pellucida* eggs present on the ld. After threshing, eggs were lost when the straw was burned or destroyed by other means. Furthermore, some of them succumbed as a result of dessication.

In cool summers an extremely small proportion of the *J. pellucida* eggs failed to hatch and consequently died during the winter.

Eggs in leaves. *J. pellucida* chiefly oviposited in the stems, but particularly in oats and barley there were also considerable numbers of eggs in the leaves as well (Tables 20—23, 55, 56). Although the absolute numbers of eggs in the leaves were greatest in the middle of the oviposition period (Fig. 61), the proportions of such eggs were highest at the beginning of oviposition and declined rapidly as soon as the stems emerged and the leafhoppers began to oviposit in them (Fig. 29). In oat stands which were suffering from drought or infested with *Oscinella frit* L. or with the viruses OSDV and EWSMV, the percentage of eggs in the leaves was considerable even at the end of the oviposition period (cf. p. 43).

The most important cause of mortality of the eggs in the leaves was *Anagrus atomus*, which right from the beginning of leafhopper oviposition destroyed a substantial proportion of the eggs, and at least 90 % of the eggs found at the end of the oviposition period (Figs. 61 and 62). Some of the eggs died as a result of dessication. This was the case especially with eggs with one end not enclosed within the leaf tissue. Such eggs occurred in places like the leaf sheaths of wheat and in the blades and sheaths of oats and barley. In experiments carried out in cages, the density of eggs in the leaves increased as the population density of OSDV-transmitting *J. pellucida* rose. Eggs in the leaves were also destroyed by nonpredators and possibly by diseases, but such factors were only of minor significance.

Nymphs. The first nymphs of *J. pellucida* hatched in July, and the nymph density was evidently at a maximum in August, just after the period of most active hatching.

Some nymphs died during the process of hatching. However, this occurred extremely seldom in the field and appeared to be most common in material which had remained for a long time in the laboratory. The nymphs hatching from eggs in the stems almost always came out onto the surface of the stem. However, among a total of 9 253 nymphs which arose from eggs in the stems, 8 (0.1 %) hatched into the stem cavity, where they lived for several weeks and ultimately died.

A high percentage of the nymphs died before autumn. During harvesting, for example, they were killed by being crushed by the harvesting machinery. Moreover, after the harvest, the microclimate of the field was altered and this apparently affected the mortality of *J. pellucida* nymphs both directly and indirectly. Drought, in particular, killed the nymphs, but predators also destroyed them to some extent.

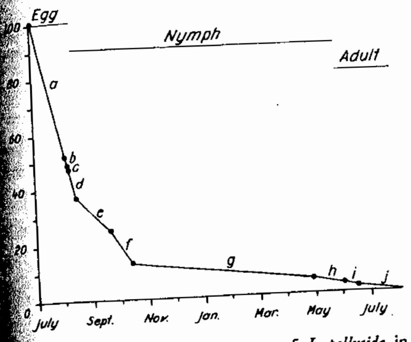
2. *Spring cereals undersown with grass in autumn and the same ley in the following year*

At the end of the summer and in autumn the nymphs moved to the edges of the fields, where their density, as judged from samples, was about 30 % of that in first-year leys (cf. p. 36).

About half of the cereal stubble in the region under investigation was without an undergrowing ley (RAATIKAINEN and TINNILÄ 1959 a, p. 53), and such fields were usually ploughed in September or October. Most of the nymphs were destroyed during ploughing or after it, and the following spring there were only small numbers of *J. pellucida* nymphs in such ploughed fields, as demonstrated by the following examinations. In the springs of 1957—1962, the numbers of *Javesella* nymphs were investigated in fields which had been under spring cereals the previous year; 35 of the fields had been ploughed in the autumn and 35 containing undergrowing ley had not been ploughed. The sampling sites were selected so that the ley and the ploughed field were adjacent to one another. A suction sample from an area of 3 × 0.1 m^2 was taken in each of the first-year leys, while nymphs were counted by eye in a corresponding area in the ploughed fields. It was found that a total of 2 280 *Javesella* nymphs were collected on the leys, while only 84 were counted on the ploughed fields. Over 95 % of these were apparently *J. pellucida* in both cases. If it is assumed that with these two methods equally large percentages of the nymphs were obtained in the samples (counting was probably more accurate), the nymph density in the ploughed fields was only 4 % of that of the leys. Since the ploughed fields were subsequently harrowed and sown, virtually no leafhopper nymphs at all remained after these operations.

Samples taken from spring cereal fields which had been undersown with grass and harvested for grain (cf. Table 89) showed that at the beginning of October in the years 1961—1963 there were over 700 *J. pellucida* nymphs per m^2. This figure represents about 25 % of the egg density of *J. pellucida*. The following spring, when these fields were first-year leys, they contained an average of slightly over 300 *J. pellucida* nymphs per m^2, as found by suction sampling. This figure is only about 8 % of the original egg density. During the course of the winter an average of at least 45 % of the nymphs succumbed in the years 1957—1960 and 1961—1964 (Tables 89 and 90).

Beginning in April and May, suction and netting samples were taken at intervals of about one week from certain first-year timothy leys established under spring cereals. There were only a few samples, so that the results do not show the slow decline in *J. pellucida* nymph density in April and May (Figs. 17 and 18). During this time nymphs were killed by spiders, mites, parasitic fungi and apparently other factors as well. Some males of *Elenchus tenuicornis* prevented the emergence of nymphs. And often a nymph which was parasitized by an *E. tenuicornis* male was infested with abundant fungal mycelium after emergence of the male parasite, and this fungal growth may sometimes have killed the nymph. However, enemies and pathogens destroyed only a very small proportion of the nymphs. Likewise, the effect of internal factors on mortality appeared to be minor, and other factors, such as weather and cultural practices, were evidently not very important causing destruction of nymphs during this e. In spring and early summer the nymphal sity dropped slowly and in June rapidly, ce the adults then emerged (Figs. 17—19). few days after emergence, the macropterous hoppers migrated away from the leys (Fig. 24) many of the brachypters likewise departed, that the adult density was much lower than nymph density. Only a small proportion of *ellucida* remained in the leys, and the number dults that moved to such leys was very small relation to the area, so that the density of lts was very low after the middle of the mmer. *Dicondylus lindbergi* and *Elenchus tenui-nis* killed adults in the leys, and in August d September the last adults finally died.



76. Diagrammatic survival curve of *J. pellucida* in fields and first-year leys established under them in —1964. Mortality factors: a = *P. oxylus*, b = *M.* us, c = *A. atomus*, d = other factors killing eggs, weather and some other factors killing nymphs, ploughing, g = winter, h = *A. gracilipes*, spiders some other factors killing nymphs, i = *E. tenuicornis* *D. lindbergi*, and j = other factors killing adults.

Mortality during one generation, 1963—1964

Attempts were made every year to ascertain thoroughly as possible the parts played by the ious mortality factors on 20 oat fields, 20 ring wheat fields and 20 leys established under above cereals. This problem was best investi- ted in 1963—1964.

As an example of these investigations and the ults, a diagrammatic presentation of the numbers of *J. pellucida* during the course of one generation is shown in Fig. 76. The diagram also shows the established or calculated mortality caused by the different factors.

According to plant samples taken from 20 places (Fig. 1, localities 1—20), the average number of *J. pellucida* eggs was found (after appropriate calculations) to be about 4 900 per square metre. According to material collected from these same plant samples, *Panstenon oxylus* apparently destroyed about 48 % of the leafhopper eggs, *Mesopolobus aequus* about 3 % and *Anagrus atomus* about 2 %. Certain other factors (crushing by the plant tissue, lethal genes, pathogens, other enemies, etc.) probably caused the destruction of some 10 % of the eggs, and only about 37 % finally hatched.

The mortality of the nymphs was probably very high. They were killed by weather conditions, predators and pathogens. Some were apparently killed by certain developmental disturbances, and evidently there were other unknown factors which also destroyed the nymphs. When suction samples were taken in October, the numbers of *J. pellucida* were only about 25 % of the original number of eggs. About half the spring cereal fields were ploughed in the autumn, and in such fields the bulk of the nymphs succumbed immediately, while by the end of May of the following year virtually all the nymphs had been destroyed. When the nymphs which were destroyed during ploughing and harrowing were designated in Fig. 76 as having died in the autumn, then less than 15 % of the original numbers of *J. pellucida* occurring in cereals in the summer of 1963 ultimately remained to hibernate. During the winter about 62 % of the nymphs in the unploughed fields died, and the following spring only slightly over 5 % of the original *J. pellucida* population of eggs in all the spring cereal fields still remained alive.

In the spring *Achorolophus gracilipes*, spiders, parasitic fungi and other factors caused further losses among the nymphs. It was calculated that less than 4 % of the eggs of *J. pellucida* developed into adults. About 5 % of the adults were apparently parasitized by *Elenchus tenuicornis*. These, as well as the small numbers of leafhoppers parasitized by *Dicondylus lindbergi*, were incapable of reproduction. Some of the adults died before the beginning of the reproductive season, and at the start of reproduction the number of females was about the same as in the previous year, or perhaps slightly greater.

Panstenon oxylus and *Mesopolobus aequus* destroyed about as large a percentage of eggs — or slightly larger — (ca. 64 %) in the stems of spring wheat as were destroyed in oats by all the mortality factors together. In wheat the other factors apparently destroyed fewer eggs than in oats. The proportion of *J. pellucida* destroyed at the egg stage appeared to be higher in wheat (70 %) than in oats (63 %).

Of the total numbers of eggs of *J. pellucida* in oats in the summer of 1963, enemies evidently caused the destruction of at least 55 %, man at least 12 % and the winter 8 %. The fate of just under 25 % was not completely known, but many factors are recognized (e.g. weather, man, enemies and pathogens, unfavourable places in which to live) which destroyed a large part of these leafhoppers. In spring wheat, enemies probably killed over 65 % of *J. pellucida*. In barley and rye the figure appeared to be the same as in wheat and oats. Consequently, enemies and pathogens evidently destroyed over half the specimens of *J. pellucida* inhabiting spring cereals during the above-mentioned period. Man and the weather (including winter mortality) probably killed about 15 % each.

The mortality caused by the chief factors in 1963—1964 appeared to be quite similar to the situation in most of the other years during the years of investigation 1957—1964, so that the year examined can be considered to be fairly representative of the normal situation.

B. Variations in spatial abundance

Considerable information has already been obtained on the abundance of *J. pellucida* in different types of vegetation (cf. e.g. Tables 12—14 and Fig. 25). In the present section a description will be given of the abundance of the species in similar crops growing at 20 different places in the years 1958—1964 (cf. Fig. 1). Samples of *J. pellucida* were taken in the stages of egg, nymph and adult.

Table 80. Mean numbers of delpbacid egg groups in the stems of oats (1958—1964) and spring wheat (1961—1964) at different localities. The numbers of the localities are tbe same as in Fig. 1. Same material as in Tables 43 and 44

Oats		Spring wheat	
Locality no.	Egg groups per 100 plants	Locality no.	Egg groups per 100 plants
3	178 a	13	91
1	127 a b	3	83
2	124 a b	2	72
13	109 a b	14	67
5	108 a b	5	66
9	98 a b	8	53
6	94 a b	6	52
14	81 a b	10	33
18	76 a b	20	30
8	51 b	18	29
11	48 b	12	28
7	48 b	9	25
10	47 b	15	23
12	42 b	11	23
15	39 b	4	18
20	38 b	17	18
17	21 b	7	17
19	20 b	1	17
4	19 b	19	9
16	10 b	16	8

Oat samples F = 3.11***, d.f. 19 and 114
Spring wheat samples F = 1.86*, d.f. 19 and 57.

E g g g r o u p s. Although only the numbers of egg groups in the stems have been used in certain of the calculations, this has no great bearing on the results, since there were generally very few eggs in the leaves (cf. Tables 55 and 56) in comparison with those in the stems. Although the egg groups of all delphacids are combined in the material, this likewise does not have a great effect on the validity of the results (cf. Table 83), since usually over 95 % of the delphacid adults in the fields investigated were *J. pellucida* (cf. Tables 85 and 86), and according to unpublished studies, as well as to the experiments reported by RAATIKAINEN (1960 a, p. 235), the number of eggs laid by *J. pellucida*, and likewise the number of its egg groups, were larger than those of the other species in the material.

ble 81. Mean numbers of *Javesella* nymphs in suction mples taken in autumn and spring 1961—1964 at ferent localities. The numbers of the localities are the me as in Fig. 1. Same material as in Tables 89 and 90

Autumn		Spring	
ocality no.	Nymphs per 0.3 m^2	Locality no.	Nymphs per 0.3 m^2
2	609 a	2	211 a
8	383 a b	5	110 b
5	357 a b	15	95 b
9	327 a b	3	78 b
3	258 a b	1	71 b
6	251 a b	6	69 b
15	228 a b	12	65 b
19	191 a b	4	64 b
14	166 a b	14	62 b
20	151 a b	20	51 b
7	149 a b	7	48 b
17	138 a b	19	47 b
13	133 a b	8	41 b
4	121 a b	13	37 b
12	117 a b	9	34 b
16	90 b	17	33 b
1	84 b	10	32 b
18	67 b	11	28 b
11	59 b	16	21 b
10	58 b	18	8 b

umn samples F = 1.81*, d.f. 19 and 57
ing » F = 1.88*, d.f. 19 and 57

Table 82. Mean numbers of *J. pellucida* adults in netting samples taken in 1961—1964 at different localities. The numbers of the localities are the same as in Fig. 1. Same material as in Tables 64 and 65

Oats		Spring wheat	
Locality no.	*J. pellucida* per 60 net sweeps	Locality no.	*J. pellucida* per 60 net sweeps
3	212 a	2	194
2	162 a b	5	130
14	124 a b	14	123
5	101 a b	20	118
6	88 a b	3	113
7	84 a b	6	86
15	76 a b	15	72
1	66 a b	8	69
8	60 a b	9	67
13	55 a b	13	64
11	51 a b	10	53
20	46 a b	1	49
10	44 a b	19	41
12	42 a b	11	39
17	40 a b	18	36
4	33 b	7	29
9	29 b	17	29
19	24 b	4	27
18	21 b	12	25
16	10 b	16	18

Samples from oats F = 2.10*, d.f. 19 and 57
» » wheat F = 1.48*, d.f. 19 and 57

In both oats and spring wheat there were er 10-fold differences between the localities regards the numbers of delphacid egg groups; ese differences were statistically significant able 80). However, according to the Tukey-artley test, only the number of egg groups in ts at locality 3 (cf. Fig. 1) was significantly ger ($P < 0.05$) than the numbers found at 11 her sites.

N y m p h s. Approximately 99 % or more of e *Javesella* nymphs were *J. pellucida*, while the cond most numerous species was *J. obscurella* Boh.) (Table 85). The percentage of *J. obscurella* ppeared to be least in the western localities and eatest in the east and southeast; the differences, owever, were not great. Although all the *avesella* nymphs are combined in the material, e numbers of nymphs found at each local-y give a good picture of the abundance of *J. llucida*.

There were over 10-fold differences in the ensity of *Javesella* nymphs between the various calities, and the differences in the samples taken in different localities were significant both in autumn and spring (Table 81). The maximum numbers of nymphs occurred at locality 2 both in autumn and spring.

A d u l t s. According to the netting samples, there were also over 10-fold differences in the numbers of adults per 60 sweeps (Table 82). The density of adults was greatest at localities 2 and 3, where the density of egg groups and nymphs, too, was greater than at the other places.

A l l s t a g e s. The density of *J. pellucida* at one and the same locality varied greatly from year to year. Even if the numbers of leafhoppers in a clearing had remained the same every year, their density would have varied in the sampling sites, since many factors, such as the situation of the sites, in the field, the position of the hibernation places in relation to the site, the wind direction during the migration period, etc., considerably influenced the numbers of leafhoppers arriving at the sampling site and also the numbers of eggs and nymphs. Evidently in

Table 83. Correlations between the numbers of *J. pellucida* adults, *Javesella* nymphs and delphacid egg groups i samples taken in 1961—1964 at the 20 localities shown in Fig. 1. The numbers of egg groups in the leav were converted to numbers of egg groups in the stems, using the coefficients 0.29 on oats and 0.19 in spring whe (cf. Table 25). Same material as in Tables 43, 44, 64, 65, 89 and 90

		1	2	3	4	5	6
Numbers of *Javesella* nymphs in 1st-year timothy	1	—	.57**	.57**	.40	.34	.62**
Numbers of *J. pellucida* adults in oats	2	.57**	—	.67**	.67**	.70***	.43
Numbers of *J. pellucida* adults in spring wheat	3	.57**	.67**	—	.61**	.79***	.68***
Numbers of delphacid egg groups in oats	4	.40	.67**	.61**	—	.73***	.29
Numbers of delphacid egg groups in spring wheat	5	.34	.70***	.79***	.73***	—	.65**
Numbers of *Javesella* nymphs in spring cereal stubble undersown with ley	6	.62**	.43	.68***	.29	.65**	—

such material the probability need not be $P < 0.05$ for the difference to be significant.

In the years 1961—1964, the correlations between the densities of eggs, nymphs and adults in the localities studied were calculated (Tables 80—82). The figures obtained from the densities were converted for the correlation computions in the following manner, using as examples the samples of nymphs collected in autumn. The numbers of *Javesella* nymphs in a sample were calculated per thousand specimens of *Javesella* in the total catch of that autumn. After this, the average frequency value from four consecutive years was calculated at each locality, and then an arc sin transformation was performed. The results (Table 83) reveal that the numbers of *J. pellucida* adults in the netting samples from oats and spring wheat were positively correlated with both the egg group densities and the nymph densities. There are two possible explanations for this: Either the overwhelming majority of the delphacid egg groups and *Javesella* nymphs were *J. pellucida*, or they mostly comprised species whose density was positively correlated with the density of *J. pellucida*. The former alternative is considered to be more correct. Determinations of the numbers of adults or delphacid egg groups would in themselves have given rather a good picture of the *J. pellucida* density of the locality. The suction samples were too small and thus did not provide as accurate a picture of the density of *J. pellucida*, as did the other samples (cf. HEIKINHEIMO and RAATIKAINEN 1962, p. 14).

According to the data in Tables 80—82, the population density of *J. pellucida* was highest on the smallish clearings usually situated at some distance from the farm buildings (localities 1 oats, 2, 3, 5, 6, 8, 13—15), while it was lowest in the larger clearings, usually along the river banks in the vicinity of the farm buildings (localities 1 wheat, 4, 7, 9—12, 16—20).

Reasons for population density. In all the localities investigated food plants for *J. pellucida* were very abundant. However, the botanical composition was different in the different clearings. In the large clearings there were hayfields and cereal fields every year, into which *J. pellucida* moved to reproduce, and particularly in the cereal fields the number of progeny appeared to be large (cf. Table 18). In the smaller clearings far from the farm buildings, on the contrary, there were often only one or a few cereal fields where leafhoppers could reproduce. In certain years there were no cereals at all, and then the leafhoppers reproduced in leys, on the edges of fields, and along the borders of the clearings. The plant species growing on leys (cf. PAATELA 1953 c) and field edges (cf. RAATIKAINEN and RAATIKAINEN 1964) were either poor food sources for *J. pellucida* (*Phleum pratense*, *Deschampsia caespitosa* and *Agrostis tenuis*) or were completely unfit (many dicotyledons), as is clear from p. 37 and Table 18. There were thus larger numbers of suitable reproduction sites for *J. pellucida* in the large clearings than in the small ones, yet the population density was just the opposite. This demonstrates that factors other than adequate food supply during the pro-

gation period had a pronounced effect on the umbers of *J. pellucida*. There were probably no eat differences between the large clearings near he farms and the small distant clearings as egards the climatic factors which influenced the eproduction of *J. pellucida* or as regards the igration of the species, so that there must have en differences in the mortality of *J. pellucida* etween these two areas.

The number of internodes inhabited by pteroalid larvae was positively correlated with the umber of internodes containing delphacid eggs f. Table 92), and the regression coefficient as larger for wheat than for oats (t = 3.52**, . 12). In wheat — and perhaps also in oats — teromalids may have been direct density-dependent mortality factors, but according to the orrelation calculations the differences were not gnificant. The material, however, comprised nly populations of moderate density (about 0 — 3 200 leafhopper eggs per 100 plants), so at on this account also the question of densitypendence remains unsettled. Calculations owed that pteromalids destroyed nearly 70 % the *J. pellucida* eggs in wheat and nearly 50 % oats. Since there was relatively more spring eat in the large clearings near the farms than the distant clearings, pteromalids apparently troyed relatively more *J. pellucida* eggs in the arby than in the distant fields. Particularly the rcentage of eggs destroyed by *Mesopolobus aequus* emed to be large in the fields near the farms. Oats damaged by OSDV and EWSMV were ore abundant in the distant fields than in the lds close to the farm buildings, and in such eased oats the pteromalids evidently did not stroy such a high proportion of the *J. pellucida* gs as in healthy oats (cf. Tables 23 and 40). espite this, however, there were probably not ore nymphs in the virotic stands of oats, since such stands *Anagrus atomus* destroyed relatively ore *J. pellucida* eggs than in healthy stands.

In different parts of the same clearing the rcentage of *J. pellucida* parasitized by *Elenchus uicornis* and *Dicondylus lindbergi* may have been fferent, but after migration of the host it ppeared to be the same in the same kind of crop, for example in oat fields. Throughout the entire region under investigation the number of parasitized leafhoppers in oats was significantly correlated with the number of *J. pellucida* (cf. Table 93), and on an average about 18 % were parasitized at all population densities. The significance which was found in the samples taken from wheat fields, too, was approximately the same, but the percentage of parasitised leafhoppers was higher, about 22 %, and it was about the same at all population densities. The frequency of *D. lindbergi* was almost the same in both cereals, but the frequency of *E. tenuicornis* was higher in wheat than in oats (cf. Tables 75 and 76 as well as p. 103), and consequently the total percentage of parasitized leafhoppers was also higher. According to the above data, *E. tenuicornis* and *D. lindbergi* did not cause distinct differences in the mortality of *J. pellucida* in different localities. Since other predators, as well, were not seen to kill *J. pellucida* in clearly different amounts among populations of different density, the predators were evidently not the principal factors accounting for differences in the density of *J. pellucida*, even though pteromalids may have been partially responsible.

Cultivation practices were definitely different in the two different types of areas. Much cereal was grown in the fields adjacent to the farm buildings, and generally considerably less than half the cereal area was undersown with grass. *J. pellucida* leafhoppers dispersed over a wide area of these nearby fields to reproduce, and when the fields were subsequently ploughed, most of the progeny were destroyed. On the distant fields, on the other hand, where the area devoted to cereals was likewise fairly large, over half of it was undersown with grass. In these distant clearings the leafhoppers were concentrated in a relatively small area for their reproduction, and since considerably less than half the reproduction sites were ploughed, most of the nymphs had good chances of survival. In this case cultural practices were probably an inverse density-dependent factor and were the chief cause of the differing densities of *J. pellucida* in the different localities.

When the area of leafhopper hibernation sites is divided by the area of reproduction sites, a figure is obtained which denotes the density of *J. pellucida* coming to the reproduction sites. This equation, slightly modified from that devised by RAATIKAINEN and TINNILÄ (1959 a, p. 53), appears to be valid, but certain amendments should be made in it. This theoretically derived equation, however, may be utilized in calculating the relative densities of the leafhoppers.

C. Fluctuation

Data on the abundance of *J. pellucida* and its natural enemies were collected eight times during each year.

Three netting apparatuses were used to determine the numbers of migrating leafhoppers (Fig. 24).

Netting samples in oats and wheat (Tables 85 and 86) were taken at the localities mentioned on p. 15. In 1958, the samples were collected from places where the leafhopper population was very dense, while the samples taken in the other years are more comparable with one another. Endeavours were made to take the samples every year when over 90 % of the macropterous *J. pellucida* had migrated and the first of the final-instar larvae of *Dicondylus lindbergi* had appeared. In general, the samples were taken at the right time, according to observations on the developmental stages of *D. lindbergi*, and in most years more than 91 % of the *J. pellucida* macropters had migrated prior to the average sampling date (weighted mean; Table 84, cf. also Fig. 24). But in 1963 only about 61 % of the macropters had migrated, and from the material obtained from the netting apparatuses it appeared that the average sampling date should have been July 4. However, there were only a few leafhoppers in the apparatuses, and their numbers were not sufficient for determining the correct date for sampling. The netting samples were probably taken too early in 1963 and slightly too late in 1960. This conclusion was based principally on observations of the frequencies of the different larval instars of *D. lindbergi*.

Table 84. Average sampling date of net sweeping in oats and spring wheat (weighted averages) and percentages of *J. pellucida* which had migrated by that date. Same material as in Fig. 24 and Tables 64 and 65

Year	Oats		Spring wheat	
	Average sampling date	% of *J. pellucida* migrated	Average sampling date	% of *J. pellucida* migrated
1958	4. VII	98.7	7. VII	99.0
1959	3. VII	96.9	—	—
1960	23. VI	96.8	27. VI	99.8
1961	23. VI	93	24. VI	95
1962	7. VII	93	6. VII	92
1963	26. VI	61	26. VI	61
1964	30. VI	96.8	30. VI	96.8

The numbers of leafhopper eggs were counted from plant samples collected in fields of oats and spring wheat (Tables 87 and 88); the sampling localities are mentioned on p. 16. Attempts were made to take samples when the oviposition period of *J. pellucida* had almost terminated but only the first adult pteromalid egg-predators had emerged. In all years nearly all the delphacids had finished ovipositing prior to the average (weighted mean) sampling date (cf. Fig. 28, Tables 43 and 44). However, in 1958—1960 the samples were collected so late that many *Mesopolobus aequus* adults and first-generation individuals of *Panstenon oxylus* had left the plants. Nevertheless, reliable data were obtained every year on the total numbers of pteromalid nymphs, although in certain years the proportions of the various species were difficult to ascertain. However, the proportions were calculated as approximations (cf. p. 68).

Suction samples of nymphs were taken in autumn and spring at the localities mentioned on p. 15. In the spring of 1958 sampling was done at the localities where the leafhopper density was apparently exceptionally high.

Netting samples of nymphs and adults were taken in late May and early June in first-year leys established under cereals; the sampling localities are mentioned on p. 15 (Table 91). The weather at the time of sampling was very different in the different years, and thus these samples did

ble 85. Abundance of *Javesella* species in oats, 1958—1964. In 1959 and 1960 200 net sweeps were made in each field, in the other years 60 sweeps. Same materials as in Table 64

Year	No. of fields	No. of delphacids	*Javesella pellucida*			*J. discolor* No.	*J. obscurella* No.
			No.	% of delphacids	No. per 60 sweeps		
58	7	1 263	1 256	99.4	—	—	5
59	10	5 266	5 210	98.9	163	—	5
60	13	4 822	3 954	82.0	95	—	38
61	20	741	684	92.3	34	—	3
62	20	1 857	1 800	96.9	90	—	10
63	20	2 015	1 951	96.8	98	2	15
64	20	1 073	1 023	95.3	51	—	5

llucida F $_{1961—1964}$ = 3.86*, d.f. 3 and 57

ot give comparable data on the abundance of *pellucida* in the various years. However, a fairly od picture is obtained of the ratios between species.

1. Fluctuations in numbers in 1958—1964

Adults. According to the samples collected n the netting apparatuses, the ratio between maximum and minimum numbers of migra- *J. pellucida* was 25:1 (Table 63). The highest mber, obtained in 1959, differed significantly m the two lowest, in 1962 and 1963. The mbers of leafhoppers found in the netting aratus samples reflect the fluctuations in ndance of *J. pellucida* from year to year but not give a good picture of the actual numbers the species.

ccording to the netting samples taken at the d of the migration period, the ratio between maximum and minimum numbers of *J. pellucida* in oats was about 5:1, while in wheat it was 2:1 (Tables 85 and 86). As shown by the samples mentioned in Tables 85 and 86 as well as other collections, the numbers of *J. pellucida* per 60 sweeps were high in 1959, dropped to a minimum in 1961 and rose thereafter. In oats, the rise was statistically significant.

Eggs. The numbers of delphacid egg groups also varied considerably in the different years (Tables 87 and 88). When the numbers were smallest, the proportion of *J. pellucida* egg groups was probably lowest; and when there were many egg groups, the proportion was highest (cf. Tables 85 and 86). In the stems of oats and wheat the ratio between the maximum and minimum numbers of egg groups of *J. pellucida* was evidently about 4:1. The numbers of egg groups in the leaves of cereals do not give such a good picture of the total numbers of *J. pellucida* eggs as do the numbers of egg groups in the stems. The reason for this is that the numbers

ble 86. Abundance of *Javesella* species in spring wheat, 1958 and 1960—1964. In 1960, 200 net sweeps were made in each field, in the other years 60 sweeps. Same material as in Table 65

Year	No. of fields	No. of delphacids	*J. pellucida*			*J. discolor* No.	*J. obscurella* No.
			No.	% of delphacids	No. per 60 sweeps		
8	5	1 377	1 357	98.5	—	—	6
60	8	1 688	1 329	78.7	51	—	5
61	20	929	829	89.3	41	—	2
62	20	1 656	1 616	97.6	81	—	3
63	20	1 734	1 661	95.8	83	1	14
4	20	1 479	1 420	96.0	71	—	4

llucida F $_{1961—1964}$ = 1.29, d.f. 3 and 57

Table 87. Numbers of delphacid egg groups in oat samples taken in 1958—1964. Every year 100 plants from each of 20 fields (2 000 plants) were examined during the period July 28—Sept. 19. Same material as in Table 43

Year	Number of egg groups				Calculated no. of eggs per 100 plants
	In stems		In leaves		
	Total	No. per 100 plants	Total	No. per 100 plants	
1958	1 259	63	62	3	734
1959	1 931	97	449	22	1 184
1960	543	27	5	0	313
1961	955	48	10	1	551
1962	1 546	77	104	5	906
1963	1 643	82	124	6	965
1964	1 766	88	627	31	1 119

Egg groups in stems F = 2.67*, d.f. 6 and 114

Table 88. Numbers of delphacid egg groups in sp wheat samples taken in 1958—1964. Every year 100 p were examined from each field; the number of fields w were 18 in 1958, 17 in 1959 and 1960, and 20 in 1961 1964. Examinations made Aug. 1—Sept. 2. Same mat as in Table 44

Year	Number of egg groups				Calculat of eggs 100 p
	In stems		In leaves		
	Total	No. per 100 plants	Total	No. per 100 plants	
1958	457	25	0	0	43
1959	1 458	86	28	2	1 481
1960	332	20	0	0	336
1961	526	26	2	0	453
1962	756	38	0	0	650
1963	546	27	6	0	471
1964	1 212	61	17	1	1 045

Egg groups in stems F = 4.60***, d.f. 6 and 125

in the leaves are readily influenced by many factors (e.g. drought, OSDV and EWSMV) as well as by the time of inspection. The total numbers of delphacid eggs in the samples were not actually counted, but calculated from the numbers of egg groups and their size on the basis of the figures mentioned in Table 25 (cf. Tables 87 and 88). In both oats and wheat the ratio between the maximum and minimum numbers of eggs was about 4:1, as in the case of the egg group ratios in the stems. According to analysis of variance, there were differences in the numbers of egg groups in the stems between the different years. The number of egg groups per 100 plants was largest in 1959 and smallest in 1960, after which there appeared to be another rise until 1964. The numbers of eggs and the numbers of egg groups in the stems are considered in this study to be the best indicato of *J. pellucida* abundance.

Nymphs. About 99 % or more of th *Javesella* nymphs were *J. pellucida* (Table 85 so that the values shown in Tables 89 and 9 satisfactorily reflect the abundance of the speci under study. According to these data, the rati between the maximum and minimum density o *J. pellucida* was 4:1 in autumn and about 5:1 i spring, excluding the samples taken in 1958 These data on nymphs indicated that the densit of *J. pellucida* was greatest in 1959, after whic there was a decrease and thereafter a gradu rise to the year 1964.

According to the netting samples (Table 91) the frequency of nymphs of *J. pellucida* was at maximum in 1958 and 1959, after which i declined and subsequently rose again. The num- of nymphs per net sweep poorly reflects the sity of *J. pellucida*, since the weather condi- s strongly influenced the numbers of nymphs ering the net. The numbers of adults and r frequency are also poor indicators of the ndance of the species.

ll stages. The population density of ellucida appeared to be high in the summer 1956 but declined the following summer ATIKAINEN and TINNILÄ 1959 a, p. 56). In the mer of 1958, the density was probably greater — or approximately the same as — in 1957, which it apparently increased (cf. Fig. 24 Tables 63, 85—91) (Fig. 77). The maximum sity occurred in 1959, but at the end of that mer it already began to decrease. This ease was not apparent, however, in the res for the nymphal density in the autumn, her was it distinct the following spring, pite the fact that the mortality appeared to high during the winter. The reason for the lack of visible population reduction was that samples of the nymphs were taken from only 7 localities and at a time when the weather was favourable, and thus they do not satisfactorily represent the entire region of investigation. The drop in density did not become clearly visible until the summer of 1960, when the numbers of adults and egg groups in the samples showed a decline.

Judging from the numbers of adults, there should have been more egg groups in 1960 than were actually found. The explanation for the discrepancy may be that the adult density estimated on the basis of the samples was too high or that oviposition was unsuccessful, or that both these causes operated. In the autumn of 1960 no samples were taken, but the following spring the density of *Javesella* nymphs was low. In 1961 the adult density was also low, but oviposition was probably successful and the density of both eggs and nymphs was evidently

Table 89. Numbers of *Javesella* nymphs in suction samples taken in autumn in spring cereal stubbles undergrown with timothy. Same material as in Tables 31 and 81

Year	Sampling period	No. of fields	No. of delphacid nymphs	*Javesella* nymphs		
				No.	%	No. per 0.3 m²
1958	24.—26. X	7	969	966	99.7	138
1959	20. X	7	1 845	1 839	99.7	263
1961	3.— 6. X	20	3 438	3 204	93.2	160
1962	15.—17. X	20	1 399	1 365	97.6	68
1963	8.—10. X	20	5 468	5 427	99.3	271
1964	7.— 8. X	20	5 825	5 741	98.6	287

F 1958—1964 = 2.83*, d.f. 5 and 88
F 1961—1964 = 5.03**, d.f. 3 and 57

90. Numbers of *Javesella* nymphs in suction samples taken in spring in first-year leys established under spring cereals. Same material as in Tables 32 and 81

Year	Sampling period	No. of fields	No. of delphacid nymphs	*Javesella* nymphs		
				No.	%	No. per 0.3 m²
	23. IV—21. V	7	875	862	98.5	123
	15.—16. IV	7	704	697	99.0	100
	28.—29. IV	7	577	576	99.8	82
	22.—24. IV	20	552	447	81.0	22
	6.— 9. V	20	1 312	1 267	96.6	63
	23.—25. IV	20	1 043	1 039	99.6	52
	27.—29. IV	20	2 103	2 057	97.8	103

—1964 = 3.27**, d.f. 6 and 94
—1964 = 5.54**, d.f. 3 and 57

ble 91. Abundance of *Javesella* nymphs and *J. pellucida* adults in first-year timothy leys established under spring cereals, 1958—1964. In 1958, 60 net sweeps were made in each field, in the other years 200 sweeps

Year	Sampling period	No. of fields	Nymphs			Adults		
			No. of delphacids	*Javesella*		No. of delphacids	*J. pellucida*	
				No.	%		No.	%
58	8. V—18. VI	20	2 647	2 642	99.8	359	330	92
59	14. V— 4. VI	20	6 316	6 303	99.8	1 388	1 307	94
60	20. V— 2. VI	17	4 796	4 662	97.2	1 217	1 193	98
61	29. V— 6. VI	20	4 755	3 756	79.0	409	373	91
62	2. VI— 7. VI	20	1 811	1 751	96.7	282	255	90
63	23. V—31. V	20	1 269	1 260	99.3	404	396	98
64	25. V—26. V	20	17 596	17 481	99.3	1 222	1 055	86

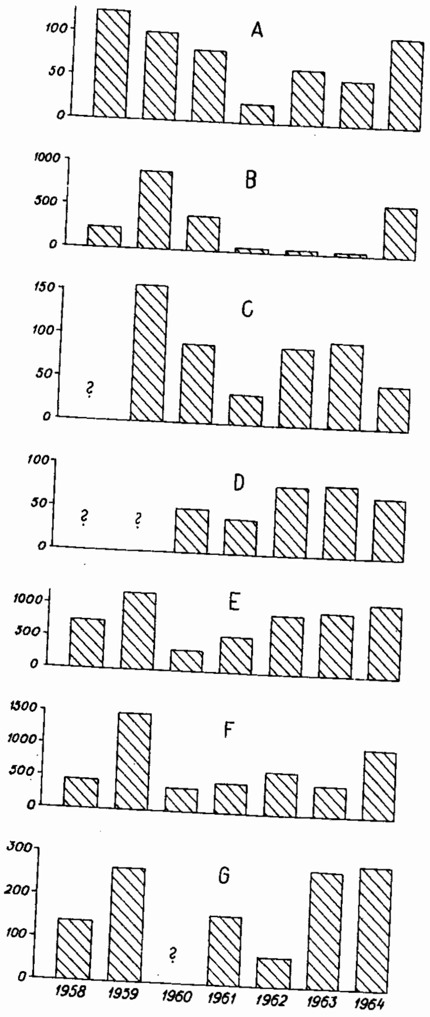


Fig. 77. Numbers of *J. pellucida* adults, *Javesella* nymphs (comprising mainly *J. pellucida*) and delphacid eggs (mainly *J. pellucida*) in 1958—1964. A = numbers of *Javesella* nymphs in spring per 0.3 m², B = migrating *J. pellucida* per netting apparatus per year, C = *J. pellucida* adults in oats per 60 net sweeps, D = *J. pellucida* adults in spring wheat per 60 net sweeps, E = delphacid eggs in oats per 100 plants, F = delphacid eggs in spring wheat per 100 plants, G = *Javesella* nymphs in autumn per 0.3 m². ? = no samples or samples uncertain. Same material as in Fig. 24 and Tables 85—90.

higher than the previous summer. In interpreting the results it must be borne in mind that in the summers of 1960 and 1961 the proportion of *J. pellucida* among delphacid eggs was lower than in the other summers (cf. Tables 85 and 86).

After the summer of 1961, the density of *J. pellucida* rose from year to year (Fig. 77; Tables 63, 85—91). At the end of the summer of 1962 there may have been a sharper drop in the density of *J. pellucida* than the average. That year, however, the nymphs were small (Tables 31 and 32), and small nymphs are obviously collected by the suction apparatus less efficiently than large ones (cf. Heikinheimo and Raatikainen 1962, p. 15). Furthermore, the weather at the time of sampling was very bad,so that the decrease in density appearing in the tables is not reliable.

2. *Reasons for fluctuations*

Food supply and its spatial distribution. In the communes of the region under investigation, about 90 % of the cultivated area was grown to crops which were a source of food for *J. pellucida* (Official statistics of Finland III 54), and in this area the leafhopper occurred. In addition, suitable host plants for the species also grew along field edges, on wasteland, etc. During the years of the investigation there was an increase of a few percent in the area devoted to cereals, particularly oats, while the area of grassland declined (cf. Official statistics of Finland III 48—52, 56—60). The change was most pronounced in 1959, and as a consequence there was apparently a slight reduction in the density of *J. pellucida*. A decrease in population density was observed in 1959 and 1960, but it was due only in small part to the change in crop cultivation mentioned above. Furthermore, the decline in abundance of *J. pellucida* did not continue after this, as might have been expected, but on the contrary rose again.

There was generally an abundant food supply for adults and nymphs of *J. pellucida* in cereal fields (cf. Raatikainen and Raatikainen 1964, 148, 149), which comprised their most portant sites of propagation. The year 1959, wever, was extremely dry (Tables 1 and 2), that summer cereals and many annual weeds ured and died early. At the same time the nsity of *J. pellucida* in the cereal fields dropped rply, and one of the main reasons for this s lack of food. For example, on a nearly ripe field only 1.0 *J. pellucida* adult per 20 net eeps on the average was collected on July 30, ile 5.0 were obtained from patches of green *ytrigia repens* growing on the same field.

During the years of the investigation underund drainage became widespread in the gion, and this to some extent diminished the bitats suitable for *J. pellucida* nymphs. A proble consequence of this change was a slight line in the density of *J. pellucida*.

The cereal and hay fields were usually small, en about 0.5—2 hectares in size, and they re generally situated in the clearings in such ay that at least macropterous *J. pellucida* could ch them. In small clearings, which were few number in the region, there was a scarcity suitable host plants in some years. However, n so adequate food plants grew along the rders of such clearings so that they were ficient to support a substantial population leafhoppers.

n general, *J. pellucida* had ample food everyere and throughout the region, so that the bile stages could easily find it. In 1959, hower, there was a scarcity of food, the result ng a great decrease in the numbers of the ecies.

M a n. *J. pellucida* is a species which has clearly rived benefit from colonization. Even today density of the species is low in wild regions high in cultivated areas. The species premably occurred in the region even before rmanent settlement, but became more abunnt after land clearing took place and increased rther in the past century, when leys began to established, first under winter cereals and er under spring cereals. The effect of man on numbers of *J. pellucida* has been both direct indirect. Among other things, the increase was at first a consequence of the expansion in the area devoted to its host plants and the increase in suitable habitats, and later of the decrease in the numbers of nymphs killed by ploughing.

Insecticides which were toxic to *J. pellucida* were used only in exceptional cases on cereals and leys in the region investigated. In 1959, however, an estimated 20 % of the area devoted to oats, 15 % of the barley area and about 5 % of the spring wheat area were treated with insecticides at the end of the migration period of *J. pellucida* in order to control *Rhopalosiphum padi* (L.) (Raatikainen and Tinnilä 1961, p. 16). The effect of these treatments is not reflected in a decline in numbers of leafhoppers in 1959 (Tables 85, 87, 88), since none of the fields investigated were treated.

The effect of the above insecticidal treatment would be expected to appear in the density of adults, eggs and nymphs in 1960, and the density that year was indeed small. The chemical treatment obviously caused a considerable reduction in numbers of *J. pellucida* in 1959, but by itself it was not sufficient to reduce the density as greatly as it actually did decrease. The density of certain species primarily inhabiting leys and even cereals rose that year, or at least seemed to rise (cf. Tables 49, 50, 64; Raatikainen and Vasarainen 1964, pp. 318, 319).

The cereals were usually harvested by binder, and the harvesting time varied widely in the different years. For example, in the warm, dry summer of 1959 about 10—15 % of the rye and barley had been cut by August 10, while the figure for oats and spring wheat was less than 10 %. In the fairly average summer of 1958 corresponding amounts of cereals had been cut about one month later, and in the cool summer of 1962 even later. Even though eggs of *J. pellucida* hatched earlier in warm summers than in cool ones, the proportion of eggs that had hatched at the time of harvesting was not the same every year. For instance, in 1960 there was probably a considerably higher proportion of hatched eggs of *J. pellucida* by the time of harvesting than in 1958 and 1957 (Fig. 78).

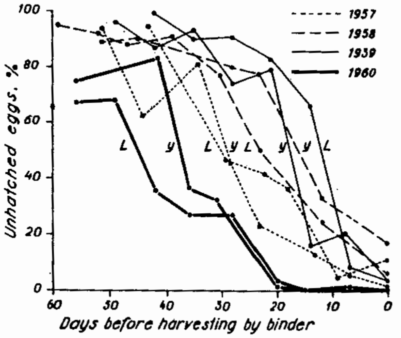


Fig. 78. Percentage of unhatched delphacid eggs in oats at Laihia (L) and Ylistaro (Y) in 1957—1960. Same material as in Fig. 16.

However, this did not greatly reduce the leafhopper density (cf. Raatikainen 1966 a).

During the course of the investigation the method of harvesting cereals shifted from the use of mowers and binders to combine harvesters, with the consequence that the time of harvesting became later and the stubble was taller (Raatikainen 1966 a). When the cereals were cut later, a greater number of nymphs managed to hatch from the eggs prior to cutting. As a result, the density of *J. pellucida* nymphs may have risen somewhat during the period of investigation, but such a rise was so small that it had virtually no effect on the actual increase in density. Moreover, a relatively larger number of leafhopper eggs remained in a tall stubble than in a short one, and the relative humidity of the microclimate in the tall stubble apparently did not decrease so much as in a short stubble. These factors, too, may have had a slight influence in raising the nymphal density of *J. pellucida*.

The cereal stubble and the vegetation along the field edges were burned quite often (Raatikainen and Raatikainen 1964, p. 136), with the consequence that a substantial proportion of the eggs and nymphs in these fields were destroyed. Such burning appeared to decrease during the course of this investigation, and the density of *J. pellucida* may have risen slightly as a result. The waste straw remaining after threshing was usually burned, and the eggs in it were thus destroyed.

The proportion of the cultivated area devoted to cereal crops used as nurse crops for leys may have declined slightly during the years of this study, but this had little effect on the density of *J. pellucida*. In 1959, however, establishment of leys failed quite generally in the region, and the same autumn or following spring many of these fields were ploughed. This meant that the proportion of *J. pellucida* nymphs destroyed was larger than usual. In 1960, more new leys than usual were established under cereals, and this measure obviously increased the population density of *J. pellucida* in 1961, although the effect was not very distinct (Tables 85—91, Fig. 77).

Biotic factors. According to Milne (1957), competition between individuals of the same species is the ultimate factor controlling increase. However, in the localities under study the density of *J. pellucida* was so low that this kind of competition was rather insignificant in all the years.

The mortality inflicted by pteromalids was large every year. During the period of investigation, cultivation of oats shifted from varieties having thin-walled stems, such as Tammi, to those with thick-walled stems, such as Pendek (cf. also Valle et al. 1958, Official statistics of Finland III: 56). This reduced the possibilities for pteromalids to feed on eggs of *J. pellucida*. The actual decrease in mortality, however, was extremely small.

As the use of combine harvesters became more common and the stubble in consequence became taller, the adult density of *Panstenon oxylus* probably increased to some extent during the period of investigation, and at the same time the opportunities for the species to destroy *J. pellucida* eggs improved slightly (Raatikainen 1966 b).

The proportions of internodes inhabited by *P. oxylus* and *Mesopolobus aequus* varied widely (Tables 43, 44, 49, 50). These predators form a pair with the characteristic that when one of the two species was abundant, the other occurred arsely, and vice versa. The numbers of del- acid egg-containing internodes inhabited by vae of these species were positively correlated th the numbers of internodes containing del- acid eggs (Table 92). Oat samples were exam- d in the years 1958—1964, and the values mbined every year; the coefficient of corre- ion was 0.92** (d.f. 5) and the regression tween the numbers of internodes inhabited by eromalids per 1 000 plants and the numbers internodes containing delphacid eggs was —11.4 + 0.49x. In the wheat samples the rresponding figures were r = 0.99*** (d.f. 5) d y = —15.0 + 0.70x. The percentage of g-containing internodes inhabited by ptero- alids also varied (Tables 49 and 50), and it peared that these predators destroyed few *pellucida* eggs in 1958, and the leafhopper pulation consequently succeeded in becoming nser. In contrast, in 1959 and 1960 they stroyed many eggs and the density of the pulation decreased. In the following years, 61 and 1962, again few eggs were destroyed d the leafhoppers increased in abundance (cf. bles 49, 50, Fig. 77). Evidently the pair of ecies *P. oxylus* — *M. aequus* was partly re- onsible for the fluctuations in abundance of *J. pellucida*, and they constituted a primary cause, which in turn was regulated by weather factors.

ble 92. Regression between numbers of internodes inhabited by pteromalids (y) and numbers of internodes taining delphacid eggs (x) as well as correlation coefficients in different years. One hundred plants were examined in each field. Same material as in Tables 43 and 44

ear	No. of fields	r	Regression between y and x	Number of internodes containing delphacid eggs per 100 plants	
				Min.	Min.
ats					
1958	20	.93***	y = —0.2 + 0.33 x	2	83
1959	20	.80***	y = 0.4 + 0.46 x	8	102
1960	20	.76***	y = 1.3 + 0.32 x	2	35
1961	20	.98***	y = —0.2 + 0.43 x	1	56
1962	20	.97***	y = —5.4 + 0.60 x	1	121
1963	20	.97***	y = —1.6 + 0.55 x	1	98
1964	20	.95***	y = —1.7 + 0.58 x	2	69
ring heat					
1958	18	.98***	y = —0.9 + 0.67 x	0	61
1959	17	.99***	y = —3.4 + 0.76 x	7	106
1960	17	.90***	y = 1.4 + 0.50 x	3	27
1961	20	.97***	y = —1.2 + 0.62 x	1	59
1962	20	.93***	y = —2.4 + 0.68 x	3	61
1963	20	.96***	y = —0.9 + 0.72 x	3	47
1964	20	.98***	y = —0.6 + 0.67 x	7	92

The abundance of *Anagrus atomus* also varied considerably (Tables 55 and 56), but since this species destroyed not more than a few percent of the eggs of *J. pellucida* at most, it had no marked effect on the fluctuations of the species. The numbers of leafhopper eggs in the leaves were largest when the density of leafhoppers transmitting OSDV was high or when the weather was very dry; and under such circumstances there were also large numbers of *A. atomus*. It seems that in the restricted area investigated, *A. atomus* was a direct density-dependent factor.

Achorolophus gracilipes killed relatively the greatest numbers of nymphs of *J. pellucida* in the spring of 1960 (Table 78). Thereafter, in relation to the leafhopper, the numbers of *A. gracilipes* were small, and consequently the density of *J. pellucida* may have increased. However, this species cannot be regarded as an actual cause of fluctuations in *J. pellucida*.

The proportion of *J. pellucida* parasitized by *Elenchus tenuicornis* was high in 1959 (Tables 74—76), and at that time relatively few *J. pellucida*

Table 93. Regression between numbers of *J. pellucida* parasitized by *E. tenuicornis* and *D. lindbergi* (y) and total number of *J. pellucida* (x) as well as correlation coefficients in different years. Netting samples (60 sweeps each) were taken in oats and spring wheat during the periods shown in Tables 64 and 65

Year	No. of fields	r	Regression between y and x	Number of *J. pellucida* per 60 net sweeps	
				Min.	Max.
Oats					
1961	20	.91***	$y = -0.3 + 0.19x$	1	134
1962	20	.92***	$y = -2.8 + 0.32x$	5	63
1963	20	.89***	$y = -1.6 + 0.18x$	3	394
1964	20	.81***	$y = 0.3 + 0.07x$	1	213
Spring wheat					
1961	20	.91***	$y = 0.2 + 0.21x$	0	171
1962	20	.97***	$y = -6.1 + 0.45x$	12	411
1963	20	.84***	$y = -0.8 + 0.19x$	5	296
1964	20	.93***	$y = -2.1 + 0.10x$	7	312

females produced eggs, but the number of eggs was great. In contrast, in 1960 and 1961 the percentage of leafhoppers parasitized by *E. tenuicornis* was low, and *J. pellucida* was thus able to increase in numbers, as actually occurred. In 1962 the frequency of parasitized leafhoppers was again high, and as a consequence there was probably a decline in the reproduction of the species. Evidently *E. tenuicornis* affected the fluctuations of *J. pellucida*, but, like the preceding species, it was probably not a major factor influencing the abundance of the leafhopper.

Dicondylus lindbergi apparently did not contribute to the decline in the population density of *J. pellucida* in 1959, but it probably slightly retarded the subsequent increase in density (Tables 63—65).

The two species *D. lindbergi* and *E. tenuicornis* formed a pair which parasitized *J. pellucida* (Table 93). Another parasite was a pipunculid, of which only one specimen was discovered parasitizing a leafhopper. The numbers of *J. pellucida* parasitized by these three species in the oat samples which were taken in 1958—1964 and combined annually were positively correlated with the numbers of *J. pellucida* ($r = 0.87^{*}$, d.f. 5). As regards the spring wheat samples, the figure was $r = 0.45$ (d.f. 4). Evidently this group of species was also partially responsible for the fluctuations in abundance of *J. pellucida*, and they likewise constituted a primary cause which in turn was regulated by weather factors.

Weather factors. The winter mortality of *J. pellucida* was studied using the material listed in Tables 89 and 90, as well as samples taken in the autumn of 1957. According to these data the winter mortality of *Javesella* nymphs in the different winters was as follows:

1957—1958 ..	27.0 %	1961—1962 ..	60.5 %
1958—1959 ..	27.8 %	1962—1963 ..	23.9 %
1959—1960 ..	68.7 %	1963—1964 ..	62.1 %

The average winter mortality of *J. pellucida* appeared to be at least 45 %, and there were great differences between the various winters. The percentage calculated for the winter of 1962—1963, however, was probably too small, since the autumn samples included fewer nymphs than usual. The mortality was not seen to be correlated with the snow depth or the severity of frost, but if adequate good samples were available, it is possible that causes could be found. The factors responsible for winter mortality may also have partly caused the fluctuations in abundance of *J. pellucida*.

The eggs of *J. pellucida* readily succumbed to desiccation when the external conditions were too dry. The eggs in the stems were not subject to such a great risk in this respect as those in the leaves, but in exceptional cases they, too, died of desiccation. For example, in the dry summer of 1959, an experiment was made comprising 18 gauze cylinders containing oats with *J. pellucida* eggs in them. Of a total of 997 eggs found in the leaves, about 813 (81.5 %) had dried up, while in the stems 3 272 eggs were found, of which 1 138 (34.8 %) had dried up. In the field the mortality due to drought was not so great, but even there a considerable proportion of the eggs succumbed to drought in 1959.

In the field the mortality of nymphs due to drought appeared to be relatively greater than that of the eggs. According to Hassan (1939, p. 352), the degree of humidity prevailing during the moulting of the nymphs is of great importance, for if the old skin becomes too dry, the insect cannot detach itself from it; and if there is too much moisture the emerging insect cannot harden properly and is susceptible to moulds, which kill it. According to Dlabola (1960, pp. 366, 367), likewise, *J. pellucida* is a typical species of moist, cool places, and its youngest nymphs tend to die when the temperature rises to 30°C and the relative humidity drops to 30 %. In cereal fields and leys, the relative atmospheric humidity at all times of the day and night is higher within the canopy of vegetation than outside it (cf. Franssila 1949, p. 180).

In the dry summer of 1959, cereals and grasses grew poorly and were lower and sparser than average. Since the leys and cereals were cut considerably earlier than usual, the nymphs of *J. pellucida* were left in a very dry environment in July and August (cf. Table 2), and many of them died of desiccation or lack of food caused by the drought. In this dry, warm summer the weather evidently influenced the population density of *J. pellucida* in many ways: It probably caused the scarcity of food supply for *J. pellucida*, the increase in *Rhopalosiphum padi* and the subsequent widespread insecticide treatment of cereal fields, the failure of many leys to become established and the ploughing up of these fields in the autumn of 1959 or spring of 1960, the increase in *M. aequus* and reduction in relative numbers of *P. oxylus*, the rise in population density of *A. atomus* in the summer of 1959, the relative increase in density of *Achorolophus gracilipes*, the rise in relative numbers of *D. lindbergi* and the concurrent relative decrease in density of *E. tenuicornis*. In addition, weather factors also had an indirect influence, through the relative areas devoted to different crops and varieties.

The exceptional weather in the summer of 1959, with its excessive warmth and drought, was probably the chief factor responsible for the reduction in the population density of *J. pellucida*. In 1959, the weather had a direct effect on the mortality of the immature stages of the species as well as an indirect effect through the agencies of natural enemies, other animals and cultural practices. The decline in the density due obviously to these latter indirect effects of weather continued even into the following year, but, starting from the middle of the summer in 1960, the weather evidently caused a renewed rise in population density.

VII DISCUSSION

On the cultivated land in the region under investigation, *Javesella pellucida* was a very successful species. The climate was favourable for it, abundant grasses and cereals were available as host plants, habitats were so situated that the species could easily reach them, and although there were predators and diseases, they were unable to destroy more than a part of the progeny.

The species is dimorphic. The brachypterous individuals moved for only short distances, while the macropters migrated for longer distances and were responsible for spreading the population into surrounding areas, as has also been demonstrated in the case of *Dicranotropis hamata* (Boh.) (Raatikainen and Vasarainen 1964, p. 320). This is a characteristic which is advantageous to the species in the region under investigation. Although the height of migration of the macropters was greater than, for example, *Laodelphax striatellus* (Fallén) (Sukhov and Petlyuk 1940, p. 484), forests constituted a considerable hindrance to migrating individuals.

There were many forests in the region, and therefore the migration of macropters was mainly within the population itself. Thus, the *J. pellucida* occurring on each more or less isolated clearing is considered to be a distinct population distributed into sub-populations in the different fields of the clearing. However, the populations were so large that the influence of any lethal genes was much smaller than in the trials of Kisimoto and Watson (1965).

Kisimoto (1956 a—c) has experimentally demonstrated that the proportion of macropters of certain leafhopper species increases as the population density rises. The same phenomenon was noted in the *J. pellucida* populations in the field in the present studies. The dispersal of the leafhopper was found to be density-dependent. The population density in first-year leys in the region studied was so high that the proportion of macropters averaged over 90 %. Even in populations of very low density the species consisted mainly of the macropterous form, so that in practice the density evidently cannot become so low as appreciably to hinder migration. Previous studies have shown that the dispersal of some other insects, e.g. locusts and butterflies, is density-dependent (e.g. Uvarov 1928, Solomon 1957, p. 133, Williams 1958, Kaisila 1962).

Only 10 animal species and two diseases were found to be natural enemies of *J. pellucida*, as well as a number of nonpredators, whose importance was quite small. The enemies were oligo- or polyphagous, and most of them were common species with a wide range. In the region of investigation they were capable of living not only in cereals and first-year leys, but also in old leys, along the borders of fields, and in natural meadows. *Panstenon oxylus*, *Mesopolobus aequus* and *Anagrus atomus* were able to follow *J. pellucida* from place to place. *Elenchus tenuicornis*, *Dicondylus lindbergi* and *Achorolophus gracilipes* were quite easily carried to new sites along with *J. pellucida* or other delphacids. The enemies attacked all developmental stages of the leafhopper and were able to destroy them in almost all possible sites. However, eggs located within thick stem walls were difficult for enemies to reach.

The abundance of the enemies varied considerably, but the most important egg-predators, *P. oxylus* and *M. aequus*, as well as the most important parasites of the mobile stages, *E. tenuicornis* and *D. lindbergi*, formed pairs of species. When the density of one species of the pair diminished, that of the other increased; and consequently the relative amount of destruction caused by the enemies remained approximately the same in different localities and different years. There was another factor, which ensured that the enemies of *J. pellucida* were always able to destroy approximately the same proportion of leafhopper offspring. If the losses of eggs caused by the egg predators had been small, the species attacking nymphs and adults would have been able to inflict greater losses than they actually produced during the years of the investigation, since, for instance, only a small fraction of the triungulinids of *E. tenuicornis* succeeded in finding a host and if there had been more hosts present, a greater proportion of them would have become parasitized.

The enemies of *J. pellucida* were very important in regulating the population of the species, since they caused the destruction of about 50—60 % of the progeny. In Czechoslovakia, on the other hand, abiotic factors have a more pronounced influence on the population density of *J. pellucida* than enemies (cf. Dlabola 1960). In the region of the present study, man should beware of destroying the natural enemies of leafhoppers and should, in fact, attempt to promote their increase. The enemies described here could evidently be used to control not only *J. pellucida* but other delphacid leafhoppers as well. The pteromalids are apparently efficient predators of eggs which extend into the cavity of the stem, and *Anagrus atomus* effectively destroys eggs in the leaves. The latter species, in particular, would obviously be very useful as a biological control agent. So far, however, little is known about the environmental requirements of these enemies. It is quite probable, for example, that *E. tenuicornis* do not thrive well in continental regions.

At the beginning of this century it was believed that the abundance of insects was principally gulated by their enemies. Later, the influence f weather factors was considered to be very ominant. Still later, attention has been paid to ternal factors within the species and competiion between individuals of the same species g. Schwerdtfeger 1941, Kanervo 1946, Milne 1957). In 1963—1964, it was calculated at 50—60 % of *J. pellucida* in the region under vestigation were destroyed by enemies, 8— % by weather factors and 12—15 % by man. urther mortality was caused by internal factors, ck of food and unsuitable places in which to e, while about 10—25 % of the mortality was e consequence of factors not well understood.

The population density of *J. pellucida* was quite fferent in the different years. The reason for is was partly variations in the production of ffspring but chiefly variations in mortality. uring the 9-year period of this study, there ere two exceptional years from the standpoint f weather, the warm, dry summer of 1959 and e cool summer of 1962 (cf. Valle 1962, 1963). he influence of weather factors was not clear, owever, and the fluctuations in population denty were obviously caused by many factors, as s been found by Schwerdtfeger (1941) and olomon (1957). According to Solomon (1957, 139), in regions with a climate relatively quable to insect life, biotic factors seem espeally important, and control by parasites and redators is clearly evident. In less favourable limates with a 'hard' season, physical factors eem more important in the determination of bundance. The present investigations demontrate that even in relatively equable climates, eather factors may sometimes influence the bundance of insects. In this study, such weather actors affected *J. pellucida* both directly and also ndirectly through the agencies of food supply, nemies and man. The whole situation is actually very complicated chain reaction, in which ertain unknown basic factors caused the weather, nd the weather, in turn, produced its effect diectly and indirectly through biotic factors, man nd food.

The population density of *J. pellucida* also aried considerably between different localities. In this case, such variations were mainly caused by cultural practices. When different proportion of fields was ploughed and tilled the proportion of leafhoppers destroyed was different, too. Furthermore, cultural practices affected the natural enemies of the species in different ways from place to place, and this was also partially responsible for variations in the mortality of the leafhoppers. In earlier times *J. pellucida* was presumably moderately frequent on virgin land, but the operations of man, principally agriculture, led to an increase in the populations; and at present, agriculture is the most important factor regulating the spatial variations in the abundance of the species in central Finland. Weather factors, competition between individuals of *J. pellucida*, enemies and food scarcity are apparently unable to prevent growth of the populations if there is an increase in the area of first-year grass leys established under cereals in relation to the area of cereals (cf. Raatikainen and Tinnilä 1959 a). Theoretically the leafhopper density can be regulated to a considerable extent, in particular by modifying the system of crop rotation, the areas devoted to different crops and the method of drainage. Such changes are difficult to carry into practice, but possibilities do exist for effecting them.

The factors influencing population size have been categorized in various ways (e.g. Schwerdtfeger 1941, Allee et al. 1950, Andrewartha and Birch 1961, Franz 1961). However, in many studies the influence of man has been given too little attention or even neglected completely. Even in investigations dealing with the fluctuations in populations of pest species, the effect of man is sometimes entirely ignored. However, it was obvious in the present study that man had a very marked influence on the size and density of the populations of *J. pellucida* and its enemies. In many other circumstances, too, man is evidently a very important factor regulating insect populations. The effect of man is to be compared to that of enemies, food supply and weather as one of the essential factors, at least in the population dynamics of agricultural pests.

VIII SUMMARY

In the period 1956—1964, studies were carried out on the bionomics and fluctuations in abundance of *Javesella pellucida* and its enemies in the region east of the city of Vaasa in western Finland. The major part of the investigation was performed in the field laboratory of the Department of Pest Investigation at Laihia and in the surrounding area. Fluctuations in the abundance of the various species were studied in 20 localities. Furthermore, data were obtained from other parts of Finland.

Javesella pellucida (F)
(Hom., Delphacidae)

J. pellucida was extremely abundant in the area investigated. The size of the egg varied according to its age and to the female. Eggs occurred from June to October. Nymphs were present throughout almost the entire year but were at a minimum in July. The species hibernated in all nymphal instars but mostly in instars IV and III. The nymphs overwintered chiefly in the same site where they had hatched, although some of them apparently moved to the borders of the fields. The mean daily temperature sum between the appearance of eggs and October 2 showed a strong positive correlation with the hibernating instar found in the autumn ($r = 0.92^{**}$). Adults occurred from May to September.

At the beginning of emergence, brachypters made up an average of 5.5 % of the leafhoppers in first-year leys. When the population density of the species increased, the proportion of macropters probably rose.

Brachypters moved for distances of at most only a few dozen metres. Macropters migrated in the daytime, in the direction of the wind, usually at heights 2—6 metres above the ground. The distances travelled by the migrating leafhoppers were probably up to several kilometres in length. It was possible to predict the onset of migration with a precision of 1.7 ± 0.5 days by means of the mean daily temperature sum of the preceding periods. Migration occurred during the period May 26—July 20, and lasted an average of at least 42 days.

J. pellucida was most abundant on open sites where grass plants were growing, particularly in spring cereals, first-year leys established under cereals, and winter cereals. The species migrated mainly to spring cereals. In spring the population density was greatest in first-year leys established the previous year under spring cereals.

The most important food plants of the nymphs were cereals and timothy, that of adults before migration timothy and after migration cereals.

The sex ratio was found to be close to 1:1. Copulation apparently took place after migration, and the male could copulate with at least two females. The pre-oviposition period at 17°C was 13—22 days, and the oviposition period in the insectary averaged 27 days. The average number of eggs produced on oats was 402 ± 38.5. Among the gramineous plants, the number of eggs laid was highest when the females were in spring cereals and lowest in ley grasses. Under natural conditions the most important plants for oviposition were spring cereals, winter cereals and ley grasses. Most of the eggs were located in the stems, but some occurred in the leaves as well. In oat fields the number of eggs per internode rose as the egg density increased.

Enemies and diseases

Panstenon oxylus (Walk.) (Hym., Pteromalidae)

P. oxylus was common and abundant in the area investigated. The length and diameter of the egg were positively correlated with the length of the wing of the female. The length of the wing was positively correlated with the number of delphacid eggs in the internodes. Males achieved their maximum size after consuming about 30 delphacid eggs, and females after consuming about 40 eggs.

P. oxylus had one complete and one incomplete generation per year. About 4 % reached the adult stage at the end of the summer. The species hibernated in the larval stage and emerged as adults in late May and early June.

The species was most abundant in spring cereals and in first-year leys established under cereals. In general, only the females migrated in June and July.

On cereal fields eggs of delphacids, particularly *J. pellucida*, comprised the chief food source of the larvae. One larva generally destroyed 20—30 eggs.

The sex ratio was about 1:1. If there were few delphacid eggs in the internodes, the sex ratio tended to be male-dominated. When females reproduced parthenogenetically, their progeny were males. The average number of eggs laid in the trials was 149 per female. This number was positively correlated with the life-span and the length of the wing. In oats and presumably also in other spring cereals, oviposition generally took place in the thinnest-walled internodes containing delphacid eggs.

The numbers of *P. oxylus* have probably increased greatly as a result of land clearance and the expansion in cultivation of cereals and hayfields. Evidently the numbers of the species were most strongly reduced by the destruction of cereal straw and stubble, while superparasitism and enemies were also important factors. Other factors decreasing the abundance of *P. oxylus* were unfavourable living sites and weather conditions as well as scarcity of food supply. Weather factors acted both directly on the fluctuation in numbers of the species and indirectly through food and the competitive species *Mesopolobus aequus*.

Mesopolobus aequus (Walk.)
(Hym., Pteromalidae)

M. aequus was quite common but not abundant in the area investigated. Only one generation per year was observed. The males emerged somewhat earlier than the females and died the same year. The females overwintered, and migrated to fields of spring cereals the following year mainly in June.

In cereal fields, eggs of delphacids, particularly *J. pellucida*, comprised the chief food source of the larvae. One larva generally destroyed 20—30 delphacid eggs.

The sex ratio was female-dominated. If the internode contained few delphacid eggs, males mainly emerged, while if there were many eggs present, females predominated. The numbers of larvae per unit of ground area as well as per number of internodes containing delphacid eggs were greater in spring wheat than in oats.

The fluctuations in abundance of *M. aequus* in the years 1958—1964 were probably chiefly caused by weather factors. In warm summers the density of larvae increased and in the cool summer of 1962 it decreased. Furthermore, in that cool summer not all the specimens succeeded in emerging as adults, while those still in the immature stages died. *Panstenon oxylus* competed with *M. aequus* for the same internodes containing delphacid eggs. In warm summers *M. aequus* apparently took possession of such internodes from *P. oxylus*, while in cool summers the situation was reversed.

Anagrus atomus (L.) (Hym., Mymaridae)

A. atomus was abundant in the region investigated. It hibernated as the immature stages in eggs of *Solenopyx sulphurellus* (Zett.) located in leys and cereal stubble. The total developmental period of the immature stages at +12.5° lasted 35 days, and the adults lived for 2—6 days. In June and July the adults of the first generation migrated to cereal fields, where 2—3 further generations arose. In cereals the chief food supply consisted of eggs of delphacid leafhoppers, particularly *J. pellucida*.

About 39 % of the specimens were males. Parthenogenetic reproduction may take place. The number of progeny was 28—42. The species principally parasitized eggs located in the leaves, but also some of those in the stems. This species was a very efficient destroyer of *J. pellucida* eggs in cereal leaves.

The food supply was an important factor causing fluctuations in the abundance of the species. If there was adequate food, i.e. delphacid eggs in the leaves, such as in oat stands infected by OSDV and EWSMV or suffering from drought, *A. atomus* was abundant. If, on the contrary, the food supply was meagre, the parasite was scarce.

Dicondylus lindbergi Heikinh. (Hym., Dryinidae)

D. lindbergi was quite abundant in the area investigated. The species was univoltine. In about 5 % of the cases studied, the larvae became visible in the nymphs of *J. pellucida*, while in the others they became visible in the adults. In the field, the larvae usually pupated on the leaves of cereals. The adults began to emerge at the end of July or later.

In early summer larvae of *D. lindbergi* were most abundant in those places where *J. pellucida*, too, was most numerous. Parasitized leafhoppers migrated during approximately the same period as healthy ones, and no differences in the height of migration were observed between parasitized and healthy leafhoppers.

On an average, the females lived over $1^1/_2$ months in the cultures and consumed nymphs of six delphacid species. The female killed at least 2.7 *J. pellucida* nymphs of instars II to IV and at most 3.8 nymphs per day.

Only 1 % of the specimens were males, and one male copulated with many females. Unfertilized females evidently produced female progeny. Usually there was only one larva in each *J. pellucida* nymph. A parasitized leafhopper was incapable of reproducing.

D. lindbergi was most numerous on cultivated land. The population fluctuated considerably during the years 1958—1964, and weather factors evidently had the greatest influence in causing such fluctuations in abundance.

Elenchus tenuicornis (Kirby) (Strepsiptera, Elenchidae)

E. tenuicornis was common and abundant, and had one generation per year. Its developmental rhythm was well adapted to that of *J. pellucida*, but differed somewhat from the latter in the different years.

E. tenuicornis hibernated as a larva in its host. Some of the male pupae already became visible in nymphs of *J. pellucida*, but most of them did not appear until the host was adult. The females became visible exclusively in adult hosts.

The males emerged between the hours of 4 a.m. and 10 p.m., and their life-span was about 6 hours. The main period of flight was in July.

The discharge of triungulinids from the female usually began in the morning and continued for an average of 44 hours. The triungulinids lived for only a few hours and readily succumbed to desiccation.

In wintertime the density of *E. tenuicornis* was greatest in leys which had been established the previous year under a cereal. After migration of leafhoppers, *Elenchus* was most abundant in cereals but also occurred to some extent in leys.

The parasite was carried to adjacent fields in nymphs and brachypters, but when its host was a macropterous leafhopper, the most important of which was *J. pellucida*, it was transported for long distances.

In Finland *E. tenuicornis* has been found in 16 species of delphacids. The chief host in the region of investigation was *J. pellucida*, and in other hosts the species made up only a few percent. In cultures offspring of a female in *Stiroma bicarinata* (H.-S.) succeeded in entering *J. pellucida* and growing to the adult stage in their new host species.

The behaviour, rate of development and life-span of parasitized *J. pellucida* was different from the normal. Furthermore, parasitized leafhoppers were incapable of reproducing.

The sex ratio appeared to be male-dominated. The progeny numbered at least 1 620 ± 110.5 triungulinids per female. Most of the triungulinids died before finding a host, and many of the parasitized leafhoppers in cereal fields succumbed when the fields were ploughed. Weather factors were apparently responsible for the fluctuations in abundance of the species in 1958—1964, acting directly and also indirectly through food supply, biotic factors and man.

Achorolophus gracilipes (Kramer) (Acar., Erythraeidae)

The mites parasitizing *J. pellucida* were mor-hologically of at least two different types, but the present work the single name *A. gracilipes* used for all the red mites encountered.

Mites were found in *J. pellucida* nymphs and dults between May 12 and July 11; they were ommon but not very abundant.

Mites were encountered in leys, edges of fields nd waste land. Among other methods of trans-ortation, they were carried from place to place their leafhopper hosts. *A. gracilipes* parasitized any species of leafhoppers.

There was usually only one mite per *Javesella* ymph. In trials, mite-infested *J. pellucida* speci-ens usually died in the nymphal stage.

The most essential factor influencing the fluc-ations in abundance was apparently the weather e previous summer. After warm summers large roportions of the leafhoppers were mite-para-tized, while after the cool summer of 1962 the tent of mite parasitization was small.

Other animals

Natural enemies of *Javesella pellucida* in the egion of investigation comprised a Dipteran f the family *Pipunculidae* as well as the spider pecies *Dicymbium nigrum* (Blackw.), *Meioneta restris* (C. L. Koch) and *Linyphia pusilla* Sundew. hey destroyed very few *J. pellucida*.

Non-predators which destroyed *J. pellucida* ere *Microtus agrestis* (L.), *M. arvalis* (Pall.), *rvicola terrestris* (L.), *Lepus timidus* L. as well the herbivorous domestic animals, cattle, orses and sheep. But these animals were quite significant in causing mortality among leaf-oppers.

Viruses and fungi

The European wheat striate mosaic virus EWSMV) and oat sterile dwarf virus (OSDV) ccurred in *J. pellucida*, but they were not found to have a directly deleterious influence. Indirectly, however, they affected the mortality.

J. pellucida was infected with the parasitic fungi *Entomophthora major* (Thaxter) M. Gustafs. and *E. sphaerosperma* Fres., which caused a slight amount of destruction to the leafhoppers. *Botrytis* sp. and ? *Cephalosporium* sp. were encountered in eggs and *Penicillium* sp. in nymphs, but they were not found to be pathogenic to the leafhopper.

Fluctuations in the abundance of J. pellucida

J. pellucida thrived well in the region of investigation. The climate was favourable for this species, its host plants were cultivated on about 90 % of the arable land, and they also grew abundantly on surrounding land. The number of progeny was large, and as the population density rose, an evidently increasing proportion of the population migrated to other fields. The host plants were distributed in such a way that the mobile stages easily found them and inhabited them. In addition to the above factors, the activities of man, especially the extensive cultivation of cereals and timothy as well as a rotation system which favoured the species, helped to bring about the high population density of *J. pellucida*, which was often as much as 4 000—5 000 eggs per square metre in oat fields.

Over 99 % of the progeny apparently succumbed. The enemy species *P. oxylus*, *M. aequus*, *A. atomus*, *D. lindbergi*, *E. tenuicornis* an unidentified pipunculid, *A. gracilipes*, *D. nigrum*, *M. rurestris* and *L. pusilla*, as well as non-predators, the parasitic fungi *Entomophthora major* and *E. sphaerosperma* and certain unknown species were responsible for the mortality of about 50—60%. The activities of man killed over 12—15 % and weather factors about 8—15 %. Some 10—25 % of the mortality could not be exactly explained. Spatial variations in abundance were caused by man, both directly and indirectly through biotic factors. The fluctuations from year to year were evidently caused by weather factors, both directly and indirectly through food supply, enemies and man.

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SELOSTUS

Viljakaskaan bionomiasta, vihollisista ja runsaudenvaihtelusta

MIKKO RAATIKAINEN
Maatalouden tutkimuskeskus, Tuhoeläintutkimuslaitos, Tikkurila

Delphacidae-heimoon kuuluva viljakaskas levittää viljakasveihin ainakin neljää virusta, joista tyviversoviruksen ja viirumosaiikkiviruksen aiheuttamat sadon menetykset ovat meillä ajoittain ja paikoitellen suuria. Tässä tutkimuksessa selvitetään kaskaan bionomiaa, vihollisia ja runsaudenvaihtelua Vaasan itäpuolella kuuden pitäjän alueella. Kenttätyöt tehtiin vuosina 1956—1964.

Viljakaskas, Javesella (Calligypona, Delphacodes) pellucida

Laji esiintyy koko viljelyalueellamme ja vuosina 1956—1964 sitä oli tutkimusalueella hyvin runsaasti. Se talvehti toukkana etenkin viljoihin perustetuissa ensimmäisen vuoden nurmissa, mutta myös vanhemmissa nurmissa, pientareilla ja muissa heinäkasveja kasvavissa paikoissa. Laji aikuistui toukokuun puolivälin ja heinäkuun puolivälin välisenä aikana. Kaskastiheyden suurentuessa pitkäsiipisten osuus suureni. Lyhytsiipiset siirtyivät enintään muutaman kymmenen metrin päähän, mutta pitkäsiipiset vaelsivat tuulen suuntaan 20. 5.—20. 7. ilmeisesti useiden kilometrien päähän tavallisimmin 2—6 metrin korkeudessa ja laskeutuivat yleensä viljapeltoihin. Vaelluksen alkamisaika kyettiin laskemaan kahden vuorokauden tarkkuudella vaellusta edeltävien kausien lämpötiloista.

Naaras muni kokeissa keskimäärin 402 munaa. Viljapelloissa valtaosa munista oli korsissa, joissa niiden pää ulottui nivelvälin onteloon. Pieni osa munista oli lehdissä. Kaurakasvustoissa nivelvälin munamäärä oli positiivisessa korrelaatiossa 100 kaurassa olevien munien määrään.

Viholliset

Panstenon oxylus -kiilupistiäinen. Pelloilla laji talvehti toukkana viljojen sängissä. Aikuiset ilmaantuivat kesäkuussa, ja lähes yksinomaan vain naarat vaelsivat kesä—heinäkuussa lisääntymispaikkoihin. Naaras muni kokeissa keskimäärin 149 munaa, ja viljapelloissa munat olivat tavallisesti kaskaiden munia sisältävissä nivelväleissä. Toukka hävitti keskimäärin 20—30 viljakaskaan munaa.

Lajin runsaus on todennäköisesti suuresti lisääntynyt viljelyalan suurennuttua ja viljojen sekä heinänurmien viljelyalan lisäännyttyä. Viljan olkien ja sängen hävittäminen vähensi ilmeisesti eniten lajin runsautta. Säätekijät vaikuttivat ravinnon ja vihollisten kautta osaksi myös välittömästi pistiäisen runsaudenvaihteluun.

Mesopolobus aequus -kiilupistiäinen. Vain naaraat talvehtivat pelloilla ja metsissä. Ne vaelsivat etupäässä kesäkuussa viljapeltoihin, joissa ne munivat samanaikaisesti ja samoihin paikkoihin kuin *P. oxylus*. Toukat hävittivät keskimäärin 20—30 viljakaskaan munaa. Lajia oli kuitenkin huomattavasti niukemmin kuin *P. oxylus* -lajia, joten se hävitti pienemmän määrän viljakaskaan munista kuin *P. oxylus*.

Pistiäisen runsaudenvaihtelun pääaiheuttajina olivat ilmeisesti säätekijät. Lämpiminä kesinä toukkatiheys suureni ja viileinä pieneni. Viileinä kesinä vain osa ehti aikuistua, ja toukiksi sekä koteloiksi jääneet tuhoutuivat. *P. oxylus* kilpaili *M. aequus* -lajin kanssa samoista kaskaiden munia sisältävistä nivelväleistä. Lämpiminä kesinä *M. aequus* näytti valloittavan niitä *P. oxylus* -lajilta, viileinä *P. oxylus* taas *M. aequus* -lajilta.

Anagrus atomus -hiukepistiäinen. Laji talvehti kaskaiden munissa ja aikuistui kesä—heinäkuussa. Tämän jälkeen aikuiset siirtyivät lisääntymispaikkoihin. Viljapelloissa ne munivat lähes yksinomaan lehdissä oleviin kaskaiden, etenkin viljakaskaan, muniin. Loisitut munat tuhoutuivat, ja viljakaskaan munasta kehittyi vain yksi pistiäisaikuinen. Lajilla oli 3—4 sukupolvea vuodessa. Kauran lehdissä sen loisimien *Delphacidae*-kaskaiden, etupäässä viljakaskaan, munien osuus nousi vähintään 90 %:iin, joten laji oli hyvin tehokas lehdissä olleiden munien tuhooja.

Ravinto oli hyvin tärkeä runsaudenvaihteluun vaikuttanut tekijä. Jos lehdissä olevia *Delphacidae*-munia oli runsaasti, kuten tyviverso- ja viirumosaiikkiviruksen saastuttamissa tai kuivuuden vaivaamissa kaurakasvuistoissa, *A. atomus* -lajiakin oli runsaasti.

Dicondylus lindbergi -pihtipistiäinen. Laji talvehti viljakaskaan toukassa ja tunkeutui toukkana näkyviin tavallisesti kaskasaikuisesta kesäkuussa. Isäntä kuoli viimeisen asteen toukan jättäessä sen. Pistiäistoukka koteloitui viljapelloissa tavallisesti viljakasveihin, ja ensimmäiset aikuiset kuoriutuivat lämpiminä kesinä heinäkuun lopulla, viileinä elokuun lopulla. Naaraat tappoivat kokeissa noin 3 viljakaskaan toukkaa vuorokaudessa ja munivat viljakaskaan toukkien takaruumiiseen.

D. lindbergi -lajin runsaus vaihteli melkoisesti, ja runsaudenvaihteluun vaikuttivat ilmeisesti voimakkaimmin säätekijät.

Kaskaskierresiipi (*Elenchus tenuicornis*). Laji talvehti monien *Delphacidae*-lajien, tavallisimmin kuitenkin viljakaskaan, toukissa. Isäntien mukana toukat kulkeutuivat peltolohkolta toiselle. Laji koteloitui yleensä aikuisissa kaskaissa. Koiraiden päälentoaika oli heinäkuussa, ja ne elivät koeoloissa noin 6 tuntia. Naarat olivat koko ikänsä isännässään, ja jälkeläiset tulivat ulos heinä—elokuussa. Naaraasta esiin tulleiden toukkien määrä oli keskimäärin 1 620. Toukat tulivat ulos noin kahden vuorokauden aikana, elivät muutaman tunnin ja kuolivat herkästi kuivuuteen.

Suurin osa toukista kuoli ennen kuin löysi isännän, ja peltoja muokattaessa kuoli todennäköisesti yli neljäsosa viljapelloilla olleista toukista. Säätekijät aiheuttivat ilmeisesti välittömästi ravinnon, kilpailevien lajien, muiden eläinten ja ihmisen välityksellä runsaudenvaihtelun.

Achorolophus gracilipes -punkki. Yksi tai useampia lajeja, joista käytetään tässä edellä mainittua nimeä. Punkit loisivat viljakaskaassa 12. 5.—11. 7. Tavallisimmin ne olivat kaskaan toukissa, mutta melko usein niitä oli aikuisissakin. Laji on moniruokainen ja esiintyi tutkimusalueella monissa eri hyönteislajeissa. Punkkien loisimat viljakaskaan toukat kuolivat tavallisesti ennen aikuistumistaan. Lajin runsaus vaihteli melkoisesti. Lämpimien kesien jälkeen loisisten kaskaantoukkien osuus oli suuri ja viileiden jälkeen pieni.

Muut eliöt. Viljakaskaassa loisi jokin *Pipunculidae*-heimon kaksisiipinen, ja kaskaan toukkia hävitti ainakin kolme hämähäkkilajia. Myös myyrät, jänis ja laitumella olevat kotieläimet hävittivät jonkin verran viljakaskaan munia. Hiukepistiäisen tuhoamien munien suhde kiilupistiäisten tuhoamiin oli suurempi viirumosaiikki- ja tyviversoviruksen saastuttamissa kauroissa kuin muissa. Kaksi loissientä *Entomophthora major* ja *E. sphaerosperma* tappoivat jonkin verran liikkuvilla kehitysasteilla olevia viljakaskaita.

Viljakaskaan runsaudenvaihtelu

Viljakaskas menestyi hyvin tutkimusalueella. Ilmasto oli sille suotuisa, sen ravintokasveja viljeltiin noin 90 %:lla viljelyalasta, ja lisäksi ravintokasveja kasvoi runsaasti viljelysten ulkopuolella. Ravintokasvit olivat jakaantuneet alalle siten, että toukat ja aikuiset löysivät ne ja voivat käyttää niitä. Edellisten lisäksi ihmisen toiminta, etenkin viljojen ja timotein viljely sekä lajille sopiva kasvijärjestys, tekivät mahdolliseksi viljakaskaan suuren tiheyden, joka oli kaurapelloissa usein 4 000—5 000 munaa/m^2.

Jälkeläismäärästä lienee kuollut yli 99 %. Viljakaskaan vihollisina oli tutkimusalueella ainakin kuusi hyönteis-, yksi punkki-, kolme hämähäkki- ja kaksi loissienilajia. Lisäksi ainakin seitsemän muuta eläinlajia ja ihminen tuhosivat sen jälkeläisiä. Lähes kaikki viholliset olivat tutkimusalueella yleisiä. Useimmat olivat yleisiä koko Etelä- ja Keski-Suomessa. Viholliset tuhosivat v. 1963—1964 noin 50—60, ihminen noin 12—15 ja säätekijät noin 8—15 % viljakaskaan jälkeläisistä. Noin 10—25 % kuolleisuutta ei kyetty tarkasti selvittämään. Paikkojen välisen runsaudenvaihtelun aiheutti ihminen välittömästi ja bioottisten tekijöiden kautta. Vuosien välisen runsaudenvaihtelun aiheuttivat ilmeisesti säätekijät välittömästi sekä ravinnon, vihollisten ja ihmisten kautta.

Viljakaskaan runsautta voidaan säännöstellä muuttamalla kasvijärjestystä, viljelykasvien suhteellisia pinta-aloja ja ojitustapaa. Käytännössä muuttaminen on vaikeaa, mutta siihen on kuitenkin mahdollisuuksia.

MS. received February 14, 1967
Printed October 26, 1967