#### POLSKA AKADEMIA NAUK

ZAKŁAD ZOOLOGII SYSTEMATYCZNEJ I DOŚWIADCZALNEJ

# A C T A Z O O L O G I C A C R A C O V I E N S I A

Tom XX

Kraków, 31. VIII. 1975

Nr 9

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Biology, Ecology, and Economic Importance of Cassids (Coleoptera, Chrysomelidae, Cassidinae) of the Ojców National Park

[Pp. 251-392, pl. XXI-XXXIII, 22 text-figs.]

Biologia, ekologia i znaczenie gospodarcze tarczyków (Coleoptera, Chrysomelidae, Cassidinae) Ojcowskiego Parku Narodowego

Биология, экология и хозяйственное значение щитоносок (Coleoptera, Chrysomelidae, Cassidinae) Ойцовского Национального Парка

Abstract: Investigations carried out in the years 1966—1971 on a meadow in the Sas-Powska Valley in the Ojców National Park showed that the maximum length of life of cassids was not one year, as was previously believed, but almost 4 years in the case of Cassida rubiginosa Müll., 3 years with C. vibex L. and C. viridis L., and 2 years with C. flaveola Thunbg.; females living always longer than males. The highest fecundity occurs with 1-year old females (200—350 eggs) decreasing with 2- and 3-years old specimens. The emergence and development of cassids depend on physical factors (temperature, insolation, rains, wind) while the biotic factors (parasites, predators, microorganisms) play a decisive role in the reduction of development stages of these beetles. In relation to the initial number of eggs the total reduction was very high (98·00—99·50 per cent). The investigated species of cassids have essential economic importance. C. rubiginosa Müll. and C. vibex L. strongly attack Cirsium arvense, C. viridis L. — Mentha arvensis, Stachys palustris, and Galeopsis pubescens, and C. flaveola <code>Thunbg.</code>— Stellaria media, moreover, it was found that C. nebulosa L. and C. nobilis L. attack Chenopodium album, while Hypocassida subferruginea Schrnk. damages Convolvulus arvensis. The above mentioned species of cassids reproduce easily and in masses under laboratory conditions, their complete development taking as little as 30 days, hence real possibility exists of using imagines and larvae of these species for biological control of troublesome field weeds.

<sup>1 -</sup> Acta Zoologica Cracoviensia XX/9

#### CONTENTS

I.	Introduction	252
II.	Description of the study area	255
III.	Method of investigation	256
IV.	Biology, ethology, and ecology of an individual	261
	A. Imago	261
	1. Description of the biotope of imago	261
	2. Phenology of emergence	262
	3. Foodplants and feeding of beetles	264
	4. Mating and egg-laying	278
	5. Length of life and sex ratio	282
	6. Ecology and ethology of imagines	284
	B. Egg	285
	C. Larva	290
	D. Pupa	295
	E. foung imago	297
V.	Ecology of population	305
	1. Dynamics of population numbers	305
	2. Fecundity	311
	3. Density	316
	4. Migrations	320
VI.	The influence of physical and biotic factors on the populations of cassids	322
	A. Physical factors.	322
	1. Temperature, rains, and wind	322
	2. Insolation	329
	B. Biotic factors	337
	1. Enemies of eggs	341
	2. Enemies of larvae and pupae .	348
	5. Enemies of imagines	355
VII.	Bioenergetics of development stages of C. rubiginosa Müll. and C. vibex L.	357
	. Consumption, excreting taeces and agginilation	357
	2. I roduction of the body	359
	of energies	363
	2. Collision of energy atticiency	365
		367
III.		370
IX.	Conclusions .	371
		376
		381
	Резюме	288

#### I. INTRODUCTION

Subfamily Cassidinae is a well distinguished group of beetles with a number of typical morphological, ecological, and nutritive features. According to Zwölfer and Eichhorn (1966) it includes about 2600 species. This group is particularly well represented in Neotropic, in Palearctic only 90 species occurring (Zwölfer, Eichhorn, 1966, Steinhausen, 1950). In temperate

zones (European part of the USSR and neighbouring European countries) the total number of about 40 species of these beetles were reported. In the majority of cases they are mesophilous species with an inclination to hygrophilosity (Palij, 1959). All Palearctic cassids live on a small number of plant families, from which the following should be mentioned: Compositae, Labiatae, Caryophyllaeae, Chenopodiaceae, and Convolvulaceae. Both in the larval and in the imaginal stage of life under optimal conditions cassids are monophagous or very narrow oligophagous animals (Palij, 1959, Lopatin, 1960, Ogloblin and Medvedev, 1971). Because of the fact that several species of cassids have essential economic importance this subfamily has for a long time been the subject of interest and investigation of numerous specialists from various countries.

The relatively greatest number of data in the literature concerns the following species of cassids:

Cassida rubiginosa Müll. (Šeremet, Gorbunov, 1969, Gorbunov, Šeremet, 1968, Zwölfer, Eichhorn, 1966, Palij, 1959, Palij and Klepikova, 1957, Kleine, 1917, 1918, and 1919, Van Emden, 1962, Dubeško, 1970, Ogloblin, Medvedev, 1971, Steinhausen, 1950, Reitter, 1912, Matis, 1968, 1971, Šapiro and Černyšenko, 1963, and Lopatin, 1960);

Cassida viridis L. (Engel, 1932, 1935, Manolache, 1938, Kleine, 1915, 1917, Palij 1959, Palij and Klepikova, 1957, Steinhausen, 1950, Van Emden, 1962, Matis, 1968, Lopatin, 1960, Reitter, 1912, Šapiro and Černyšenko, 1963, Ogloblin and Medvedev, 1971);

Cassida nebulosa L. (Kleine, 1914, 1915, 1916, 1918, and 1920), Manolache, 1936, Steinhausen, 1950, Palij and Klepikova, 1957, Palij, 1959, Matis, 1968, 1971, Šapiro and Černyšenko, 1963, Reitter, 1912, Dubeško, 1970, Ogloblin and Medvedev, 1971, Nietzke, 1939, Wilke, 1923, Lopatin, 1960);

Cassida nobilis L. (Kleine, 1919, Kaufmann, 1933, Steinhausen, 1950, Palij and Klepikova, 1957, Palij, 1959, Lopatin, 1960, Reitter, 1912, Matis, 1968, Šapiro and Černyšenko, 1963, Ogloblin and Medvedev, 1971, Menozzi, 1938);

Hypocassida subferruginea Schrnk. (Šeremet, Gorbunov, 1969, Gorbunov and Šeremet, 1868, Palij and Klepikova, 1957, Palij, 1959, Steinhausen, 1950, Matis, 1968, Šapiro and Černyšenko, 1963);

Cassida vibex L. (OGLOBLIN and MEDVEDEV, 1971, STEINHAUSEN, 1950, VAN EMDEN, 1962, ZWÖLFER and EICHHORN, 1966, PALIJ and KLEPIKOVA, 1957, PALIJ, 1959, REITTER, 1912, LOPATIN, 1960, MATIS, 1968, ŠAPIRO and ČERNYŠENKO, 1963).

The following species were investigated in a smaller degree:

Cassida prasina Ill. (Palij, 1959, Palij and Klepikova, 1957, Šapiro and Černyšenko, 1963, Lopatin, 1960, Steinhausen, 1950, Kleine, 1917, Matis, 1968, Ogloblin and Medvedev, 1971, Reitter, 1912);

Cassida flaveola Thunbg. (Kleine, 1917, Steinhausen, 1950, Van Emden, 1962, Palij and Klepikova, 1957, Reitter, 1912, Matis, 1968, Šapiro and Černyšenko, 1963);

Cassida sanguinolenta MÜLL. (OGLOBLIN and MEDVEDEV, 1971, VAN EMDEN, 1962, STEINHAUSEN 1950, REITTER, 1912);

Cassida rufovirens Suffr. (Palij and Klepikova, 1957, Steinhausen, 1950, Reitter, 1912).

The biology of Cassida hemisphaerica HBST. is so far quite unknown from a few informations about the foodplants of this species (STEINHAUSEN, 1950, REITTER, 1912, OGLOBLIN and MEDVEDEV, 1971).

Up to the present the most comprehensive and detailed reports concern the results of investigations on the taxonomy and morphology of cassids (Reitter, 1912, KLEINE, 1917, SIMM, 1948, STEINHAUSEN, 1950, PALIJ and KLEPIKOVA, 1957, Palij, 1959, Zwölfer and Eichhorn, 1966). Data on the biology of the above-mentioned species are in the main limited to list of foodplants of beetles and larvae, description of feeding and behaviour, phenology of the emergence of development stages, migration of imagines to winter-quarters (in a rather general way), description of the structure of egg batches, of numbers of eggs in batches, and of places where the eggs are laid on plants, and to a rather insufficient discussion of the development cycle of cassids under field and laboratory conditions. Informations on the ecology of cassids are scant. The descriptions of biotopes of particular species are relatively precise while the influence of physical and biotic factors on the development and degree of reduction of development stages of cassids has been too generally approached. The problem of the economic importance of cassids has been discussed with full particulars but the opinions of various workers are different and often contradictory.

In our country the data on the subfamily of cassids are very scant (Markiewicz, 1948, Simm, 1948, Żurańska, 1959). The only information on the occurrence of cassids in Ojców is found in the work of Eichler (1914).

In spite of a rich literature on this beetle subfamily and of numerous investigations carried out on them, serious gaps occur especially in the biology and ecology of cassids. The evaluation of the life length, sex ratio, and size of the population of imagines, rate of survival of beetles throughout the period of wintering, the phenomenon of "complementary feeding" in the spring period, the evaluation of the fertility of females of different age, the phenology of emergence, the process of development and changes in the degree of density of consecutive development stages of cassids, the influence of abiotic and biotic factors on the reduction of these stages and on the occurrence and course of diapause in young imagines, as well as the bioenergetics of development stages of cassids should be thoroughly investigated. The problems mentioned above were the aim of the present work.

Acknowledgements: Author wishes to thank Prof. Dr. W. SZYMCZAKOWSKI for his care, valuable remarks and suggestions, and for the identification of predatory bugs, Dr. A. Draber-Mońko for the identification of parasitic diptera, Dr J. Łuczak for the identification of spiders, Dr. W. Micherdziński for the identification of predatory mites, Dr. B. Burakowski for the identification

of predatory larvae of Cantharidae, Prof. Dr. W. Grodziński for making accessible his laboratory with air conditioning for the study of the respiration of cassids, Dr. S. Stanuszek, for the identification of parasitic nematodes, Mr. J. Wagner, M. Sc. for the identification of parasitic hymenoptera, Dr. M. Niemirowski for the drawings, and Dr. A. Warchałowski for checking the identification of several species of cassids.

#### II. DESCRIPTION OF THE STUDY AREA

The study area (pl. XXI, A, B) includes a plot in a meadow Arrhenatheretum elatioris alchemilletosum (Medwecka-Kornaś, 1963) in the Ojców National Park on the bottom of the Sąspowska Valley. The Valley runs from west to east and in the cross-section is characterized by a flat bottom, cut by the deep bed of a stream and steep rocky slopes. The spaces between little rocks are occupied by a hornbeam of the subassociation Tilio-Carpinetum typicum widely spread in the Ojców National Park and much drier than Tilio-Carpinetum stachyetosum (Medwecka-Kornaś, Kornaś, 1963). Beginning from the border of the forest up to the middle of the slope height considerable numbers of fir young undergrowth occur and favour the gathering of great amounts of litter in the successive years.

The investigated area is a mid-forest meadow from the east bordered by a slope of the Chełmowa Góra Mt., and from the north neighbouring on a slope of the Złota Góra Mt. (pl. XXI, A). The northern line of the meadow is the river bed of the stream Sąspówka, on whose banks strips of a river-side forest Alno-Padion (Medwecka-Kornaś, Kornaś, 1963) occur. On the south side the stream Młynówka flows partly overflowing the south-east border of the meadow in the periods of storms and spring thaws. The surface of the meadow shows certain differentiation which is particularly marked in the south-east part, the soil being more wet and alkaline (Karkanis, 1967). The species composition of plants within this area is in general not different from the rest of the meadow (Jankowska, 1967) with the exception of the presence of Cirsium oleraceum (L.) Scop., which only here occurs.

At present the unmown surface of the meadow is in the state of succession, which is chiefly marked by the change of the quantitative and qualitative share of separate species of plants (Jankowska, 1967). In the first year grasses constituted 52 per cent of the overground biomass of plants and dicotyledonous plants 48 per cent in the uncut meadow. After 3 years the share of monocotyledonous plants increased by 13 per cent at the cost of dicotyledonous ones. At the same time seedlings of trees and bushes appeared (Carpinus betulus L., Alnus glutinosa (L.) Gaertn., Corylus avellana L., Salix caprea L., Quercus sp.). The share of separate species of plants increased or decreased in the total biomass (e.g. Dactylis glomerata L. from 8 to 23 per cent). Decrease in the number of green shoots was very distinct; the process of a decrease in the total number

of species being also observed: in 1964 in one sample of the surface of 1/16 sq. m. the average number of 24 species of vascular plants were recorded and in 1966 14 species. The rate of succession of the meadow, which may be identified as secondary, influences the quantitative decrease in the vegetal production (Jankowska, 1971) (the difference amounting to 18 per cent in the years 1964—1968). In the years of the investigation new species of plants also appeared in the uncut meadow: Geranium phaeum L., Polygala comosa Schkr., Urtica dioica L., Myosotis palustris (L.) Nathorst., Cirsium rivulare (Jacq.) All., Mentha longifolia (L.) Huds., Impatiens noli-tangere L., Hypericum maculatum Cr., Aegopodium podagraria L., Potentilla anserina L., Circaea lutetiana L., Agrostis alba L., Festuca arundinacea Schreb., Chrysosplenium alternifolium L., Galium aparine L., Poa annua L. Moreover, within the area the following hygrophilous plants occur: Alopecurus pratensis L., Ranunculus repens L., and others.

This character of the vegetation is connected with the relatively cool and wet climate on the bottom of the Saspowska Valley (Klein, 1967). The microclimatic relations are formed by the influence of radiation and insolation factors. The active surface is the sward reaching 40 cm in full vegetation season and owing to high slopes the meadow is in the zone of calm. In the microclimatic regionalization of the Ojców National Park (Klein, Niedźwiedź, Sztyler, 1965). the study area was included in the cool region of valley bottoms, characterized by great 24-hour amplitudes, about 5—10°C greater than those on the upland. The masses of cool air, often persisting all days, occasionally bring about temperatures lower by 10°C than in the upland. Characteristic radiation frosts occur in spring and autumn. Because of the situation of the meadow on the bottom of the Sąspowska Valley the shading of the study area by the Chełmowa Góra Mt. undergoes constant changes throughout the year and considerably influences the development of the vegetation and invertebrates on the meadow. In consequence of complete shading of the valley bottom in winter the sun radiation is much weaker here, this fact together with low temperatures bringing about longer persistence of the snow-cover than in the upland (on the average by 12—14days longer). The air humidity is great (often by 30 per cent greater than in the open upland) especially in the period of thermic inversions when radiation foggs persist in the valley.

## III. METHOD OF INVESTIGATION

The investigation was carried out in the years 1966—1971, the year 1966 being regarded as preliminary, while proper investigation methods were elaborated, precise identification of larvae of particular species in the first and second instar of their life and the spectrum of foodplants which occurred in the region of the investigation were studied in detail. In the period of investigation temperatures and air humidity were registered at the altitude of 2 m above soil surface using

a weekly thermohygrograph installed in a climatologic box while the rains were measured using a rain gauge.

In the successive years from April to October at 7-30 day intervals 6 species of cassids were observed and examined: Cassida rubiginosa Müll., C. vibex L., C. viridis L., C. flaveola Thunbó., C. prasina Ill. and C. hemisphaerica Hbst. (the last two species occurring outside the study area). The first two species feed on the leaves of Cirsium oleraceum (L.) Scop. (pl. XXI, C), C. viridis L. on the leaves of Mentha longifolia (L.) Huds. (pl. XXI, D), and C. flaveola Thunbg. on the leaves of Stellaria graminea L. (pl. XXI, E). Within the study area the leaves of all specimens of foodplants of cassids were carefully examined, the phenology of the emergence and the numbers of individuals in all development stages of these beetles being noted. Moreover, supplementary observations were carried out outside the study area (in the Sąspowska and in the Prądnik Valley) on the biology of Cassida nebulosa L., and C. nobilis L., and (outside the Ojców National Park) on Hypocassida subferruginea Schrnk. The observations carried out on these species were only concerned with their foodplants and had the aim to determine the actual role of these beetles in the economy of man. Besides, both on the investigated meadow and in the territory of the Ojców National Park the eatch with a sweep net was used as an additional method in the investigation on the occurrence and numbers of cassids.

In the period of the investigation (with the exception of 1969) within the area the method of marking and recapturing of beetles of the investigated species was used. A leather paint "Wilbra" in a few colours was used for marking in the successive terms of investigation. It was found that the paints stuck well to the elytrae of imagines even throughout a year and had no negative influence on their life functions. In the years 1969—1971 in the periods of the maximum emergence of imagines of the 4 investigated species a complete catch of beetles was carried out in the whole area throughout 5 days in order to determine the size of population of these species. In the years 1966—1971 the observations of the maturation of imagines in spring, of the time and course of copulation, and of the sex ratio in old and young beetles were conducted in round boxes of the diameter of 40 cm and the height of 10 cm, made of wire and covered with nylon gauze.

The investigations on the fertility of females at different age and on the length of life of imagines of both sexes were carried out in the years 1969—1971 in permanent observation stations on the meadow,  $20 \times 10$  cm sacs of nylon gauze being used. Single specimens of fertilized females were placed on leaves of foodplants, the leaves being carefully put into the sacs which were tied with a string at their base. At 3—9 day intervals the sacs with females were placed on new leaves, the number of egg batches and the number of eggs on the old leaves being noted. The procedure was repeated throughout the vegetation season up to the end of October while, after the fertility of females ended, the survival rate of beetles was only observed.

The investigations on the development and rate of the reduction of eggs, larvae, and pupae of cassids by physical factors were also carried out in the

years 1969—1971 in permanent observation stations. The leaves of the foodplants of cassids where the eggs were laid, were surveyed at 3—7 day intervals and the rate of development of eggs was recorded up to the moment of hatching on the first and the last larvae. Afterwards all batches which escaped destruction were gathered from leaves and observed in the laboratory in order to determine the quantitative and qualitative composition of parasites of eggs of the cassids. The percentage of eggs reduced by the physical factors (rains, wind) were calculated from the difference between the initial and final number of eggs.

The newly hatched larvae were placed on separate plants in the number from a few to several on one specimen, the plants being then surveyed at the intervals of 3—7 days and the number, length of the time of development, and the degree of reduction of individual larval stages, pre-pupae, and pupae were noted up to the moment of hatching of young imagines. In the years 1970-1971 the death rate of young imagines from the moment of emergence to the beginning of wintering was investigated in sacs of nylon gauze (of the dimensions of  $50\times25$  cm) which were put on whole plants, the beetles collected in the area and placed inside. When a given plant was strongly damaged by the eassids, the sac was moved on another specimen.

In order to determine the death rate of imagines of the investigated species of cassids, as well of the young ones hatched in the vegetation period as of the old ones, in the years 1968—1972 controlled wintering of these beetles was carried out in the litter of the lime-hornbeam forest on a slope of a south exposition in the Sąspowska Valley (pl. XXI, A). Beginning from the edge of the forest up to the middle of the slope height three horizontal lines were drawn in the distance of 5 m from each other and along them at the intervals of  $3.5~\mathrm{m}$  1-litre jars were placed, the bottoms of the jars being previously cut off. Round the jars the litter was cut with a sharp knife, the jars were thrusted deeply and the beetles put inside, the mouth of jars being covered with nylon gauze and tightened with a rubber. For the first wintering 100 jars were used, 10 beetles being placed in each, and in the next years 49 jars and 5 to 7 beetles in each were used. The jars were covered with a small amount of litter in order to protect them from damage. In the spring period (the first decade of May) the jars with the litter and beetles were placed in bags, then the samples were carefully examined in the laboratory, the percentage of living and dead specimens being calculated. The beetles of the two sexes, which survived the first wintering, were put into the round boxes described above and, after the copulation, the females were placed on leaves in the bags, one specimen in each bag. In a similar way the survived males were disposed. In autumn (October) living specimens were captured in the study area and put into jars in the forest for repeated wintering. This procedure was continued up to the death of the last old beetle and its aim was to evaluate the length of life of imagines of the investigated species.

In order to determine the quantitative changes in the foodplants of cassids within the study area the measurements of their distribution on the meadow were carried out in the years 1966, 1968, and 1970. Since it was assumed that

a dependence exists between the occurrence of the development stages of the investigated species of cassids and the degree of shading of the study area on the meadow, special measurements were carried out in the vegetation season of 1970. From March 21 (the beginning of the astronomical spring) at 1-month intervals the degree of shading of the meadow from sunrise to sunset was measured every hour. A plan of the study area in the scale of 1:200 was prepared on the plotting paper and the range of shading of the meadow, measured every hour with the use of a tape, was drawn on it. After the observation was finished it was accepted that the parts of the meadow shaded throughout 8 consecutive hours or longer, are within the zone of permanent shade. Similar schemes were prepared for the next months up to 21st September. In the figures presenting the changes in the degree of shading of the meadow in the successive months of investigation, the stations of the development stages of cassids were marked in accordance with their occurrence on foodplants throughout the vegetation season.

In the course of several-year studies the observations on the degree of the reduction of the development stages of cassids by parasites, predators, and microorganisms were carried out under laboratory conditions. The investigated material partly came from the study area and in a great measure was collected outside it in the Sąspowska Valley and in the Prądnik Valley. Moreover, specimens were made of the batches of eggs, larvae, pre-pupae, and pupae of these species to determine the number of parasites which did not managed to get out of the bodies of host animals.

Additional observations on the biology of these beetles under laboratory conditions were also carried out, the process of the maturation of imagines in spring, the length of time of the copulation, the period of laying eggs by females as well as the sex ratio being particularly considered. Moreover, the course of development of successive stages of cassids at various temperatures and relative humidities of air was also studied.

Besides the field observations in order to determine the actual foodplants of eassids and the role of the beetles in the control of some common field weeds, mass culture of these beetles was conducted on selected plants as quoted by different authors and also on some suggested by the present author.

The study of the bioenergetics of cassids was carried out under laboratory conditions (at the temperature of  $20^{\circ}\text{C}\pm2\cdot0$ ) in the period from 25th June to 25th September, 1969. The larvae and young imagines of the two species of cassids were only included: of Cassida rubiginosa MÜLL. and C. vibex L. because it was easy to catch a suitable number of beetles and larvae of these two species and also because they had a common foodplant: Cirsium oleraceum (L.) Scop. In the period of investigation the fluctuations in the temperature and air humidity in the laboratory were recorded using a weekly thermohygrograph.

The culture was carried out in Petri dishes of 10 cm diameter. The starting point of the study was the hatching of larvae from eggs. 70 larvae were taken from the respective species, each 10 specimens being placed in a sepa-

rate dish. In 24-hour intervals the larvae were weighed on a torsion balance with accuracy of 0·1 mg, the changes in their biomass (together with faeces which after being excreted are carried by the animal on the abdominal furca) were noted, the area of feeding on leaf blades was calculated in square milimetres and re-counted in miligrams of biomass and dry mass (Łomnicki, Kosior, Kaźmierczak, 1965), fresh undamaged leaves being placed in the dishes. Larval exuviae with excrements were taken off the larvae which were passing successive moults and then the larvae themselves, their exuviae and excrements were separately weighed. Then these larvae were placed in a separate dish, their further development being watched. After their complete development the larvae stopped feeding and passed into the pre-pupal and then into the pupal stage. The initial period of the pre-pupal stage was regarded as the maximum of larval development. Larvae of the investigated species pass 4 moulting, the fifth one being to the pupal stage.

At the moment of hatching of imagines from pupae (12 specimens of Cassida rubiginosa Müll. and 7 of Cassida vibex L.) the study of their bioenergetics was began and carried out — in a way parallel to that of the larvae — for the period of 45 days of the life of beetles, i.e. up to the moment when the biomass of their bodies already only slightly changed and the consumption of food was minimal. Certain difficulty was caused by the fact that the beetles excreted fluid faeces leaving them as well on plant leaves as on the walls of jars. Their number was always noted and, after drying, hundreds of them were carefully scraped off with a blade from the walls of jars, weighed, and dried in a drier, their dry matter being calculated.

In order to determine the content of dry matter and free water in the bodies of all development stages of cassids, 30 specimens of eggs, larvae of consecutive instars, pre-pupae, pupae, and newly hatched and 45-day old imagines were weighed, dried for 2 days in a drier at 85°C and then for 1 hr at 105°C. Then they were weighed on an analytical balance with the accuracy of 0·0001 g and the percentage of dry matter and free water was calculated. In a similar way the content of dry matter of larval exuviae and of excrements of larvae and beetles was determined. The calorific value of the dried material was calculated on the basis of the results of combustions in a Philipson microbomb.

The measurements of the respiration metabolism of the development stages of both species were carried out in manometric microrespirometers (according to ZADIN, 1966) at a constant temperature of  $20^{\circ}\text{C}\pm0.1$ . On the whole 1331 specimens from all stages (with the exception of eggs) were examined. A few to several specimens were put in a bottle and a strip of blotting paper saturated with 2 ml of 30 per cent solution of KOH was placed in a coupler above it, a control bottle being left empty. The respirometer prepared for the measurement was dipped in an aquarium into the water of  $20^{\circ}\text{C}$ . After the equilization period (15—20 min.) the process of the oxygen consumption was measured, the readings being made every 5 minutes during 1 hour. The obtained

results were reduced to standard conditions of temperature, air pressure, and air humidity. The specimens were weighed with the accuracy of 0.1 mg immediately after having been taken out of the respirometer.

#### IV. BIOLOGY, ETHOLOGY, AND ECOLOGY OF AN INDIVIDUAL

### A. Imago

## 1. Description of the biotope of imago

In the years 1966—1971 investigations were carried out within the study area on the meadow in the Sąspowska Valley of the Ojców National Park, the occurrence of 4 species of cassids being noted: Cassida rubiginosa Müll. (pl. XXII, D), C. vibex L. (pl. XXIII, D), C. viridis L. and C. flaveola Thunbe. (pl. XXIV, C, D). Moreover, outside the area C. prasina Ill. and C. hemisphaerica Hbst. occurred on the meadow. The observations were also carried out in the whole territory of the Park and the presence of species mentioned above was recorded in various habitats: in cereals and root crops, on fallows, on the borders of forests and streams, on wet and dampened meadows, and even on tussocks of plants emerging from water. The above-mentioned range of habitats allows to classify the investigated species of cassids to the group of meso- and hygrophilous insects, Cassida viridis L., C. prasina Ill. and C. flaveola Thunbe. showing greater inclination to hygrophilousness. Cassida hemisphaerica Hbst. is distinctly mesophilous species with a fairly strong inclination to xerophilousness. C. vibex L. occurs in various biotopes.

In the majority of cases the opinions of other workers (Gorbunov, Šeremet, 1968, Reitter, 1912, Šapiro and Černyšenko, 1963, Lopatin, 1960, Kleine, 1917, Palij, 1959, Palij and Klepikova, 1957, Ogloblin and Medvedev, 1971, Zwölfer and Eichhorn, 1966) on the adaptation of the investigated species of cassids to given biotopes are similar to the views of the present author. Certain differences in the opinions concern only Cassida flaveola Thunbg., which according to Palij and Klepikova (1957) and Šapiro and Černyšenko (1963) occurs in the biotopes from the most wet to xerothermic.

The adaptation of certain species of cassids to the conditions of habitat is fairly considerable and in a great degree this fact makes them possible to pass on other substitute plants (Kleine, 1917), but on the other hand, cassids as chiefly mesophilous beetles are (according to Lopatin, 1960) particularly sensitive to moisture conditions in the region of their occurrence and hence in certain districts particular species are often encountered while in others they are rare, occurring as single specimens. According to Opyrchalowa (1972) the ranges of the distribution of herbivorous species are in general smaller than the spread of foodplants. The range of occurrence of given species is rather identical with

the range of certain types of the vegetation. On the other hand Zwölfer and Eichhorn (1966) are of the opinion that the ranges of the distribution of cassids agree with the primary distribution of their foodplants, e.g. the Mediterranean and West-Asiatic region, the geographical centre of *Cynareae*, is also the centre of *Cassida rubiginosa* Müll. and *C. vibex* L.

The investigation in the Ojców National Park showed that Cassida rubiginosa MÜLL. is a species encountered often and in very great numbers, C. vibex L. and C. viridis L. fairly often and in lesser numbers, C. flaveola Thunbg. rarely and in scarce numbers, while C. prasina Ill. and C. hemisphaerica HBST. very rarely and as individual specimens. With regard to the occurrence of Cassida rubiginosa Müll. the opinions of the above-mentioned workers are in accordance with the results of the present author, nevertheless, there are differences in views with regard to the numbers of other species resulting from their geographical distribution. According to Reitter (1912) Cassida vibex L. is very common, according to Palij (1959) — common, according to Zwölfer and Eichhorn (1966) fairly common, and according to Palij and Klepikova (1957) fairly rare. According to Palij (1959) and Palij and Klepikova (1957) C. viridis L. is common and numerous, according to Reitter (1912) it is frequent. C. flaveola THUNBG. is frequent according to Reitter (1912) and Kleine (1917) but it is rare according to Palij and Klepikova (1957). C. prasina Ill. is very numerous according to Palij and Klepikova (1957), common according to Šapiro and ČERNYŠENKO (1963) and Kleine (1917) but not very frequent according to REITTER (1912). C. hemisphaerica HBST. is widely spread according to OGLOBLIN and Medvedev (1971) but rare according to Reitter (1912). However, the intensity of the occurrence of these individual species may considerably differ in various regions, in agreement with the above-mentioned view of Lopatin (1960).

# 2. Phenology of emergence

In spring the emergence of imagines of cassids within the area on the meadow depends above all on climatic factors and among them a decisive role is played by temperature, insolation, rains, and wind, while the humidity of air is less important. It is supported by several-year investigation of the present author and by other workers who were interested in cassids (Lopatin, 1960, Kleine, 1916, 1917) as well as those who studied other herbivorous groups (Dmoch, 1959, Szujecki, 1966, Węgorek, 1959, Starzyk, 1970, 1971, Wilski, 1951). Spring activation of cassids chiefly depends on the temperature. On the basis of the data of Dmoch (1959) and Ruszkowska and Opyrchalowa (1969) the values of temperature from 7—9°C were accepted for cassids as the term of their return to vital activity. At this term the beetles show slow movements, creep out of litter and hide again in it. As the temperature rises to 10—15°C the period of incomplete vital activity occurs when short flies of beetles and the beginning of feeding are observed.

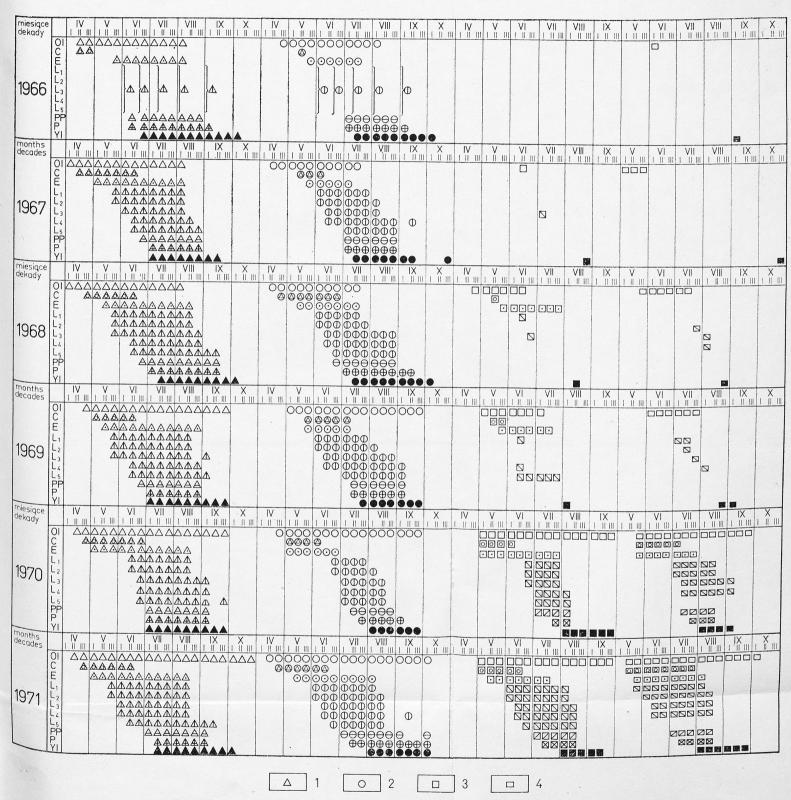


Fig. 1. Phenology of appearance of the development stages of Cassids in the study area on the meadow in the Saspowska Valley of the Ojców National Park in the years 1966—1971. Explanations: 1 — Cassida rubiginosa Müll., 2 — C. vibex L., 3 — C. viridis L., 4 — C. flaveola Thunbeg., OI — old imagines, C — copulation, E — eggs, L1—L5 — successive larval instars, PP — prepupae, P — pupae, YI — young imagines, }—in 1966 no larval instars were distinguished

 $A.~Kosior \ Acta~Zoologica~Cracoviensia~XX/9$ 

The emergence of cassids on the meadow occurs in the period when maximum air temperature exceeds +13°C this being a threshold value for the investigated species (i.e. under conditions of the meadow microclimate in the Sąspowska Valley). In April on the meadow the temperatures higher than 13°C usually prevail (Kosior, Klein, 1970) creating favourable bioclimatic conditions for the occurrence of cassids which begin to remigrate from winter chambers to the meadow. However, the basic role is played by maximum day temperatures and the insolation, this opinion being supported by the investigations of Wegorek (1959) on the Colorado beetle. The essential fact is whether the days of higher temperatures occur in succession or are separated by days of lower temperatures. Certain constancy of the temperature is indispensable to secure an undisturbed course of the emergence of beetles.

The influence of the climate is directly marked (but it can also be indirect) since it delays or hastens the growth of foodplants and in consequence the term of the emergence of beetles may be considerably shifted. Therefore, the presence of cassids on the meadow also depends on the degree of development of their foodplants. The beetles do not emerge as late as the necessary amount of food is available. A distinct relation exists between these two factors, this being supported by the investigations of Kleine (1917) and Žurańska (1968) on the pests of culture plants.

Several year investigation on the meadow showed that Cassida rubiginosa MÜLL. is the earliest species appearing on the study area (fig. 1). The earliest emergence was recorded in the first decade of April, while the latest in the third decade of that month. The cassids C. vibex L., C. viridis L., and C. flaveola Thunbg. appear on the meadow successively in weakly intervals (fig. 1). The maximum numbers of C. rubiginosa Müll. and C. vibex L. occur in May and June, of C. viridis L. in may, and of C. flaveola Thunba. as late as in June. The emergence of beetles and the intensity of its course may be inhibited or even interrupted if worse climatic conditions befall. The influence of low temperature connected with continuous rains and wind is most strongly marked. In such case the beetles sink into an apparent diapause and hide at the bases of plants or even in the upper layer of the soil. Old beetles of the investigated species are encountered as late as at the end of summer or even in autumn. It was found that imagines of C. rubiginosa Müll. occur on the meadow from 5.5—6 months, C. vibex L. 5—5.5 months, C. viridis L. 4.5—5 months, C. flaveola Thunbg. 4—5 months. In the Years 1966—1971 only a few specimens of C. prasina Ill. and C. hemisphaerica HBST. were caught within the Saspowska Valley. Their occurrence was noted in spring in the month of May but no other details were obtained since these species are extremely rare in the territory o the Park.

The opinions of various authors on the phenology of the emergence of cassids in spring are fairly discrepant. According to Kleine (1917), Palij and Klepikova (1957) and Zwölfer and Eichhorn (1966) Cassida rubiginosa Müll. is a species appearing as early as in April, but Gorbunov and Šeremet (1968) claim that it appears fairly late, as late as the second half of May but this

fact does not seem probable. Zwölfer and Eichhorn (1966) and Palij and Klepikova (1957) note an early emergence (April) of C. vibex L., while Lopatin (1960) quotes the occurrence of this species as late as in June, this being quite inacceptable. The only reference to the term of the emergence of C. viridis L. and C. flaveola Thunbg. is given by Palij and Klepikova (1957). The appearance of C. viridis L. in April is partly consistent with the observations of the present author while the reported emergence of C. flaveola Thunbg. in the same month is in a certain degree disputable since this species is classified among those which appear at the latest term. As far as the length of the occurrence of adult beetles is concerned scarce data are found in the literature. The results of the investigations of Palij and Klepikova (1957) are very inaccurate in this case while those presented by Zwölfer and Eichhorn (1966) are by far consistent with the observations of the present author.

# 3. Foodplants and feeding of beetles

Within the study area Cassida rubiginosa Müll. and C. vibex L. fed on the leaves of Cirsium oleraceum (L.) Scop. (pl. XXI, C), C. viridis L. on the leaves of Mentha longifolia (L.) Huds. (pl. XXI, D), C. flaveola Thunber. on the leaves of Stellaria graminea L. (pl. XXI, E). On the basis of measurements of the spread of foodplants of cassids carried out in the years 1966, 1968, and 1970, distinct quantitative changes were found in these plants (fig. 2, 3, and 4). Under the influence of the meadow not having been mown in the period of investigation the first two plants showed a distinct tendency to increase their spread on it while Stellaria graminea L. reached its maximum number in 1968 (fig. 3) and then its range of distribution on the meadow gradually dicreased. In consequence of strong mineralization of dead organic matter on the meadow the share of Urtica dioica L. increases in the total biomass from year to year, and, morever, this species supersedes other plants from the places of their primary occurrence (fig. 4).

The list of foodplants of beetles and larvae of cassids quoted by various workers as well as of plants found by the present author in the territory of the Ojców National Park is given in Table I. The list of foodplants presented by the author on the basis of field observations and laboratory cultures contains as well some plants mentioned by other authors as those found for the first time. Only these species on which the complete development of cassids occurs are regarded as foodplants. It is unquestionable that Cassida rubiginosa Mülland C. vibex L. are connected with plants of the family Compositae, this being supported by the data of the majority of authors and by the present author's own investigation. Hence the occurrence of C. rubiginosa Müll. on plants of the family Rosaceae reported by Ogloblin and Medvedev (1971) or on Papilionaceae reported by Żurańska (1959) are questionable. According to Zwölfer and Eichhorn (1966) both species of cassids show the greatest preference for the plants of the genera Cirsium, Carduus, and Silybum, and, besides, C. vibex L. considerably prefers the species of the subfamily Centaureinae. Cirsium arvense (L.)

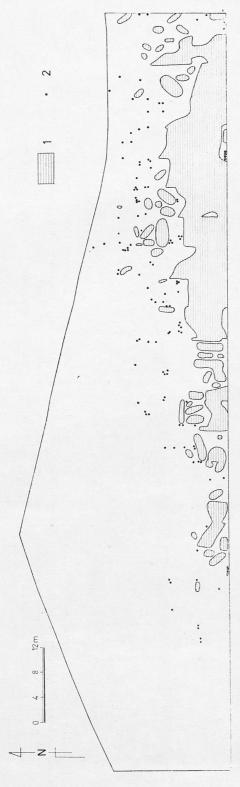


Fig. 2. The range of Cirsium oleraceum (L.) Scop. in the study area on the meadow in the Sąspowska Valley of the Ojców National Park in September 17, 1966, 1 — Mass occurrence, 2 — single specimens

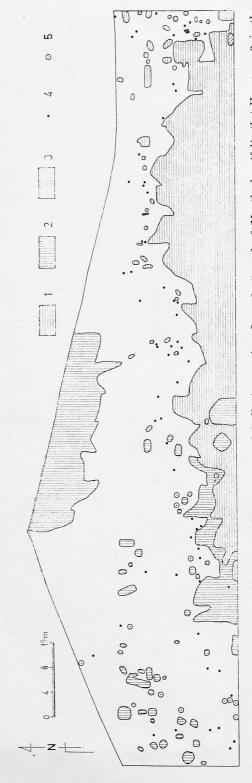


Fig. 3. The range of Cirsium oleraceum (L.) Scop. — 1, 4, of Stellaria graminea L. — 2, 5, and of Mentha longifolia (L.) Huds. — 3, in the study area on the meadow in the Sąspowska Valley of the Ojców National Park in August 20. 1968. 1—Cirsium oleraceum (L.) Scop. — mass occurrence, 2 — Stellaria graminea L. — mass occurrence, 3 — Mentha longifolia (L.) Huds. — mass occurrence, 4 — Cirsium oleraceum (L.) Scor. — single specimens, 5 — Stellaria graminea L. — single specimens

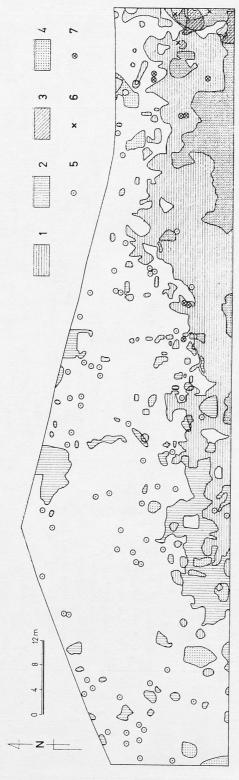


Fig. 4. The range of Cirsium oleraceum (L.) Scop. — 1, of Stellaria graminea L. — 2, 5, of Mentha longifolia (L.) Huds. — 3, 6, and of Urtica dioica L. — 4, 7, in the study area on the meadow in the Sąspowska Valley of the Ojców National Park in September 28. 1970. 1 -- Cirsium oleraceum (L.) Scop. -- mass occurrence and tussocks, 2 -- Stellaria graminea L. -- mass occurrence, 3 -- Mentha longifolia (L.) Huds. — mass occurrence, 4 — Urtica dioica L. — mass occurrence, 5 — Stellaria graminea L. — single specimens, 6 Mentha longifolia (L.) Huds. — single specimens, 7 — Urtica dioica L. — single specimens

Foodplants of imagines and larvae of Cassidinae

Observations of the present author	Author Author Author Author Author
Data according to other authors	OGLOBLIN, MEDVEDEV, 1971  ŽURAŃSKA, 1959  ŽURAŃSKA, 1959  ŽURAŃSKA, 1959  ŽURAŃSKA, 1959  ŽURAŃSKA, 1959  ZWÖLFER, EICHHORN, 1966  KLEINE, 1917, OGLOBLIN, MEDVEDEV, 1971, PALIJ, 1959, PALIJ and KLEPIKOVA, 1957, RAMMNER, 1932, REITTER, 1912, STEINHAUSEN, 1966  KLEINE, 1917, PALIJ, 1959, REITTER, 1912 ZWÖLFER, EICHHORN, 1966  KLEINE, 1917, PALIJ, 1959, REITTER, 1971, STEINHAUSEN, 1950  KLEINE, 1917  VAN EMDEN, 1962, OGLOBLIN, MEDVEDEV, 1971, STEINHAUSEN, 1950  KLEINE, 1917  KLEINE, 1917, MATIS, 1968, PALIJ, 1959, PALIJ and KLEPIKOVA, 1957, ŠEREMET, GORBUNOV, 1966*  ZWÖLFER, EICHHORN, 1966  ,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,
Foodplant	F. Rosaceae Agrimonia L. F. Papilionaceae Pisum L. Medicago L. Trifolium L. Trifolium L. Arctium minus (HLL.) Bernh. Arctium L. Arctium L. Carduus glaucus BMG. Carduus personata (L.) JACQ. Carduus reniflorus CURT. Carduus acanthoides L. Carduus acanthoides L. Carduus L. Carduus L. Carduus acanthoides L.) Scop. Cirsium acantle (L.) Scop. Cirsium acantle (L.) Scop.
Species of the cassid	Cassida rubigi- nosa Müll.

Author?	Author Author Author Author Author
""  LOPATIN, 1960  VAN EMDEN, 1962, RAMMNER, 1932, REITTER, 1912, STEIN-HAUSEN, 1950  ZWÖLFER, EICHHORN, 1966*, KLEINE, 1917  "" PALIJ and KLEPIKOVA, 1957, REITTER, 1912  REITTER, 1912  ZWÖLFER, EICHHORN, 1966  DUBEŠKO, 1970	ZWÖLFER, EICHHORN, 1966  EMDEN VAN, 1962, OGLOBLIN, MEDVEDEV, 1971, PALIJ and KLEPIKOVA, 1957, STEINHAUSEN, 1950  ZWÖLFER, EICHHORN, 1966  ""  VAN EMDEN, 1962, STEINHAUSEN, 1950  ZWÖLFER, EICHHORN, 1966*  ""  ""  ""  ""  ""  ""  ""  ""  ""
Cirsium rivulare (JACQ.) All Cirsium canum (L.) M. B. Cirsium heterophyllum (L.) All Cirsium tuberosum (L.) All Cirsium tuberosum (L.) All Cirsium incanum Bieb Cirsium Mill Silybum Marianum (L.) Gaerty. Cynara Scolymus L. Onopordon acanthium L. Onopordon L. Sonchus arvensis L. Sonchus L. Tanacetum L. Centaurea jacea L. Centaurea nigra L. Centaurea nigra L. Centaurea nigra L.	F. Compositae Arctium minus (HIIL.) BERNH. Arctium L. Carduus glaucus BMG. Carduus tenuiflorus CURT. Carduus erispus L. Carduus L. Carduus L. Corduus L. Cirsium arvense (L.) Scop. Cirsium palustre (L.) Scop. Cirsium palustre (L.) Scop. Cirsium palustre (L.) Scop. Cirsium rivulare (JACQ.) Scop. Cirsium monspessulanum All. Cirsium rivulare (JACQ.) ALL.
	Cassida vibex L.

Observations of the present author	Author INHAUSEN, Author Author	Author Author Author , 1971, Pa- SEN, 1950,
Data according to other authors	LOPATIN, 1960  VAN EMDEN, 1962, MATIS, 1968, REITTER, 1912, STEINHAUSEN, 1950  ZWÖLFER, EICHHORN, 1966*  ", REITTER, 1912  OGLOBLIN, MEDVEDEV, 1971  ZWÖLFER, EICHHORN, 1966  ", ", ", ", ", ", ", ", ", ", ", ", ",	Matis, 1968?  Żurańska, 1959  van Emden, 1962, Reitter, 1912  Engel, 1932, Kleine, 1917*  Kleine, 1917  Lopatin, 1960, Matis, 1968, Ogloblin, Medvedev, 1971, Palij, 1959, Palij and Kleptkova, 1957, Steinhausen, 1950, Zwölfer, Eichhorn, 1966
Foodplant	Cirsium lanceolatum (L.) Scop. Cirsium incanum BIEB. Cirsium MILL. Silybum Marianum (L.) GAERTN. Cynara Scolymus L. Onopordon acanthium L. Serratula tinctoria L. Tanacetum L. S. F. Centaureinae Centaurea jacea L. Centaurea nigra L. Centaurea scabiosa L. Centaurea scabiosa L. Centaurea L.	F. Chenopodiaceae Beta vulgaris L. F. Papilionaceae Trifolium L. F. Labiatae Mentha aquatica L. Mentha piperita L. Mentha arvensis L. Mentha L.
Species of the cassid		Cassida viridis L.

Author	Author Author	Author Author Author Author	
", ", ", ", ", ", ", ", ", ", ", ", ", "	KLEINE, 1917  ENGEL, 1932, KLEINE, 1917  KLEINE, 1917  KLEINE, 1917  MATIS, 1968, STEINHAUSEN, 1950  KLEINE, 1917  MATIS, 1968, OGLOBLIN, MEDVEDEY, 1971, PALIJ, 1959, PALIJ and KLEPIKOVA, 1957, STEINHAUSEN, 1950  KLEINE, 1917, STEINHAUSEN, 1950  STEINHAUSEN, 1950  KEITTER, 1912  MATIS, 1968, after TARBIŃSKI	VAN EMDEN, 1962, KLEINE, 1919, MATIS, 1968, OGLOBLIN, MEDVEDEV, 1971, PALIJ and KLEPIKOVA, 1957 KLEINE, 1917, after Weise KLEINE, 1917, after Weise KLEINE, 1917, after Weise Steinhausen, 1950 KLEINE, 1917, after Weise Steinhausen, 1950 KLEINE, 1917, after Weise, Steinhausen, 1950 KLEINE, 1917, after Weise, Steinhausen, 1950 KLEINE, 1917, after Weise, Steinhausen, 1950	Kleine, 1917
Stachys palustris L. Stachys recta L. Stachys germanica L. Stachys L.	Galeopsis pubescens BESS. Galeopsis tetrahit L. Galeopsis speciosa Mill. Galeopsis versicolor Curt. Galeopsis ladanum L. Galeopsis L. Salvia pratensis L. Salvia L. Nelissa L. Lycopus L. Lycopus L. Nepeta L. Compositae Cynara Scolymus L. Cirsium Mill.	Cassida flaveola  Thunbb.  Stellaria graminea L. Stellaria media Vill. Stellaria nemorum L. Stellaria nemorum L. Stellaria uliginosa Murr. Stellaria uliginosa L. Stellaria L. Gerastium aquaticum L. Cerastium aquaticum L. Cerastium aquaticum L. Spergula arvensis L.	Spergula L.

Observations of the present	author	Author, after Dr. Bo- RUSIEWICZ	•	- Author			Author!						Author	
Data googing to other authors	Data according to other authors	KLEINE, 1917, KLEINE, 1917, after Weise, Steinhausen, 1950	Kleine, 1917 ", Reitter, 1912	VAN EMDEN, 1962, KLEINE, 1919 KLEINE, 1914, 1915, 1916, 1918, KLEINE, 1914, after KAL- TENBACH, PALIJ, 1959	Pally, 1959*, Matis, 1968*, Ogloblin, Medvedev, 1971, Pally and Klepikova, 1957*, Steinhausen, 1950*	KLEINE, 1914, 1915, 1916, 1918, KLEINE, 1914, after KAL- TENBACH, LOPATIN, 1960, MATIS, 1968, OGLOBLIN, MEDVE-	DEV, 1971, PALIJ, 1959, PALIJ and KLEPIKOVA, 1957, REITTER, 1912, SIMM, 1948, STEINHAUSEN, 1950	KLEINE, 1914, after KALTENBACH, STEINHAUSEN, 1950	Kleine, 1914, after Kaltenbach	ŻURAŃSKA, 1959	a	Dubeško, 1970	VAN EMDEN, 1962 KLEINE, 1919	LOPATIN, 1960, OGLOBLIN, MEDVEDEV, 1971, PALIJ, 1959, PALIJ and KLEPIKOVA, 1957*, RAMMNER, 1932, REITTER, 1912
to Carlos Fr	тооарын	Honckenya peploides (L.) EBRH.	Melandrium album (MILL.) GARCKE Minuartia LOEFL.	F. Chenopodiaceae Chenopodium album L.	Chenopodium L.	Beta vulgaris L.		Atriplex I.	F. Caryophyllaceae Silene L.	F. Papilionaceae Ornithonns I.,	Trifolium L.	F. Compositae Artemisia L.	F. Chenopodiaceae Chenopodium album L.	Ohenopodium glaucum L. Ohenopodium L.
Species	of the cassid			Cassida nebulosa L.									Cassida nobilis L.	

	KLEINE, 1919, MATIS, 1968, OGLOBLIN, MEDVEDEV, 1971, PALIJ, 1959, PALIJ and KLEPIKOVA, 1957, STEINHAUSEN, 1950 KLEINE, 1919  PALIJ, 1959 EMDEN, VAN 1962 KLEINE, 1919 STEINHAUSEN, 1950  ,,, ŻURAŃSKA, 1959 ,,, ,,,	Palij, 1959, Palij and Klepikova, 1957, Steinhausen, 1950, Kleine, 1917, Matis, 1968, Ogloblin, Medvedev, Author 1971, Reitter, 1912 Steinhausen, 1950, Kleine, 1917 Palij, 1959, Palij and Klepikova, 1957, Kleine, 1917, Ogloblin, Medvedev, 1971	Reitter, 1912 Ogloblin, Medvedev, 1971, Steinhausen, 1950 ,,	>
a con		olium L. ica L. gare L.		Convolvulaceae Connoluilie amonois I.  Datit and Kiedicota 1057 September 1050 September

Explanations: \*— the main foodplant

?—feeding on this plant doubtful

!— doubtful damage of cassids on this plant, rather of secondary character

Scop. is a plant particularly favoured by these species of beetles. The present author also found the greatest preference of both species in relation to Cirsium arvense (L.) Scop. and C. oleraceum (L.) Scop., while it was a little weaker in relation to the remaining species of plants. The report of Zwölfer and Eichhorn (1966) concerning Centaurea jacea L., and C. nigra L. as foodplants of Cassida rubiginosa Müll. was not confirmed by the investigation of the present author.

Cassida viridis L. is closely connected with the plants of the family Labiatae (Tab. I), particularly with the species of the genera Mentha, Stachys, and Galeopsis, as it may be seen from the results of the investigations of various workers and of the present author. The investigation in Ojców indicates a marked preference of this beetle in relation to Mentha aquatica L. and M. longifolia (L.) Huds. The latter was for the first time used as a foodplant of C. viridis L. A fairly strong preference is also observed in relation to Stachys silvatica L., Galeopsis pubescens Bess., G. tetrahit L., and Salvia L. Therefore, the report of Zurańska (1959) concerning the plants of the family Papilionaceae, of Reitter (1912) and Matis (1968) concerning those of the family Compositae, and of Matis (1968) of the family Chenopodiaceae as foodplants of C. viridis L. seem strongly disputable.

Cassida flaveola Thunbg. occurs on plants of the family Caryophyllaceae (Tab. I) this being confirmed by other authors. This beetle mostly prefers the species of the genera Stellaria, Spergula, and Honckenya. In the territory of Ojców the mostly preferred plant is Stellaria graminea L. while S. nemorum L. and S. media VILL. were taken less willingly and they were for the first time reported as foodplants. An attempt failed to feed cassids on the specimens of Stellaria holostea L. thus the respective report of Kleine (1917) seemed doubtful.

According to the opinions of the majority of authors and to the observations of the present author Cassida nebulosa L. occurs on the plants of the family Chenopodiaceae only (Tab. I), showing strong preference of the plants of the genera Chenopodium and Beta. With regard to its chief foodplant contradictory opinions are found in the literature. The observations in the vicinity of Ojców indicated decisive preference of Chenopodium L. The reports of Kleine (1914) on the plants of the family Caryophyllaceae, of Żurańska (1959) on those of the family Papilionaceae, and of Dubeško (1970) of the family Compositae are practically out of the question.

Considerable discrepances are found in the opinions of various authors regarding the foodplants of Cassida nobilis L. (Tab. I). The majority of them and the present author as well, quote the species of the family Chenopodiaceae as the actual foodplants of this beetle, the plant of the genera Chenopodium and Beta coming into consideration as particularly preferred ones. However, other workers suggest the species of the family Caryophyllaceae, especially the genus Spergula. This beetle is relatively rare in the territory of the Ojców National Park nevertheless it was only found on root crops considerably infested with weeds of the genus Chenopodium.

It seems that under conditions of the Ojców National Park Chenopodium

album L. is the chief foodplant of this beetle. The report of Żurańska (1959) about the plants of the family Papilionaceae is strongly disputable.

Cassida prasina ILL. is closely connected with the plants of the family Compositae (Tab. I), particularly with species of the genus Achillea and more rarely Tanacetum, this being shown by the results of the investigations of various workers and of the present author.

Scarce data are available on the problem of foodplants of Cassida hemisphaerica Hbst. (Tab. I). According to various workers the plants of the family Caryophyllaceae come into consideration, this being supported by the observations of the present author. Food tests carried out on various plants of this family seem to indicate Silene nutans L. as its possible foodplant.

The cassids presented and discussed so far are narrow oligophagous animals limited to a small number of plant species, while *Hypocassida subferruginea* Schrnk., observed outside the territory of the Ojców National Park, is a real monophagous animal and occurs on *Convolvulus arvensis* L. of the family *Convolvulaceae* (Tab. I), this being confirmed by all authors.

One more fact should be mentioned here: according to the opinions of Steinhausen (1950) the most primitive forms of cassids live on Caryophyllaceae (C. flaveola Thunbg., C. hemisphaerica Hbbst.) and Chenopodiaceae (C. nebulosa L., C. nobilis L.) while specialized forms occur on Compositae (C. rubiginosa Müll., C. vibex L., C. prasina Ill.), Labiatae (C. viridis L.), and Convolvulaceae (H. subferruginea Schrnk.).

The problem of how do the cassids find their foodplants is so far inexplained. It is supposed that the smell of these plants plays a great role. The investigations on the Colorado beetle proved that in spring migrations as well its sense of smell as the smell of potato plants (Willsz et al., 1958) play a great role in finding food (Kaczmarek, 1955). Olfactory organs of the antennae of insects enable them to orientate in what direction and distance the food, scented owing to its volatile chemical compounds, may be found.

An interesting phenomenon of the so called "complementary feeding" was found in cassids migrating from winter chambers to the territory of the meadow in spring. This fact is confirmed by other investigators of cassids (Rammer, 1934, Kleine, 1915, 1917, 1919, Gorbunov and Šeremet, 1968) and on other groups of herbivorous animals (Opyrchalowa, 1970, Warchalowski, 1958, 1959, 1960, Szujecki, 1966, Żurańska, 1968, Dmoch, 1959, Starzyk, 1970). In this period during intense feeding sexual gland maturate, insects begin to mate and at last to lay eggs. However in the first days on the meadow the cassids do not feed much on youngest leaves of plants but more often they warm in the sun sitting on old plant shoots or on fallen leaves. The observations of Warchalowski (1959) on the genus Longitarsus Late. showed that warming of insects in the sun is extremely important for the process of normal reproduction, particular role being played here by the ultraviolet radiation. The radiation effects certain physiological processes in the bodies of insects, among others influences the metabolism of carotenoids which in the period of "comple-

mentary feeding" are stored up in the fat body and transferred from there to eggs as they maturate. Hence a conclusion may be drawn on the nutritive origin of carotenoids in the bodies of insects, this being supported by the results of the investigations of Czeczuga (1971) on the Colorado beetle. The physiological importance of carotene was defined by Kleine (1917) as a reserve substance which gets to eggs and serves to produce sperm, moreover, as a reserve energy for the period of mating. Starvation may completely inhibit the formation of carotene in the insects.

As it was already mentioned, with the beginning of feeding the sex glands of insects maturated. In this period the beetles very intensely feed on youngest top parts of plants which in spring contain great amounts of tocopherols (vitamines E) (Kowalska, 1969, Opyrchalowa, 1970). These compounds have a great influence on the maturation of sex glands of insects and on the intensification of their biological activity. The maturation of beetles is also connected with a change in the amount of free water in their bodies. In the investigated species of cassids the content of free water reaches its lowest level in the period just before wintering (Kosior, Klein, 1970), gradually increases throughout the wintering (chiefly in consequence of fat combustion) and amounts to 65—70 per cent in spring, when the maturation of sex glands and the laying of eggs occur. According to Łarczenko (1957) the content of free water in the Colorado beetle amounts to 70 per cent at this period, thus being a little greater than in cassids.

With cassids the intensity of the course of the complementary feeding above all depends on climatic factors, especially on temperature, insolation, rains, and wind, while the decisive role is played by the maximum day temperature and insolation. On the meadow in Ojców the feeding of cassids was intense at the temperatures exceeding 15°C, the most intense at 20°C and more, with clear weather and strong insolation. Great decreases in the temperature connected with rains and wind brought about decreases in the activity and an inhibition of feeding of beetles which hid in the meadow turf.

The climate also decides about the term of the beginning and length of this feeding, as it was found in several-year studies of the present author. In the years 1966—1971 the length of complementary feeding on the investigated cassid species was: Cassida rubiginosa Müll. 15—40 days, C. vibex L. 15—35 days, C. viridis L. 9—12 days, C. flaveola Thunber. 8—15 days. The above list indicates that the length of this feeding depends on the period of the emergence of beetles. A simple dependence occurs here and according to it the later a given species emerges the shorter complementary feeding lasts and the faster the beetles maturate. The contributions of different workers to this problem, though not numerous, are greatly in agreement with the results of the present author. Kleine (1917) reports that the length of this period is 2 weeks for C. murraea L. and above 2 weeks for C. rubiginosa Müll. According to Gorbunov and Šeremet (1968) Hypocassida subferruginea Schrnk. begins to lay eggs already after 1—1.5 week. Warchalowski (1959) found that in Longitarsus Late. the length of this period was several to more than twenty days.

In consequence of feeding of the imagines of cassids pictures of feeding remain on the leaves of food plants, which, according to Kleine (1917, 1919), are very characteristic for given species. The investigations of Kleine supply most information to this problem, Cassida rubiginosa Müll. and C. flaveola Thunbe. being particularly considered. According to the opinion of this author almost all species of beetles which attack plants of the family Compositae perform oval superficial feeding mixed with marginal one, while the species occurring on the plants of the family Caryophyllaceae perform both marginal and superficial feeding. The results of investigations presented by Kleine (1917) agree with the present author's observations.

Field observations carried out on 4 species of eassids which appear within the study area on the meadow, as well as the laboratory cultures enabled to prepare sets of pictures of their feeding. Plate XXV presents the pictures of the feeding of adult imagines of Cassida rubiginosa Müll. (A, B) and C. vibex L. (C, D) which feed on the same plants of the family Compositae, with the exception of one, i.e. Centaurea jacea L. The striking feature is the superficial (primary) feeding while the marginal (secondary) one rarely occurs and is performed from the surface, never from the margin. The feeding chiefly takes place on the upper leaf surface and in a less degree on the lower one. The feeding marks are round, oval or even elongated and always begin as points. They are encountered on the whole leaf surface so that no part of the leaf is preferred. The pictures of feeding of both species differ by the more uniform distribution of feeding marks on the surface and by greater damage on leaf margins made by C. rubiginosa Müll. while the feeding marks of C. vibex L. are often concentrated in the form of groups, the leaf margins being more rarely damaged. Moreover, in the pictures of feeding of C. rubiginosa MÜLL. scrape feeding (feeding on leaf tissue to opposite epidermis) occurs more often than the perforation feeding (right through a leaf) while with C. vibex L. an opposite situation is observed. In the period of complementary feeding much scrape feeding is observed in both Species however with C. rubiginosa Müll. it always prevails over the perforation one. Throughout the vegetation period the intensity of feeding of imagines decreased and at the end of summer traces of their feeding were very scarce. In 1972 additional laboratory cultures showed that the beetles of C. vibex L. also fed willingly on the leaves of Carduus acanthoides L. Mereover, it was found that both species fed on the leaves of Cirsium lanceolatum (L.) Scop., and Arctium lappa L. in a degree greater than that presented in plate XXV, B, D, the traces of feeding being always very irregular on the leaves of Arctium.

On the plants of the family Labiatae (pl. XXVI, A, B) the pictures of feeding of adult imagines of *C. viridis* L. are very similar to those described above. Superficial feeding is primary while the marginal one is secondary and always started from the surface. The basic difference is that with *C. viridis* L. always and exclusively the perforation feeding occurs but never the scrape feeding. Moreover, the damages to leaf margins and smaller nerves are much more frequent. The places of feeding are round, oval, and even irregular and are chiefly

distributed on the whole surface of leaves with a slight tendency to the formation of groups.

On the plants of the family Caryophyllaceae the pictures of feeding by adult imagines of C. flaveola Thunbg. (pl. XXVI, C, D) are characterized by primary marginal feeding, the superficial one having a secondary character. Both the perforation and scrape feeding occur with these imagines but the latter very rarely. Feeding points are of different size and very irregular shape. Attempts failed to feed the adult beetles with the leaves of Cerastium vulgatum L.

## 4. Mating and egg-laying

The moment of sexual maturity occurs almost at the same time in females and males of herbivorous insects and they begin to mate then (WARCHALOWSKI, 1958, STARZYK, 1970, WEGOREK, 1959). This fact was also observed in the investigated species of cassids, the earliest copulation being observed in the beetles of Cassida rubiginosa Müll. (second half of April); afterwards other species begin mating at almost equal intervals, in accordance with the terms of their emergence on the meadow (fig. 1).

Mating of cassids, its way, and length depend to a great degree on climatic conditions (temperature, insolation, rains, wind) this being distinctly stressed by Kleine (1914-1915). In Ceuthorrhynchus quadridens Panz. similar dependence was observed by DMOCH (1959). The first mating pairs of beetles were observed on the meadow on days with maximum air temperatures above 18°C, the maximum number of copulating cassids being noted at temperatures above 20°C. WEGOREK (1959) also observed the copulation of the Colorado beetle at temperatures exceeding 18°C. A decrease in the temperature to 15°C did not yet stop the mating of cassids but at a further decrease to 13°C and lower, the process was stopped. Low temperatures connected with rains and winds most strongly influenced the beetles, bringing about an inhibition of their activity and the phenomenon of their hiding at the bases of foodplants.

The investigations in Ojców showed that the month of May and the first half of June are decisive for cassids since in that period mass copulation and egg-laying occur with the studied species. The mating is carried out during the day and the greatest number of pairs are observed at noon at high temperatures and considerable insolation. Mating pairs were also encountered soon after sunrise and just before sunset. In individual pairs the time of copulation was from a few to several hours. Kleine (1915) reported a similar length of time for Cassida nebulosa L., but Wradatsch (1919) claimed that the pairs of C. splendidula Suffr. mated as long as 24 hrs. Szujecki (1966) reported the length of 1-3 hrs for other chrysomelids and DMoCH (1959) a few to several hours for Ceuthorrhynchus quadridens PANZ., but they both stressed that the copulation was repeated throughout the whole period of egg-laying. In the investigated cassids repeated copulations were observed but in the majority of cases this process occurs only once, this being proved by the fact that one mating was enough for a female to produce fertilized eggs throughout the whole period of egg-laying. A similar example is quoted by Balli (1943) for *Melasoma populi* L. Also Warchalowski (1958) reports that in *Longitarsus suturellus* Dft. a single copulation of 2—8 hrs occurs. The above data indicate that in various herbivorous animals the course of mating shows considerable differences, especially with regard to its multiplicity.

In the investigated species of cassids an interesting phenomenon was observed consisting in longer periods of mating than that of egg-laying. Kleine (1917) explains this seeming copulation with longer inclination to mating in males which tend to sexual connexion when in females the reserve of eggs has been already exhausted.

It was found in the course of the investigation that the period of mating is different in various species (fig. 1). With Cassida rubiginosa Müll it amounted to 7—8 weeks, with C. vibex L. 6—7, with C. viridis L. 4—6, and with C. flaveola Thunbe. 6—7 weeks. The length of this period depends on the term of the emergence of a given species on the meadow; the later the emergence occurs the shorter is the mating period, only with C. flaveola Thunbe. a contrary situation being observed. In the literature on cassids scarce informations on this problem are found. Šeremet and Gorbunov (1969) and Kleine (1917) only noted the copulation of C. rubiginosa Müll in May, moreover, Kleine reported that with C. flaveola Thunge. it occurred up to the middle of August. The report of Kleine (1915) that with C. flaveola Thunbe. the copulation was continued for more than a few weeks, was also worth noting. According to Starzyk (1970) in Gaurotes virginea L. the period of copulation is as long as 14 weeks thus considerably exceeds the results obtained with cassids.

Some days after mating the females of cassids begin to lay eggs. In the investigated species it happens after 3-7 days under field conditions and after 2-5 days in the laboratory. According to KACZMAREK (1955) and MIKSIE-WICZ (1948) in the Colorado beetle an average period between the copulation and the beginning of egg-laying is 3 days while with Ceuthorrhynchus quadridens Panz. (DMoch, 1959) a few days. Thus the above-mentioned data agree with the Observations of the present author. The climatic factors especially temperature, air humidity, length of day, rains, and wind have an essential influence on the term and course of egg-laying by cassid females. The egg-laying occurs at the temperature above 18°C, optimum temperatures being within 20-25°C. A decrease in the temperature below 15°C inhibits this process while at 13°C and lower the egg-laying is stopped. Similar effect have high temperatures of about 30°C. The investigations on the Colorado beetle (Kowalska, 1969, Wegorek, 1959) and on Xyletinus peltatus Harris (Moore, 1970) support the Observations of the present author. The influence of air humidity is also fairly distinct. An optimum humidity which favours the egg-laying by females of cassids ranges from 60-90 per cent, while as well the high (about 100 per cent) as the low (less than 50 per cent) humidity inhibits the process of egg-laying. Very similar results were obtained by Wegorek (1959) and Kowalska (1969)

in their studies on the Colorado beetle. Rains connected with low temperatures and winds influence very unfavourably the course of this phenomenon, bring about its inhibition, and strongly lengthen its time. The length of day very strongly influences the beginning, course, and length of the period of egg-laying. Under climatic conditions of the meadow the egg-laying occurs always at the day length of over 15 hrs (Tab. II), the threshold value being the day length of 15 beginning and end of this process. Identical results for the Colorado beetle are reported by Weggrek (1959) and Kowalska (1969).

Table II

Changes in day length throughout the investigation season

Date of observations	Sunrise (hr.)	Sunset (hr.)	Day length (hrs,)
8. IV	454	1822	1328
21. IV	426	1845	1419
8. V	352	1913	$15^{21}$
21. V	332	1934	$16^{02}$
8. VI	316	1955	1639
21. VI	314	2001	1647
8. VII	324	1957	1633
21. VII	340	1944	1604
8. VIII	407	1915	. 1508
21. VIII	429	1848	1419
8. IX	458	1808	1396
21. IX	520	$17^{37}$	1217

The eggs of cassids are laid in batches on the foodplants and only sporadically on other, neighbouring plants, e.g. Urtica dioica L., Veronica chamaedrys L., Alchemilla sp., Alopecurus pratensis L. Detailed descriptions of the way of egg-laying of cassids are presented by Kleine (1915, 1917), Rammer (1937), Engel (1932), Palij and Klepikova (1957), and Ogloblin and Medvedev (1971). Cassida rubiginosa Müll. deposited eggs on the leaves of Cirsium oleraceum (L.) Scop. usually on the under surface, more rarely on the upper one, and sporadically on the stem. The majority of batches were found on the forepart of leaves, often near the main nerve or at the end of the blade. Up to 3 batches of eggs were found on one leaf. The number of eggs in a batch ranged from 2 to 17. Cassida vibex L. also laid eggs on the leaves of Cirsium oleraceum (L.) Scop.; the number of eggs in batches ranged from 1—3 but most often was one. The eggs were usually deposited on the under part of leaves and on their foreparts, on the margins of leaf blades, or more rarely on the upper leaf surface. Often a few batches were found on one leaf.

The batches of eggs of *C. viridis* L. were deposited on *Mentha longifolia* (L.) Huds. in the majority of cases on the stem of these plants, more rarely on the

under surface of leaf blades, and very rarely on their upper surface. On one specimen of mint even 3 batches were found which, if deposited on the stem, were in a distance of 15—20 cm from each other. The number of eggs in a batch was 5—16. C. flaveola Thunber laid eggs on Stellaria graminea L. usually on the under surface of leaves, fairly often on stems, and rarely on the upper surface of leaves. The number of eggs in batches ranged from 1—3, most often being one. In this species egg-laying on leaves of other species of plants occurred frequently.

With all discussed species the striking feature is that the females lay eggs on the under surface of leaves. This way of depositing egg-batches probably plays a protective role. According to Szujecki (1966) in this way chrysomelids protect their batches of eggs from enemies and unfavourable atmospheric factors. The time of proper egg-laying ranged from a few minutes (C. flaveola Thunbg., C. vibex L.) to several minutes (C. rubiginosa Müll. and C. viridis L.). The obtained results are fairly consistent with the observations of Rammner (1934) who found the span of about 10 minutes for C. murraea L. After depositing eggs the females rest for a few minutes and afterwards intensively feed. It should be stressed that throughout the whole period of egg-laying intense feeding is observed with females of cassids, the batches of eggs and traces of feeding being usually found on the same leaf. The batches of eggs of the investigated species were most often encountered on solitary plants, on plants growing in small groups, or on well exposed tufts of plants, this being also stressed by Šeremet and Gorbunov (1969).

The opinions of various authors (Engel, 1932, Steinhausen, 1950, Kleine, 1917, OGLOBLIN, MEDVEDEV, 1971, ŠEREMET, GORBUNOV, 1969) on the problem. of the distribution of egg-batches of cassids on their foodplants are essentially consistent with the results of the present author. Only the report of Kleine. (1917) who claims that the eggs of C. rubiginosa Müll. are always deposited on the upper surface of leaves, seems doubtful. Strong controversies arise from the views of certain authors concerning the number of eggs in batches. The number of eggs in the batches of C. rubiginosa Müll (Palij and Klepikova, 1957, STEINHAUSEN, 1950) and C. viridis L. (ENGEL, 1932, KLEINE, 1917, STEINHAUSEN, 1950) are too low as compared with those found by the present author, while the report of Engel (1935) that the number of eggs in a batch of C. viridis L. amounts to 15, agrees with the author's own results. On the other hand the data of Kleine (1917) and Steinhausen (1950) on the numbers of eggs in the batches of C. flaveola Thunbg. seem very doubtful. According to the opinion of these workers the batches of this species on the average contain three eggs while the present author usually found batches with one egg. It is also impossible to agree with the view of Ogloblin and Medvedev (1971) that the eggs of cassids are deposited in batches sometimes containing several dozen eggs.

It was found in the course of investigations on the meadow in Ojców that period of egg-laying by the females of *C. rubiginosa* Müll. amounts to 12 weeks. *C. vibex* L. 8—10, *C. viridis* L. 8—9, and *C. flaveola* Thunbg. 8—9 weeks,

An interesting dependence occurs here: the later is the emergence of a given species on the meadow the shorter is the period of egg-laying by the females (fig. 1). The investigated species of cassids lay eggs from the middle of May to the middle of August, with the exception of C. viridis L. always finishing this process in July. At the same time it is distinctly visible that the process of egg-laying by the females is very extended, the climatic factors deciding about it. With regard to the length of egg-laying discrepant opinions prevail among various workers. The length of this process found by Zwölfer and Eichhorn (1966) with C. rubiqinosa Müll. and C. vibex L. fully agrees with the findings of the present author, while the results of Palij and Klepikowa (1957) obtained for these two species and for C. viridis L. greatly differ from the data of the author; these differences are most probably effected by different climatic conditions in the regions of their occurrence. With regard to C. flaveola Thunber the discussed problem was not studied by these authors while general informations reported by Ogloblin and Medvedev (1971) on the period of egg-laying in the subfamily of cassids are partly consistent with the results of the present author.

## 5. Length of life and sex ratio

Little attention was paid by various workers to the problem of the length of life of beetles under field conditions. Lindroth (1945) claims that the species of the genus Carabus in adult stage as a rule live longer than one year. According to Miksiewicz (1948) and Wegorek (1959) separate cases are known of the imagines of the Colorado beetle living for two years, while Trouvelot (1935) reports that even the cases of 3-year lifetime of this insect are noted, the normal length of life of the Colorado beetle being one year. According to Starzyk (1970) the average length of life of Gaurotes virginea L. (Cerambycidae) amounts to 28 days, a maximum being 30 days.

Only two short references are found in the literature with regard to the problem of the lifetime of cassids. Rammer (1934) reports that after a period of reproduction adult imagines of *C. murraea* L. gradually die and from the middle of July are slowly vanishing from plants. According to Kleine (1915) adult imagines of *C. nebulosa* L. died shortly after egg-laying.

In the years 1968—1972 in the investigation of cassids special method of observation was applied (sacks of nylon gauze on leaves and controlled wintering in jars without bottom, placed in the forest litter and covered with gauze) which made possible a study of the actual length of life with imagines of the investigated species of cassids (Tab. III). It was found that the average length of life of cassids was about one year in the case of *C. rubiginosa* MÜLL. and a little more with the remaining species. In all species the minimal length of life amounts to about one month. The problem of the maximum life length of these beetles seems very interesting. The longest life, almost 4 years, was found among the females of *C. rubiginosa* MÜLL., *C. vibex* L. live 3 years, *C. viridis* L. almost equally long, and *C. flaveola* Thunber. only 2 years. In all species males live shorter than

Life length of females and males of Cassidinae within the study area on the meadow in the Sąspowska Valley of the Ojców National Park

Species	Cassi	ida rubi Müll	iginosa	Cass	ida vil	bex L.	Cassi	da viri	idis L.		rida fl	aveola
Life length in months  Sex	$\overline{\mathbf{x}}$	max.	min.	$\overline{\mathbf{x}}$	max.	min.	$\overline{\mathbf{x}}$	max.	min.	x	max.	min.
female	9.4	45	1	13.7	36	1	12.8	33	1	13.9	24	1
male	9.2	24	1	11.1	24	1	12.3	24	1	12.6	22	1

females, the differences between the two sexes ranging from 2 months with C. flaveola Thunbe. to almost 2 years with C. rubiginosa Müll.

In was found in the investigations of DMOCH (1959) on Ceuthorrhynchus quadridens Panz. (Curculionidae) and Starzyk (1970) on Gaurotes virginea L. (Cerambycidae) that the males also lived shorter than the females but the differences in the life length were insignificant. Ruszkowska and Opyrchałowa (1969) explain shorter life of males by the fact that with the insects the rate of metabolism measured by CO released by organisms, is higher in males than in females.

It should be particularly stressed that sexual dimorphism is observed in the beetles of the investigated species of cassids. In general the females are larger than males and only sporadically the situation is contrary. The prothorax and elytrae of females are ovate and more arched, those of males more rounded and fairly flat. The prothorax of females is broader and in its forepart more sharply ended than that of males, and, moreover, its length is almost equal to the breadth of elytrae, while in males it is much narrower and its length is greater than the breadth of elytrae, with the exception of *C. viridis* L. and *C. flaveola* Thunbe. Morphological features described above are the basis of a precise evaluation of sex ratio in the investigated species throughout the vegetation season.

In the light of the results quoted above the problem of sex ratio with cassids and also with other herbivorous animals seems interesting. In the period of several year investigation of these species this ratio usually shows an insignificant prevalence of females (1·2—1). In several cases a slightly greater differences were noted in this ratio, especially with *C. viridis* L. (1·3:1). In general, the prevalence of females is also observed in other herbivorous beetles. In the Colorado beetle the sex ratio amounts to 2:1 for females (Willusz et al. 1968, Karg, Trojan, 1968) while contrary to it with *Gaurotes virginea* (L.) 3:1 and 2:1 for males, however, this is a transitory situation since males die relatively earlier, distinct prevalence of females being observed then.

<sup>3 —</sup> Acta Zoologica Cracoviensia XX/9

## 6. Ecology and ethology of imagines

The cassids occurring within the study area on the meadow may be classified to the group of insects of day activity. The beginning of this activity is observed soon after sunrise, an increase and a maximum include the middle part of day, a decrease occurring at sunset. The beetles feed during the day only and at nightfall hide between the stem and leaf just at its bottom or under a leaf. The typical course of 24-hour rythm of the activity depends on climatic conditions (temperature, humidity, insolation, rains) this being supported by the observations of Starzyk (1970) on Gaurotes virginea (L.) and of DMOCH (1959) on Ceuthorrhynchus quadridens Panz. Day temperatures play a basic role since these insects show the day activity. An increase in the activity of cassids was noted at temperatures higher than 18°C, and the optimal conditions of activity at the range of temperatures of 20—25°C, the beetles being often found on foodplants then while at the temperatures of 30°C and higher the insects hide under leaves or even go down into the sward.

The role of air humidity seems equally essential, the range of 60—90 per cent being most favourable for the insects. Rains connected with a decrease in temperature (about 13°C) bring about a decrease in the activity of cassids. At a further decrease in the temperature a complete inhibition of the activity of cassids is noted. The activity of cassids also greatly depends on their physical condition. In the time of spring emergence at the beginning of the period of full vital activity the beetles of the investigated species are very mobile and perform frequent flies. Gradually their activity and frequency of flights decrease and in the period of mating and egg-laying imagines do not fly much, this being supported by the investigations of Kleine (1917) and Engel (1932). According to the latter C. nebulosa L. which also flies very fast and on great distances, shows greatest activity of all species of cassids.

The phenomenon of akinesis commonly occurs as well among cassids (Engel, 1932) as among other groups of herbivorous insects (Dmoch, 1959, Starzyk, 1970). Alarmed insects fall down from plants into the sward and become motionless for a certain time. In the investigated species of cassids the time of immobility ranges from several seconds to a few minutes.

Particular liking of cassids for sunlight should be stressed (Engel, 1932, Rammer, 1934) this being also noted in the field investigations in Ojców. The beetles were most often encountered on the borders of meadows and on sides of ditches and within the study area in places well exposed to sun light (solitary specimens of plants, tussocks and less compact patches of vegetation) and only very rarely in the zone of half-light. The investigated species also show a distinct positive photoactivity.

Detailed description of the morphology of eggs of cassids are presented in the works of Wradatsch (1919), Kleine (1915, 1919), Ogloblin and Medve-Dev (1971), the structure of egg batches being discussed by Rammer (1937), Engel (1932), Steinhausen (1950), Kleine (1915, 1917), and Gorbunov and Šeremet (1968). Particular attention should be paid to a special protective covering which is laid by females over deposited eggs so that it reaches the surface of the leaf. The covering is very strong and has the properties of parchment. According to Kleine (1915) and Engel (1932) it plays an important role in protecting eggs from unfavourable weather conditions and enemies. According to the present author these opinions are only true to a certain moment since as the eggs maturate the batches stick out slightly on one side from the surface of the leaf and are then exposed to damage by strong winds and rains, or may be attacked by parasites.

The embrional development of eggs depends above all on temperature, air humidity, and rains. Since in the development of eggs certain span of time was needed, mean (and not maximum) temperatures and air humidities were considered and computed for the period of the observations. Table IV presents the results of field investigations on the length of egg incubation of the investigated species of cassids, carried out in 1969—1971. The mean length of the time of egg incubation computed for the whole period of observations shows slight differences in separate years. In 1971 the shortest time of the development was noted under the influence of unusually favourable weather conditions in the month of May. Similar result was found in 1969, however, a slight lengthening of development was brought about by a strong decrease in the air temperature on the turn of May. In 1970 the reason of the longest period of the development of eggs was the influence of low temperatures and great rains in May.

The problem of the length of the development of eggs is extremely interesting in comparing various values of mean decade temperatures and air humidities. At the temperature of 11.2°C and air humidity of 85.80 per cent the length of the development of eggs was 33 days, at 13.4°C and 83.80 per cent — 21 days, at 15.2°C and 82.70 per cent — 11 days. The above data distinctly show that With an increase in the temperature and a decrease in the air humidity the period of the development of eggs shortens as much as 3 times. In comparing the <sup>ob</sup>tained results with the data of other authors it was found that they greatly agree with regard to the evaluation of the length of eggs development. According to Engel (1932) the incubation of eggs of C. viridis L. took 32 days under field conditions, and according to RABOUD (1915) 28 days, the same number being reported for C. rubiginosa Müll. Wegorek (1950) reported that at the temperature of 15°C the egg development of the Colorado beetle took 19 days, a result approximating that of the present author. At the temperatures higher than 15°C Kleine (1917) observed the development of eggs of C. murraea L. Within 10-14 days, ŠEREMET and GORBUNOV (1968) within 8-15 days with

Length of development of Cassidinae within the study area on the meadow in the Saspowska Valley

In the vegetation season 1969.	The period of the observations May-August			a-		14.5°C 79.40%									•	In the vegetation	season 1970. The pe-	riod of the observa-	tions May-August			tempera- humi-	ture dity 14.0°C 85.80%
veola	max.			•											24		<b>∞</b>	9	10			6	
Cassida flaveola Thung.	x/spec. min. max.														14	4	9	5	9			7	
Cass	z/spec														18.2	5.5	6.1	5.1	7.7	×	3.0	8.0	
s L.*	max.														33	6	7	00	12	12	9	111	
Cassida viridis L.*	x/spec. min. max.														13	4	က	က	5	9	3	6	
Casside	x/spec														24,1	8.9	4.1	5.3	9.4	9.4	4.3	10.0	- Ng
v L.	max.	30	4	4	7	7	6		6	42				72	33	7	∞	10	00	7	4	10	
Cassida vibex L.	min.	111	3	က	က	က	4		7	25				36	.14	4	က	က	4	20	63	00	
Cassic	x/spec. min. max.	8.02	3.5	3.3	4.7	5.0	5.8	2.0	8.0	32.2				53.1	25.1	5.8	5.9	6.5	0.9	0.9	3.0	0.6	
inosa	max.	31	9	5	50	5	7	1	œ	38				69	33	oo	00	6	6	6	4	12	
la rubig Müll.	min.	11	3	3	က	က	4	1	7	25				36	11	4	က	က	9	5	22	1	
Cassida rubiginosa Müll.	x/spec. min. max.	20.0	4.3	4.1	4.2	4.0	4.8	2.0	7.2	30.8				9.09	20.7	6.1	5.0	0.9	9.2	6.7	3.2	×.50	)
Species	Number of days of develop- ment Stage	Eggs	Larvae L.	์ เ	ี่ ำ	L,	Ľ,	Prepupae	Pupae	Young imagines	Complete develop-	ment (from the	moment of egg lay-	ing)	Eggs	Larvae L.	1 1	N _	î ⊢	Ţ,	Prenimae	Pinae	

			In the vegetation	season 1971.	The period of the	observations May-	August		tempera- numi-	11.8°C 85.70%				
43	67	29	7	6	10	00		4	10		48	a		77
31	7.4	13	5	4	7	55		က	<b>∞</b>		32			45
35.1	23.00	18.0	2.9	6.5	7.5	0.7	X	3.2	0.6		39.9			57.9
65	86	28	13	10	7	6	7	4	12		62			06
33	46	18	9	8	5	7	9	3	10		45			63
47.5	717.6	21.2	9.8	9.5	5.4	8.5	6.3	3.7	11.0		52.4			73.6
54	× 7	33	14	10	7	9	6	4	12		62			95
59	43	14	4	က	4	4	7	6.1	6		33			47
41.9	67.0	22.2	7.5	5.5	5.9	5.5	8.0	3.0	11.0		46.1		,	68.3
59	66	29	13	10	_	6	10	4	12		65			94
30	41	=	4	4	4	4	20	67	7		30			41
44.3	65.0	19.1	8.8	7.2	4.9	9.9	8.8	3.6	9.5		49.4			68.5
Young imagines	Complete development (from the moment of egg laying)	Eggs	Larvae L <sub>1</sub>	IJ	L3	Ľ.	L,	Prepupae	Pupae		Young imagines	Complete develop- ment (from the	moment of egg lay-	ing)

Explanations: \*—in 1969 the development of C. viridis L. and C. flaveola Thunbg. was not investigated.  $\times$ —with C. flaveola Thunbg. only 4 larval instars were found.

Length of development of Cassidinae under laboratory conditions

		The period of the	observations	25. VI—9. VIII. 1971		$\overline{x}$ air temperature	$17.0^{\circ}\mathrm{C}{\pm}2.0$	$\overline{\mathbf{x}}$ air humidity	$88.00\%\pm5.00$							The period of the	observations	25.VI—30.VIII.1969	ouritonound air x		x air humidity	$87.00\% \pm 7.00$	
eola	max.		9	. 9	9	9		4	10	38				52	1								
Cassida flaveola Thunbg.	min.	ı	4	4	4	4		<b>c</b> 1	∞	26				40	1								
Cassic Tr	$\overline{x}/\mathrm{spec}$ .	14.0	5.0	5.5	5.5	5.3	×	3.0	0.6	32.7				46.7	10.5	*							
is L.	max.		9	9	7	7	7	4	10	47				64	1								
Cassida viridis L.	min.	1	5	4	20	50	5	63	∞	34				51	1								
Cassid	$\overline{x}/\mathrm{spec}$ .	17.0	5.4	5.5	5.3	9.9	5.8	3.0	0.6	39.3				56.3	12.5	*							
° L.	max.	18	6	1-	7	7	oo	4	10	52				70		5	5	2	10	11	4	10	52
Cassida vibex L.	min.	17	5	4	53	30	9	22	0.8	35				52	1	3	60	က	4	5	22	8	28
Cassic	x/spec. min. max.	17.5	6.5	5.8	0.9	6.5	7.1	3.0	0.6	43.3				8.09	13.0	4.0	4.0	5.0	0.7	8.0	3.0	0.6	40.0
inosa	max.		6	1	7	7	œ	4	10	52				69	1	3	5	7	00	13	4	6	51
Cassida rubiginosa Müll.	min.	1	5	70	20	5	9	21	œ	36				53	1	က	က	အ	4	5	23	7	27
Casside	x/spec.	17.0	6.3	5.8	5.9	6.1	1.0	3.0	0.6	43.1				60.1	12.5	4.0	4.0	5.0	0.9	0.6	3.0	8.0	39.0
Species	Number of days of develop- ment Stage	Eggs	Larvae L <sub>1</sub>	Ĺ.	_่า	Ľ,	Ľ,	Prepupae	Pupae	Young imagines	Complete develop-	ment (from the	moment of egg lay-	ing)	Eggs	Larvae L <sub>1</sub>	Ļ	่าำ	Ľ,	Ļ	Prepupae	Pupae	Young imagines

			The period of the observations	19. VI—7. IX, 1971		$egin{array}{ll} { m x} & { m arr} & { m temperature} \ 23.9^{\circ}{ m C}\pm4.0 \ \hline egin{array}{c} { m z} & { m air} & { m humidity} \end{array}$	00·6 <del>+</del> %00·11	
		6	15	1	9	23		32
		5	13		4	19		24
		0.7	14.0	2.0	0.9	21.0		28.0
		6	18	1	7	27		36
		7	17	1	5	24		31
		8.7	17.5	2.0	0.9	25.5		33.3
	65	6	20	1	7	29		38
	41	9	18		10	25		31
	53.0	8.7	19.0	2.0	0.9	27.0		34.8
	39.5 63.5	6	19	1	7	28		37
	39.5	9	17		5	24		30
	51.5	9.7	18.0	2.0	0.9	26.0		33.6
Complete development (from the moment of egg lay-	ing)	Eggs	Larvae L <sub>1</sub> —L <sub>5</sub>	Prepupae	Pupae	Young imagines	Complete develop- ment (from the	moment of egg laying)

Explanations: \*—in 1969 the development of the larvae of C, viridis L. and C, flaveola Thunbe. was not investigated.  $\times$ —with C, flaveola Thunbe. only 4 larval instars were found.

H. subferruginea SCHRNK.; with the Colorado beetle Wegorek (1959) found 8-14 days, Wegorek (1957a) 9-12 days, and Łarczenko (1958) within 8-9 days, moreover, with Ceuthorrhynchus quadridens Panz. Dmoch (1959) noted 11 days, and with Gaurotes virginea (L.) STARZYK (1970) 14-15 days. The report of Ogloblin and Medvedev (1970) that the length of the development of eggs of cassids amounts to 4-6 days seems rather surprising. Laboratory observations on the development of eggs of cassids were carried out under almost constant conditions of temperature and air humidity (Tab. V). It was found that at temperature 17.9°C and air humidity of 88.00 per cent this period amounted to 14—17.5 days, at 20.3°C and 87.00 per cent — to 10.5—13 days, at 23.9°C and 77.00 per cent — to 7.0—7.8 days. The results of the laboratory investigation support the opinion that an increase in the air temperature and a decrease in the humidity stimulate the development of eggs, this dependence having been already found under field conditions. In the laboratory the development was twice as short and the results obtained by other workers were also very similar. According to RAMMNER (1937) the development of eggs of C. murraea L. took 11 days at 20°C, according to STARZYK (1970) with Gaurotes virginea L. only 8—10 days. In the latter case course of the development was probably shortened by lower air humidity (70 per cent). DMOCH (1959) found that the length of egg development of Ceuthorrhynchus quadridens Panz. was on the average 6·1 days at 25°C, this also corresponding with the results of the present author.

The above results indicate that the influence of temperature on the period of egg development is probably more essential than the humidity, this being supported by the results of Moore (1970) and Becker (1940).

### C. Larva

A detailed description of the larvae of cassids was presented in the works of Kleine (1915, 1917), Engel (1932), Rammner (1934), Steinhausen (1950), PALIJ (1959), and OGLOBLIN and MEDVEDEV (1971). However, considering the occurrence of a particular formation in the larvae: a covering from exuviae and excrements, this description should be shortly given once more. The body of larva is dorsally and ventrally flattened, variably elongated. The head usually not visible from above, is ventrally curved. At the body sides 16 featherlike spines are set while the anal segment has a pair of long hairs, the so-called abdominal furca, which serve as base for the formation and carrying of the corvering from excrements. Anus is situated on the ventral side on a protruding pusher. The basis of the covering is formed of successive larval exuviae and from excrements collected on them. Abdominal furca of one moult are stuck in a former smaller one and the furca of the smallest moult freely protrude or are covered by excrements. Excrements are deposited on the moults with an elastic anal segment. The kind and way of depositing excrements are very characteristic with separate species (Steinhausen, 1950).

From the investigated species of cassids only *C. flaveola* Thunbg. does not form any covering from excrements at all, it casts them and also the moults on the surface of leaves, while the other three species form compact massive coverings. Among other this covering from excrements is a characteristic feature of the subfamily *Cassidinae* and makes possible a rapid and precise evaluation of the age of a larva by counting the number of exuviae. The opinions of various authors are quite contradictory with regard to the role of this covering in the life of a larva. Some of them (Engel, 1932, Matis, 1968) claim that because of the free and open way of the life of larvae the covering does not protect them from enemies and parasites; while others (Wradatsch, 1919, Palij, 1959, Kleine, 1917, Ogloblin and Medvedev, 1971) are of the opinion that it plays a protective role against predators, especially small ones. The present author's opinion is that it can partly hide a larva from enemies but does not really protect it.

After 11—33 days larvae emerge from eggs laid on the leaves of foodplants, they punch through egg membranes in the direction of the leaf since they find the least resistance here and can immediately begin feeding. Egg membranes and protective coats are first dissolved with saliva and then perforated (Kleine, 1915). Observations of hatching larvae of the investigated species of cassids showed that they really behave in the way presented by the above-mentioned author.

Figure No 1 presents the phenology of the emergence of larvae of the investigated species within the study area in the period of investigation. The earliest emergence was observed in the third decade of May and they were larvae of C. rubiginosa Müll. and C. flaveola Thunbe., while the other two species appear as late as the beginning of June. Gradually the number of appearing larvae increases and in July their maximum numbers are noted, while all development stages are encountered at the same time at this period. This phenomenon is explained by Kleine (1920) with delayed egg laying by females and with an unequal development of the larvae of cassids, this being fully supported by the investigation of Węgorek (1959) and Łarczenko (1958) on the Colorado beetle. In the investigation in Ojców considerable differences were found in the development of eggs (3—5 days) and larvae (3—7 days) from the same egg batch.

The following length of the period of the occurrence of the larvae of cassids was noted on the investigated meadow: the larvae of *C. rubiginosa* Müll. occur throughout 3—3·5 months, of *C. vibex* L. 2·5—3 months, *C. viridis* L. 1·5—2 months, *C. flaveola* Thunbg. 2—2·5 months. Confirmity is principally observed between the phenology of the emergence of a given species and the length of the occurrence of its larvae (fig. 1). However, certain discrepancy arises in the case of *C. viridis* L., whose larvae, of all species, occur on the meadow for the shortest period, even shorter than that of *C. flaveola* Thunbg., which always comes last from wintering. The reports of other authors (Palij, 1959, Palij and Klepikova, 1957, Steinhausen, 1950) on the emergence and period of the occurrence of the larvae of the investigated species considerably differ from

the results of the present author. According to their opinion the emergence of the larvae of these species (with the exception of *C. flaveola* Thunbg. which was not investigated) occurs 2—4 weeks earlier than in Ojców; this phenomenon may be explained with differences in the climate of the regions of investigations. On the other hand, Steinhausen (1950) reports a period of the appearance of larvae fairly similar to that found in Ojców by the present author, while Palij (1959) and Palij and Klepikova (1957) report the periods of the occurrence of the larvae of these species shorter by 1—2 months than those found in Ojców, but their results seem questionable.

Immediately after hatching larvae begin to feed on foodplants. Two elements of their behaviour are most striking: the feeding chiefly occurs on the under side of leaves and, moreover, the sociability of feeding observed at that time, takes only place up to the end of the second instar. This behaviour of new hatched larvae of cassids is also reported in the works of RAMMNER (1934, 1937), ENGEL (1932), KLEINE (1915, 1917), PALIJ (1959), PALIJ and KLEPIKOVA (1957), and OGLOBLIN and MEDVEDEV (1971); in the larvae of the Colorado beetle by WEGOREK (1959) and SIMM (1948); and with the larvae of chrysomelids in the work of SZUJECKI (1966). Beginning from the third instar larvae pass on other leaves of foodplants and even on neighbouring specimens of plants. At that period they do not only feed on the under side of leaves but also more often on the upper surface. In the fourth and fifth instar the feeding of larvae occurs on both sides of leaves.

The pictures of feeding of consecutive larval instar of C. rubiginosa MÜLL. on the leaves of foodplants are presented in plate XXVII, C, of C. vibex L. in plate XXVIII, C, of C. viridis L. in plate XXIX, A, B, and C. flaveola Thunbg. in plate XXIX, C, D. Larvae of the first instar are hardly active, feed round themselves, eat out small holes (rather near each other) on the surface of the leaf (the so-called scrape feeding) and very rarely make perforations. In the next stages the activity of a larvae increases, the holes are greater and greater and more scattered; the scrape feeding still dominates but perforation is more and more frequent. In the fourth instar the feeding of larvae is very strong, the holes are still greater the perforation feeding dominates over scraping, marginal feeding already occurring in places. In the fifth instar the holes are very great, perforation dominates while the scrape feeding is infrequent and the marginal one fairly often. The damage in smaller leaf nerves is also encountered. The difference between C. viridis L. and C. rubiginosa Müll. as well as C. vibex L. lies in the fact that in the first species no scrape feeding occurs only perforation and strong injury to leaf nerves being noted.

The surface feeding is of the primary character, while the marginal one is secondary since it is begun from the middle; the scrape feeding is also primary (occurs throughout the whole larval period) while the perforation one secondary. The feeding of the larvae of *C. rubiginosa* MÜLL., *C. vibex* L., and *C. viridis* L. on other foodplants (pls. XXVII, C, XXVIII, C, and XXIX, B) is very similar to that on *Cirsium oleraceum* (L.) Scop. and *Mentha longifolia* (L.) Huds. while the

dominance of the perforation over scrape feeding on leaf blades depends on the age and thickness of leaves, this being strongly stressed by KLEINE (1915, 1917). Moreover, he claims that these more or less variable pictures of feeding exclusively depend on the structure of leaves and thus do not origin from the nature of larvae. E.g. delicate leaves of Cirsium rivulare (JACQ.) ALL., Centaurea jacea L., or Stachys silvatica L. are distinctly perforated by the larvae while on the leaves of Carduus acanthoides L., Cirsium lanceolatum (L.) Scop., and on Stachys palustris L., which have somewhat thicker blades, the dominance of scrape feeding is observed.

The larvae of *C. flaveola* Thunber. fed on the leaves of *Stellaria graminea* L. (pl. XXIX, C). Contrary to the species mentioned above the larvae of the first and second instar feed as well on the under as on the upper leaf surface, besides. they show relatively weak sociability. The picture of feeding of this species is quite different. The marginal feeding has a primary character while that on the surface is secondary; moreover, perforation feeding decisively prevails while scraping occurs rarely. The larvae of the first instar feed similarly like those of the other three species, but strong injuries are already observed from the second instar including the injuries of leaf blades. The larvae also make similar picture of feeding on other food plants (pl. XXIX, D), the weakest feeding being found on the leaves of *Cerastium vulgatum* L.

Additional laboratory cultures, carried out in 1972, showed that Sonchus arvensis L. (pl. XXVII, C) was a doubtful foodplant of C. rubiginosa MÜLL. since on its leaves feeding was found in an insignificant degree, while Carduus acanthoides L. and Cirsium lanceolatum (L.) Scop. (pl. XXVIII, C) were real foodplants of C. vibex L. which fed on them in a considerable degree.

In comparing the pictures of feeding of four investigated species it may be observed that the picture left by the larvae on the leaves is characteristic for each species. The differences in these pictures are particularly strong in the fourth and fifth larval instars and are visible in the shape of feeding, its size, density, and spread on the surface of leaf blades. It should be also stressed that the basic structure of feeding, i.e. the type and way of making holes, does not change in any instar, this being distinctly supported by the observations of Kleine (1917).

In this period the larvae of cassids undergo successive moults each of them being connected with a decrease in their activity and a strong reduction in food consumption. After each moult the larva begins intense feeding again its maximum intensity occurring in the fourth and fifth development instar. In the period of investigation it was found that the larvae of *C. rubiginosa* MÜLL., *C. vibex* L., and *C. viridis* L. moulted as much as 5 times throughout their lifetime (fifth moulting ending in the pupation), while the larvae of *C. flaveola* Thunber only 4 times. Therefore 5 larval instars occur in the first three species, and only four in the last one.

This is fully supported by the data of RAMMNER (1932, 1934), STEINHAUSEN (1950), ENGEL (1935), KAUFMANN (1933), MANOLACHE (1938), NIETZKE (1939),

and KLEINE (1920), while the data of PALIJ (1959) and of OGLOBLIN and MEDVE-DEV (1971) reporting the number of 3—4 larval instars of cassids are incorrect.

The course of development of larvae depends above all on the influence of climatic factors, the main role being played by temperature, air humidity, and rains. This is also supported by the results of Kleine (1920) and Rammner (1934) on cassids; of Wegorek (1950, 1959), Miksiewicz (1948), Kaczmarek (1955), and SIMM (1948) on the Colorado beetle; of STARZYK (1970) on Gaurotes virginea (L.), and of DMOCH (1959) on Ceuthorrhynchus quadridens PANZ. The influence of these factors was investigated on the meadow in Ojców in the years 1969-1971 (Tab. IV) and the shortest course of the larval development was found at the mean temperature of 14.5°C and air humidity of 79.40 per cent while at temperature 11.8°C and air humidity of 85.70 per cent it was 1.5—2 times longer. The table clearly shows that the rate of the larval development of cassids depends on temperature and air humidity. The influence of rains, especially if connected with strong decrease in the temperature, is also strongly marked. In 1970 the cool and rainy May and the beginning of June significantly influenced the larval development, which was lengthened by about 10 days as compared with that of the preceding year. In 1971 the still longer development of larvae was recorded under the influence of very low temperatures and strong rains in June and at the beginning of July.

Against this background extremely interesting are the results of investigations of other workers on the development of larvae. Palij and Klepikova (1957) and Ogloblin and Medvedev (1971) report that under field conditions the development of the larvae of cassids takes 12—20 days, this seeming a somewhat lowered value. According to Steinhausen (1950) the development of the larvae of C. flaveola Thunbg. takes 18 days, according to Engel (1932) of C. viridis 27 days, according to Rabaud (1915) of C. rubiginosa Müll. and C. viridis L. 21 days, according to Gorbunov and Šeremet (1968) 30—40 days. Results obtained with other herbivorous insects are also interesting. According to Wegorek (1950) the larvae of the Colorado beetle take 25 days to complete their development, those of Longitarsus suturellus Dft. 28—35 days according to Warcholowski (1958), those of chrysomelids 17—25 days (Szujecki, 1966), and of Ceuthorrhynchus quadridens Panz. 25—40 days (Dmoch, 1959). The presented results are highly consistent with the data of the present author.

In the years 1969—1971 laboratory investigation was carried out on the length of the larval development of the investigated species of cassids (Tab. V). The observations showed that as the temperature increases and the air humidity decreases the rate of the development is faster and faster. At the constant temperature of 17.9°C and humidity of 80.00 per cent it amounted to 21—31 days while at 23.9° and 77.00 per cent it was shortened 1.5—2 times and amounted to 14—19 days. The results obtained by other workers under laboratory conditions are also worth noting. According to RAMMNER (1934) the larvae of C. murraea L. took 21 days to complete their development at room temperature, of C. nebulosa L. — 17 days (KLEINE, 1920), of C. nobilis L. 29 days at 18°C

(Kaufmann, 1933), of Ceuthorrhynchus quadridens Panz. 25 days at 21°C (Dmoch, 1959). The above-given data are very similar to those obtained by the author of the present work.

In comparing the length of the development of the larvae of cassids under field (Tab. IV) and laboratory conditions (Tab. V) it may be said that in both cases the larvae of *C. flaveola* Thunbg. show the shortest period of development, while those of *C. viridis* L. a relatively short period in the laboratory but the longest one in the field. The larvae of the other two species have very similar periods of development both in the field and in the laboratory.

### D. Pupa

Considerable restlessness is observed in the behaviour of larvae which have completed their development; they cast the covering from excrements and show a tendency to migrations, this being also supported by the results of RAMMNER (1934) and Engel (1932) and in chrysomelids by Szujecki (1966). They usually select for pupation other leaves of their host plants, never those on which they have fed. Pupation fairly often occurs on grasses and on various dicotyledones which grow nearby, this having been observed with *C. flaveola* Thunbg. Throughout the period of several-year investigation it was found that in the investigated species the pupation takes place at inflorescences or in the middle of the height of plants, chiefly under a leaf, here the only exception being *C. vibex* L. which often pupates also on the upper leaf surface. The observations of the author are fully supported by the results of the investigations of RAMMNER (1934), Engel (1932), Palij and Klepikova (1957), Ogloblin and Medvedev (1971), and Gorbunov and Šeremet (1968).

The period of the pupa is preceded by the pre-pupal stage. The larvae sit motionless on the under side of leaves, stuck to the substratum with a brown sticky substance excreted from the fifth to seventh segments. Outdoors the length of this stage (Tab. IV) ranges with various species from 2 to 4.5 days and in the laboratory (Tab. V) from 2 to 3 days. According to Engel (1932) under field conditions this stage lasts 36 hours with C. viridis L., while according to Szujecki (1966) its length ranges from 36 hrs. to 4-6 days with various chrysomelids and this observation is consistent with author's own data. Figure presents the time of emergence and occurrence of the pre-pupae of cassids on the study area. The pre-pupae of C. rubiginosa Müll. were the earliest ones found While those of other species appeared in 1-week intervals. The variation in the terms of the appearance of pre-pupae amounted to 1-2 weeks in separate years. The period of the occurrence of pre-pupae was 2.5 month in C. rubiginosa MÜLL., 2—2.5 months with C. vibex L., 1—1.5 months with C. viridis L., and 1-1.5 months with C. flaveola Thunbg. No data were found in the literature on the phenology of the occurrence of this stage of cassids.

The moulting to pupa is very short taking 2-3 minutes, this being also

supported by the observations of Engel (1932). The pre-pupa makes violent movements with its body, alternately bending and constricting it, while the fifth larval skin bursts and is pulled back above the pupa. Hence the pupa is in two ways protected from being hurled down from a leaf since the back of its body is stuck to the leaf surface and besides, its cerci are strongly inserted in the cerci of the fifth larval skin. According to the opinion of WRADATSCH (1919) this protects the pupae from being thrown down by strong rains and winds.

Detailed descriptions of pupae are presented in the works of RAMNER (1932), PALIJ and KLEPIKOVA (1957), KLEINE (1915), and OGLOBLIN and MEDVEDEV (1971) therefore it is unnecessary to repeat them here. The pupae of the investigated species of cassids were found on plants just at inflorescences or in the middle of the height of plants and almost always hanging upside down, this being distinctly mentioned by the workers quoted above. In the period of the investigations the present author was finding single pupae on the leaves of plants. The only exception was *C. rubiginosa* MÜLL. whose pupae were sometimes found in the number of 1—3 specimens on one leaf. The report of Engel (1932) that 1—9 specimens of the pupae of *C. viridis* L. were found on one leaf is strongly questionable.

The phenology of the appearance of the pupae of cassids is presented in figure 1. In relation to pre-pupae the time of their appearance ranges within only a few days, while in separate years strong fluctuations amounting to 10—30 days are observed in the time of the appearance of the proper pupae. The pupae of *C. rubiginosa* Müll. were first observed within the study area while those of the other species only 10—15 days later. The only report on the phenology of the appearance of the pupae of the investigated species (with the exception of *C. flaveola* Thunbg.) was the work of Palij and Klepikova (1957). The terms of the appearance given by these workers agree with the results obtained by the present author, though they do not quote any data on the length of the occurrence of this stage under field conditions.

The term of the appearance and the length of development both of the pre-pupae and of pupae of cassids above all depend on temperature and air humidity. Field investigations (Tab. IV) showed that low temperatures and rains (May and the beginning of June in 1970, June and the beginning of July 1971) distinctly delay the appearance and lengthen the time of development of pre-pupae and pupae. As the temperature rises and the air humidity slightly decreases the time of their development is considerably shortened, in the case of *C. rubiginosa* Müll and *C. vibex* L. even by 2—3 days. In individual years the period of the development of pupae of the investigated species ranged from 7—11 days. The most rapid development was found with the pupae of *C. flaveola* Thungs. while the slowest one with *C. viridis* L. A comparison of the obtained results with the results of other workers is interesting; according to Rabaud (1915) the development of the pupae of *C. viridis* L. takes 8 days, according to Engel (1932) 6 days, according to Rupertsberger (quoted according to Engel 1932) 8—20 days. The result of the last author is most accurate while

that of Engel is distinctly too low. According to Kleine (1917) the development of the pupae of *C. murraea* L. takes 10 days under field conditions, of the pupae of *C. nebulosa* 10 days at the mean temperature of 14·4°C (Kleine 1920), and of other chrysomelids 5—11 days (Szujecki, 1966). The results given above are consistent with the observations of the present author.

The investigations carried out on the length of development of cassid pupae under laboratory conditions (Tab. V) also showed a distinct dependence of the length of development on the temperature and air humidity. Similarly like outdoors, a more rapid development of pupae occurred at a higher temperature and lower air humidity, C. flaveola Thunber. of all species also here taking the shortest time to develop. The length of the development of the pupae ranged from 5—9 days. The results of other authors are quoted here for the sake of comparison: according to Rammer (1934) the development of the pupa of C. murraea L. takes 5—8 days under laboratory conditions, according to Kleine (1920) C. nebulosa L. 9 days, and at a mean temperature of 24·4°C only 5 days; according to Starzyk (1970) Gaurotes virginea L. 10 days at 18—20°C. The above data are highly consistent with the results of the present author.

## E. Young imago

The development of the generations of cassids are decisively influenced by temperature, air humidity, and rains, this being particularly stressed by Kleine (1920) and Palij and Klepikova (1957) as well as by Węgorek (1957a, 1959) in his study on the Colorado beetle. In the years 1969—1971 in the investigations on the meadow in Ojców actual influence of these three factors was found (Tab. IV). The shortest development cycle of cassids was observed at a mean air temperature of 14.5°C and humidity of 79.40 per cent, while the longest one at the mean temperature of 11.8°C and humidity of 85.70 per cent. Longer periods of development found in the last two years were brought about by chilly weather and long rains in spring 1970 and in the spring-summer period of 1971. The differences in the length of a complete development between the two years (1969 and 1970) amounted to 15—18 days. Thus a successful development of cassids depends on a certain level of temperature, which plays an essential role here, but above all on its uniform distribution throughout the vegetation period. The most favourable distribution of temperatures for the development of cassids occurred in 1969 and therefore this average value of temperature was accepted as a probable development optimum of these species. Several-year investigation of Kleine (1920) showed that this optimum really lies within the limits of 14—15°C. According to Ogloblin and Medvedev (1971) the length of development of cassids is 28-35 days, according to Wradatsch (1919) of C. splendidula Suffr. 47 days, according to Kleine (1917) of C. murraea <sup>56</sup> days, according to Gorbunov and Seremet (1968) of H. subferruginea SCHRNK. 64 days, according to WEGOREK (1959) of the Colorado beetle 48 days,

according to Warchalowski (1958) of *Longitarsus suturellus* Dft. 67 days. The above-mentioned data are fairly consistent with the results of the present author.

Under laboratory conditions at various systems of constant temperatures and air humidities (Tab. V) the development of cassids showed dependences similar to those found in the field. The longest period of development was found at the temperature of  $17.9^{\circ}$ C and the humidity of 88.00 per cent, while at the temperature of  $23.9^{\circ}$ C and the humidity of 77.00 per cent it was shortened almost a half. From the investigated species the most rapid development both under laboratory and field conditions was found with C. flaveola Thunber. while with C. viridis L. it was longest in the field and relatively short in the laboratory (as compared with other species). According to RAMMNER (1937) C. murraea L. took 37-38 days to complete its development at  $20^{\circ}$ C, this period being much shorter at the same temperature than in the investigation of the present author (Tab. V), however, it was supposed that high air humidity occurring in the laboratory played a serious role here.

The problem of the number of generations in a year is connected with the length of development of cassids. In separate years under microclimatic conditions of the meadow this development ranges within 1—3 months in the species under investigation (Tab. IV). According to the present author this irregularity and extension of the development are the best argument for the occurrence of one generation with the investigated cassids throughout a year, this being also stressed by Kleine (1915). On the other hand the opinions of other authors are sometimes different: some of them (Kleine, 1915, 1916, 1917, Šeremet and Gorbunov, 1969, Gorbunov and Šeremet, 1968) claim that only one generation of cassids occurs throughout a year, while others think probable the occurrence of two generations with certain species in some years, e.g. C. murraea L. (Rammer, 1934), C. viridis L. and C. nobilis L. (Palij and Klepikova, 1957, Ogloblin and Medvedev, 1971) in southern regions.

The author suggests that under climatic conditions of Poland the development of only one generation in a year is possible. However, in laboratory cultures under conditions of favourable temperature (24—25°C) and air humidity (70—80 per cent) maturation, copulation, and even egg-laying by the females of young beetles of cassids were observed but a further development and the emergence of a second generation of beetles was only found with *C. flaveola* Thunbg. The above considerations clearly indicate that under field conditions climatic factors play a basic role in the development of cassids and decide about the number of generations of these beetles throughout a year.

In the period of investigations the term of the emergence of young imagines within the study area ranged from 2 weeks with  $C.\ vibex\ L.$  to 3 weeks with  $C.\ rubiginosa\ MÜLL.$  while with the other species it occurred at a constant period (fig. 1). The imagines of  $C.\ rubiginosa\ MÜLL.$  emerged on the meadow at the earliest term (the end of June and the beginning of July), then 3 other species appeared at 2-week intervals. The most intense emergence of young

beetles was observed at the end of July and throughout the month of August, afterwards a slow decline was noted in September. The observations of RAMMNER (1937), Kleine (1915, 1916), Šeremet and Gorbunov (1969), and Palij and Klepikowa (1957) on eassids, of Wegorek (1959) on the Colorado beetle, and of Warchałowski (1958) on Longitarsus suturellus Dft. showed that in general the time of the emergence and intense occurrence of these beetles agree with the results of the present author.

The course of the hatching of young imagines from pupae is presented in detail in the work of Engel (1932). Under field conditions the hatching (from a pupa stuck to a leaf) takes about 5 minutes while in the laboratory (a pupa freely lying on a dish) 5 to 10 minutes. The newly hatched specimens of the investigated species are characterized with different colouring, which is worth discussing here. The imagines of C. rubiginosa Müll. are whitish yellow on the upper side and pink on the under side, C. vibex L. are yellow-willow green on both sides, C. viridis L. willow green on both sides, and C. flaveola Thunba. light creamy on the upper and under side. The common features of all these specimens are: dark eyes and bases of antennae, light brown colouring of mandibles, dark ashy or blackish bases of femures (in the case of C. vibex L. even whole femures are dark). As they grow older a change in the colouring of the cuticula occurs, this being stressed by Rammner (1934), Engel (1932), Wradatsch (1919), and Kleine (1917). In the first six hours of their life young beetles quietly sit on the under side of leaves and their cuticula slowly grows darker. First traces of feeding may be observed after 6-9 hours and intense feeding as late as after a few days. Warchalowski (1958) observed newly hatches, imagines of Longitarsus suturellus Dft. feeding after a few to several hours thus in the period almost identical with that observed by the present author.

After the first 24 hours of life of imagines of the investigated species following colours of cuticula were found on prothorax and elytrae: with *C. rubiginosa* Müll. greenish yellow, with *C. vibex* L. light green with a dark triangle on elytrae, with *C. viridis* L. light green, and with *C. flaveola* Thunbg. light brown. With the first two species the under side was black and with the two others also black, the side margins of abdomen showing a narrow yellow streak on the under side. The colour of the cuticula of prothorax and elytrae of beetles did not change in the next days of their life, with the exception of *C. rubiginosa* Müll. with which it turned from light green to green. The elytrae which were very soft and delicate after hatching, hardened in 5—7 days, this being consistent with the data of Rammer (1934) and Engel (1932).

Field observations in Ojców showed that full colouring of beetles, in certain species connected with a metallic lustre of elytrae, is observed as late as after wintering, in spring in the mating period. Hence it may be concluded that this process must take a certain period of time and, moreover, that the lack of full colour of the cuticula of prothorax and elytrae indicates sexual immaturity of imagines. Throughout several-year investigations it was found that the full colouring of cassids is never observed in the year of their hatching, this being

<sup>4 —</sup> Acta Zoologica Cracoviensia XX/9

also confirmed in the works of WRADATSCH (1919) and KLEINE (1920). The opinion of RAMMNER (1934) that depending on climatic conditions a complete change in the colour of *C. murraea* L. occurs in 4—12 weeks seems questionable, as he admits the possibility of the completeness of this process under field conditions in the year of hatching of beetles, this being distinctly inconsistent with the results of the present author.

Complete colouring of the cuticula depends on intense feeding of young imagines. The observations of the author as well as the report of Kleine (1917) indicate that starvation of specimens inhibits the process of changing colour. Hence it may be suggested that it depends on certain components occurring in the leaves of foodplants. The components which bring about changes in the colour of young imagines are carotenoids accumulating in the fat body and hemolymph of insects. This fact distinctly indicates the nutritive origin of carotenoids with cassids, as is also supported by the results of CZECZUGA (1971) in his investigation on the Colorado beetle. The feeding favours the formation of carotene in the body of beetles and thus ensures the possibility of a change in the colour as the time passes. A detailed description of a complete colouring of C. murraea L. is given by Kleine (1917). The process is very slow and has a following course: mellow green colour of cuticula of prothorax and elytrae passes into mucky green because a reddish pigment appears besides the green one, their arrangement originating the mucky green colour. Gradually the amount of the red pigment increases and that of green one decreases, the bettles getting brick red at last.

Under laboratory conditions at temperature 20—25°C and the air humidity of 70—80 per cent the complete colouring of beetles occurred in the period of 30—60 days of their life and even the metallic lustre on their elytrae was observed (*C. flaveola* Thunbg.) though it was normally found in the mating period. The final colours of cassids are: dark green with *C. rubiginosa* Müll., golden-hued with a dark brown triangle with *C. vibex* L., brownish green with *C. viridis* L., and light brown with *C. flaveola* Thunbg.

Already in the first days of their life young imagines of cassids feed fairly intensely. The intensity of feeding increases in the next days and attains its maximum in the period of the first 2—3 weeks of life, distinctly decreasing afterwards. Usually the beetles feed in early forenoon hours, and then in the afternoon up to the sunset. The pictures of feeding of young imagines of C. rubiginosa Müll. and C. ribex L. are presented in plate XXX, of C. viridis L. and C. flaveola Thunbg. in plate XXXI. The range of host plants of the two first species (pl. XXX, A, B, and C, D) is almost identical with the exception of Centaurea jacea L. which is only damaged by C. vibex L.

The essential features of feeding of these beetles are: surface feeding as primary and marginal feeding as secondary, always performed from the middle; moreover, scrape feeding as primary and perforation feeding as secondary. Scraping of leaf tissue always prevails over perforation with *C. rubiginosa* MÜLL and with *C. vibex* L. vice versa. No sooner than in a later period of life (about the second month) the perforation of leaf blade decisively occurs in both species.

The shape of feeding marks is basically similar with both species but the pictures of feeding differ, greater regularity in the distribution of places of feeding on the leaf blade being observed with  $C.\ vibex$  L. than with  $C.\ vibiginosa$  MÜLL. and, moreover, in the latter very intense and wide feeding is observed on certain parts of the leaf. The weakest feeding was found on the leaves of  $C.\ vibex$  L., on Carduus acanthoides L. Additional laboratory cultures carried out on the leaves of these plants showed that both species of cassids successfully completed their development cycle on them.

The picture of feeding of young imagines of *C. viridis* L.(pl. XXXI, A,B) is also characterized by the occurrence of surface feeding as primary and marginal one as secondary. As opposed to the two above-mentioned species perforation feeding is always found here, often connected with injuries to leaf nerves. The perforations are often very irregular. The picture of feeding of *C. flaveola* Thunbg. (pl. XXXI, C, D) is quite different: marginal feeding occurs as primary here, while surface feeding has a secondary character; moreover, perforation feeding decisively prevails over scraping and is also a primary feature. The places of feeding considerably differ in size and their shape is very irregular. The weakest feeding was observed on the leaves of *Cerastium vulgatum* L., however, laboratory cultures showed that *C. flaveola* Thunbg. successfully completed its development on them.

In comparing the pictures of feeding of these four species it may be said that they are distinctly specific and that their structure is very characteristic for a given species. It is also interesting to compare the picture of feeding of adult larvae (pl. XXVII—XXIX) with those of imagines (pl. XXX—XXXI) of the investigated species. Strong similarity is distinctly visible in the structure, shape, and distribution of places of feeding on the leaf surface, especially with *C. viridis* L., *C. rubiginosa* MÜLL., and *C. flaveola* Thunbg., being less distinct with *C. vibex* L. With regard to the feeding of young imagines RAMMNER (1937) claims that newly hatched specimens of *C. murraea* L. perform only the perforation feeding all the time from the beginning, this being consistent with the results of the present author, but only in the case of feeding of the imagines of *C. viridis* L.

The behaviour of young imagines of cassids in the field is also worth noting. In the investigation on the meadow it was found that young beetles are hardly mobile sitting on the same place for hours (near the place of hatching), most often just at the inflorescence or in the middle of the height of a plant and usually on the upper side of leaves. This way of behaving of young beetles of cassids as well as their intense feeding in the first weeks of their life were also stressed in the works of Kleine (1916, 1919), Rammner (1934), Engel (1932), and Palij and Klepikova (1957), and with the Colorado beetle it was found by Wegorek (1959) and Miksiewicz (1948).

With very numerous insects and among them also with cassids which do not reach the state of sexual maturity in the year of hatching, the phenomenon of diapause is very common. This problem was mentioned by the workers who

studied the cassids (Palij and Klepikova, 1957, Kleine, 1917, and Engel, 1932) and was discussed at large in the investigations on the Colorado beetle (Wegorek, 1957a, 1959, Łarczenko, 1957, and Kowalska, 1960), and on the insects in general (Ruszkowska and Opyrchalowa, 1969, Opyrchalowa, 1972). According to Kowalska (1960) the characteristic features of this physiological period are: general decrease in metabolism, a decrease in the content of free water in the organisms, in the intensity of respiration, in the activity of enzymens, an increase in the osmotic pressure, and great content of reserve (fat) substances.

As well the process of the origination of diapause as its course are very complicated phenomena and depend on the influence of various factors. According to the opinion of Wegorek (1959), Larczenko (1957), Kowalska (1960), Ruszkowska and Opyrchałowa (1969), and Opyrchałowa (1972) a complex of ecological factors such as the length of day, food, temperature, and humidity, prevailing at the end of summer and in autumn induces the mass diapause with the Colorado beetle and with other insects. Among these factors, according to Kowalska (1960), a decisive role is played by light in the generation of diapause, while according to Larczenko (1957) by the quality of food. On the base of the results of several-year studies the author of the present work suggests that the diapause of cassids originates under the influence of day length and quality of food, while the term of its occurrence, closely connected with the migration of beetles for wintering, depends on temperature, humidity, and day length.

The day length connected with the date of hatching of imagines exerts a decisive influence on their activity, period of feeding, and staying within the study area. The earlier is the term of hatching of imagines and the longer is the photoperiod, the longer is the activity of beetles in the field. The observations of Wegorek (1959) indicate that young beetles of the Colorado beetle hatched at a short day prepare for wintering already after 7—8 days, while those hatched at a long day preserve their activity for a long period, migrating as late as after 45 days.

The method of marking and recapturing applied in the years 1967—1968 (Kosior, Klein, 1970) showed that young imagines which emerged earlier (at the long day) fed and stayed on the meadow for about 2 months, while those hatched later (at the short day) for only about 2 weeks. The period from the beginning of June to the middle of July was accepted as the long day (up to 17 hrs.), while that from the middle of August as the short day (below 15 hrs.). Kowalska (1960) used an identical classification in the investigations on the Colorado beetle. The above consideration suggests that the short day activates the generation of diapause, moreover, a change in the taxis (from the negative to positive geotaxis) and biochemical processes specific for the diapause occur under its influence. Kowalska (1960) reports that a positive correlation exists between the production of eggs and the size of corpera allata. In the period of diapause their size is smallest and in the period of the formation of eggs—the largest. On this basis one may suppose that the hormone of corpora allata

is the direct reason of a depression in the production of eggs (DE VILDE, 1954). This is supported by the investigations of Ruszkowska and Opvrchałowa (1969) who found that certain cells of the gland corpora allata may excrete hormones inducing the diapause with insects.

Another factor which inhibits the process of the production of eggs and contributes to the occurrence of diapause is the quality of food (biochemical composition of the leaves of host plants). Since no biochemical analyses were carried out on the content of fats and albuminous nitrogen in the leaves of host plants of cassids and in the bedies of new hatched beetles, of those migrating for hibernation, and of hibernating ones, the reasons of the occurrence of diapause under the influence of the changes in food quality were studied on the basis of investigations of Wegorek (1957, 1959), Łarczenko (1957), and Kowalska (1960) on the Colorado beetle and of Opyrchaeowa (1972) on the insects in general. In the active period of development as well as in the period of diapause the physiological state of cassids depends on the biochemical composition of food which changes throughout the vegetation season. The index of these changes is the lipoidal coefficient L/N determining the quantitative relation of fatty bodies to albuminous ones. In the spring period the beetles feed on young leaves of a low lipoidal coefficient which favourably influences the maturation of females and the egg laying. As the leaves grow older the value of the coefficient increases and since the beetles consume food of greater content of lipoids, fats are accumulated in their fat body and the changes occur in the course of metabolism. The synthesis of fats in an organism is accompanied by the passing of free water into metabolic one, this being highly important for an insect as the percentage share of free water is decisive for the process of egg maturation. In the newly hatched imagines of cassids the amout of free water is over 80 per cent of the body weight (Kosior, Klein, 1970). In the course of development the beetles intensively feed, the content of reserve substances increasing and that of the water decreasing in their bodies. In connection with the accumulation of reserve substances the body weight of betles increases. In the period of the accumulation of reserve substances, with the water content of up to 60 per cent, the maturation of cassids occurs and the laying of eggs is observed. With the decrease in the free water content to 55 per cent, the maturation of eggs is inhibited, the activity and feeding are weakened and the beetles gradually fall in diapause. The above facts support the opinion of Wegorek (1959) who claims that the factors which induce the beetles to stop feeding and to leave the plants have their origin in the organisms of insects and are of physiological character.

As it was already mentioned the term of the occurrence of diapause is influenced by temperature, humidity, and length of the day. Before falling in this state young beetles migrate from the meadow into the forest to seek suitable places for wintering. The most important role is played by the day length which decides that the specimens hatched as last migrate first, while those hatched earlier do it much later. The periods of the migration of beetles to winter

quarters slightly differs in individual years, however, they usually begin at the end of August, intensively occur in September, and end at the beginning of October. Several-year observations also showed that young imagines of C. rubiginosa Müll. stay on the meadow for  $2\cdot 5$ —3 months, of C. vibex L. 2— $2\cdot 5$  months, of C. viridis L.  $1\cdot 5$ —2 months, and C. flaveola Thungs. 1— $2\cdot 5$  months. This list showes almost ideal regularity according to which the later young beetles emerge, the shorter they stay on the meadow.

At the end of the vegetation period the meadow on the bottom of the Saspowska Valley is under much worse climatic conditions than the forest on the slope of south exposition. It does not receive any more energy from direct solar radiation, since it is in the zone of shade of the Chełmowa Góra Mt. In the second half of August and in September the inversion of temperatures and the radiation frosts connected with it very often occur here, while in the higher situated and well insolated lime-hornbeam forest the more favourable conditions of higher temperatures and lower humidity prevail (Klein, unpublished). The frosts of early autumn bring about considerable worsening of bioclimatic conditions on the meadow. As it was found in several-year investigation in September the minimal air temperatures almost never exceeded the threshold of  $+13.0^{\circ}$ C. Probably these low temperatures influence the migration of cassids for wintering into the forest region.

In the investigation carried out in 1967—1968 it was found that the hibernation grounds of young imagines of cassids lay in a lime-hornbeam forest on a slope of south exposition in the Sąspowska Valley, where favourable conditions for the wintering of these beetles prevail. The cassids hibernate in the forest litter at the depth of 5—8 cm in the imago stage and in the state of diapause (Kosior, Klein, 1970). This fact is fully supported by the results of Palij and Klepikova (1957), Kleine (1917), Šeremet and Gorbunov (1969), Gorbunov and Šere-

MET (1968), and by ENGEL (1932).

According to Kowalska (1969) wintering beetles being in the state of proper diapause are characterized with great resistance to unfavourable conditions, i.e. low temperature, high humidity, and fungal infection. She also claims that the most stable diapause is shown by the specimens which are the earliest to begin it and those which have the least content of free water and the greatest one of lipoids, the highest lipoidal coefficient and the greatest resistance to thermic reactivation. In the bodies of hibernating cassids slow metabolic processes (chiefly the combustion of fats) occur resulting in the production of water. Its amount gradually increases throughout wintering and in spring reaches the value of 60—70 per cent, the spring reactivation of beetles and then their maturation taking place then.

#### V. ECOLOGY OF POPULATION

# 1. Dynamics of population numbers

In the years 1966—1971 observations and reviews of host plants were carried out within the study area on the meadow at the intervals of 7—30 days, making possible the investigation of the seasonal dynamics in the numbers of development stages of four species of cassids. The results of these investigations are presented in figures 5—10. The old imagines of *C. rubiginosa* Müll. alwaye appear first on the meadow. Their emergence as well as that of other species shows certain fluctuations in the successive years. The earliest appearance of beetles was found on 7th April, 1967, the latest on 25th April, 1969. The corresponding maximum numbers are recorded at the end of April or in the first half of May. In the consecutive years in the month of May a strong decrease in the numbers of beetles of this species regularly occurs, their number slowly decreasing in June and July, and at the end of the season only single specimens were found on the area.

The first specimens of C. vibex L. flew on the meadow 6—12 days later than those of C. rubiginosa Müll. The earliest emergence was noted on 13th April, 1967, the latest on 6th May, 1969, the maximum numbers basically occurred at the end of May or at the beginning of June, then a slow decrease in the numbers was observed, so that in the final period of investigation only single specimens of C. vibex L. were encountered. Since scarce numbers of C. viridis L. and C. flaveola Thunber. were found on the meadow, the dynamics of the number of these species was only presented to such a degree as was possible. The appearance of the first specimens of C. viridis L. decisively occurred in the first decade of May, thus in relation to C. vibex L. it was delayed by 0 (1969) to 14 (1971) days, the maximum numbers being observed in the first decade of May (1968) and in the second half of June (1970). In summer the number of adult beetles gradually decreases and at the end of September only single specimens are encountered. The date of the emergence of beetles of C. flaveola Thunba. considerably ranged in the period of investigations. The earliest appearance was noted on 9th May, 1967, the latest on 7th June, 1966; the maximum number was observed in the second half of the months of May and June, then a slow decline followed and at the end of the investigation season old beetles were only sporadically encountered.

In the period of investigation it was found that the term of the appearance of old imagines of the investigated species, the course and intensification of the return from winter-quarters, and the fluctuations in the numbers of these beetles depend above all on climatic conditions: temperature, rains, and wind. It is supported by the investigations of KLEINE (1916—1917) on cassids, of Miksiewicz (1948) and Wilusz (1958) on the Colorado beetle, and of Starzyk (1970, 1971) on Gaurotes virginea L. Strong rains connected with a great decline of temperature and with winds inhibited the return of beetles which hid again

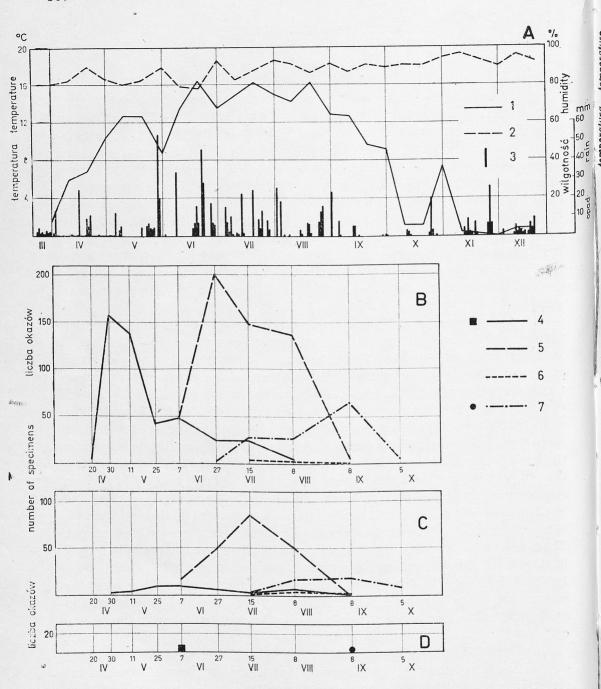


Fig. 5. Influence of climatic factors (A) on the fluctuations of quantity of Cassids (B, C, D) in the study area on the meadow in the Saspowska Valley in the vegetation season of the year 1966. B — Cassida rubiginosa Müll., C — C. vibex L., D — C. flaveola Thunbe., 1 — temperature, 2 — humidity, 3 — rains, 4 — old imagines, 5 — larvae, 6 — pupae, 7 — young imagines

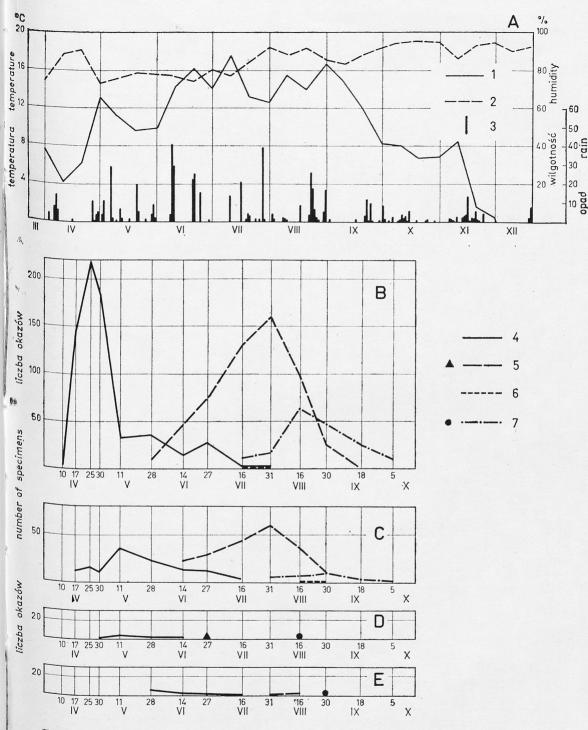
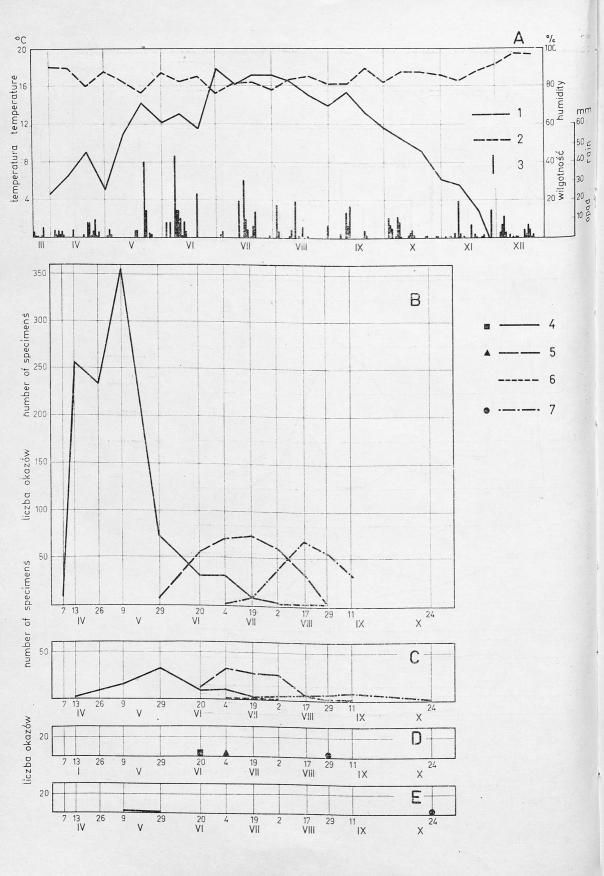


Fig. 6. Influence of climatic factors (A) on the fluctuations of quantity of Cassids (B, C, D, E) in the study area on the meadow in the Sąspowska Valley in the vegetation season of the year 1967. B—Cassida rubiginosa Müll., C—C. vibex L., D—C. viridis L., E—C. flaveola Thunber, 1—temperature, 2—humidity, 3—rains, 4—old imagines, 5—larvae, 6—pupae, 7—young imagines



in the litter or into the meadow turf, influenced their activity, and hence their number in separate periods of investigation, and also the period of their stay on the meadow. In comparing seasonal fluctuations in the number of old beetles in consecutive years considerable differences in the maximum values of recorded specimens are striking, the investigation season of 1970 being most remarkable.

The problem of the emergence of the larvae of cassids within the study area throughout successive years appears very interesting. In general, the larvae of C. rubiginosa Müll. hatch first, the earliest term being 27th May, 1971, the latest 10th June, 1970. The periods of maximum numbers also range from 26th June in 1970 to 2nd August in 1971. Then in August a great decrease in the numbers of larvae generally occurs and in September only single specimens of larvae may be encountered strongly stunted in the development. The larvae of C. vibex L. were found several to more than twenty days later than those of C. rubiginosa Müll., but in the years 1966 and 1970 their simultaneous emergence was noted. In 1970 the greatest number of the larvae of C. vibex L. was recorded as early as 26 June but in 1971 as late as 2nd August. A decrease in the number of larvae occurs throughout the month of August usually at a rapid rate, so that in September few specimens were only encountered.

In 1969—1971 the terms of hatching and emergence of the larvae of C. viridis L. are identical with those of C. vibex L. in spite of the fact that the former appear on the meadow a little later. The greatest numbers occur in the second half of June, in July a strong decrease and at the end of August a complete disappearance of the larvae of this species are observed. The appearance of the larvae of C. flaveola Thunbg. on the meadow takes place more than two weeks later than that of the larvae of C. viridis L., though in 1971 it was noted at the same time. The maximum number was recorded on 15th July in 1971 and as late as 4th August in 1970. In August a slight decrease in the numbers was found and the last larvae were observed in the first days of September. The dynamics of the number of the larvae of cassids show a marked dependence on climatic conditions. High temperature brings about a simultaneous emergence of larvae of various species from eggs laid at different terms, as was dinstinctly showed in the years 1970-1971. Great rains, low temperatures, and winds significantly influence the decreases in the numbers of larvae in the periods of their maximum development, which were observed in all years of the investigation.

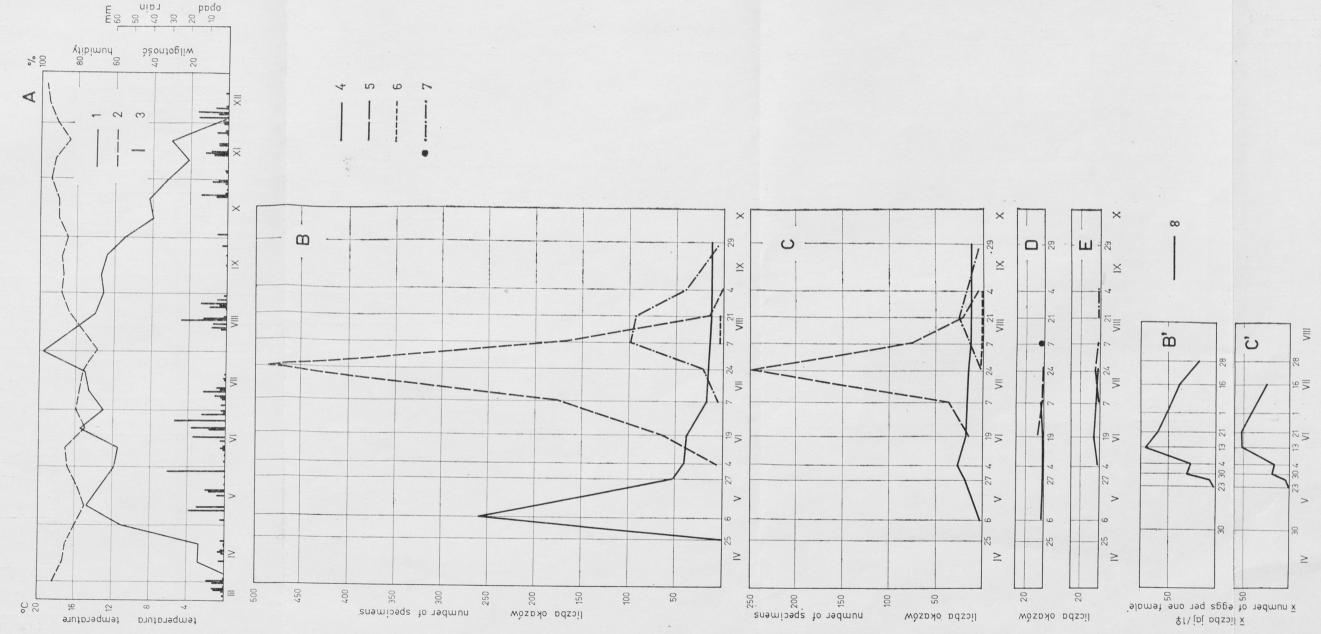
The earliest emergence of young imagines of *C. rubiginosa* Müll. was noted on 27th April, 1966 and the latest on 16th August, 1968, the greatest numbers being observed in August (usually in the second half of this month) and in the first days of September. In September a decrease in the numbers occurs more or

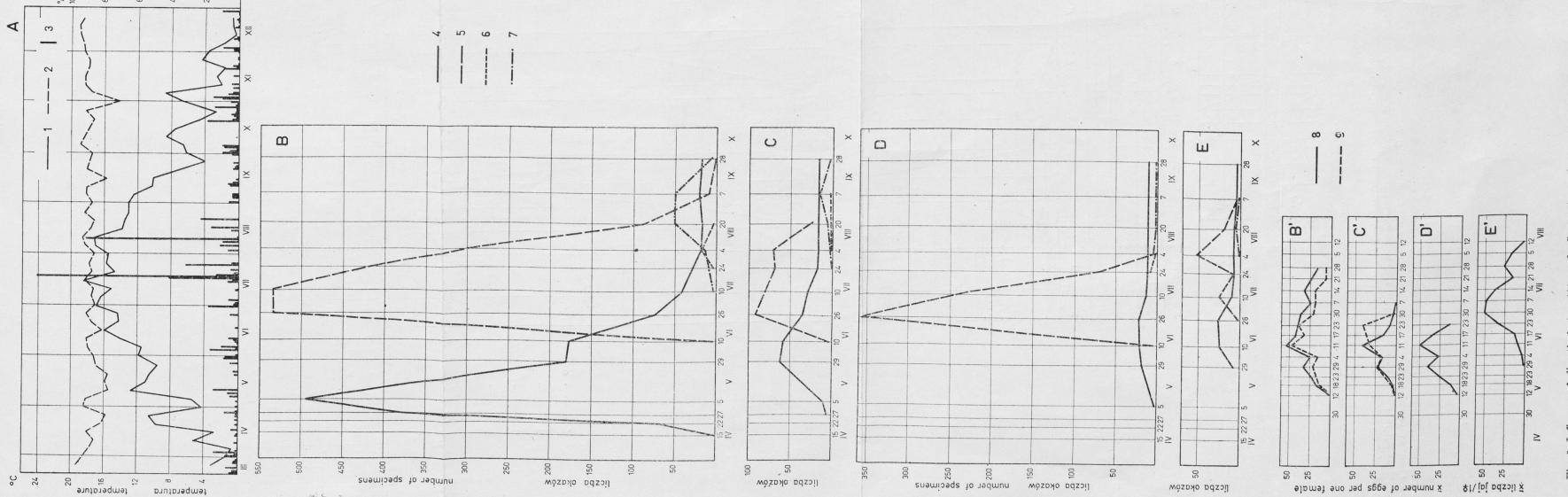
Fig. 7. Influence of climatic factors (A) on the fluctuations of quantity of Cassids (B, C, D, E) in the study area on the meadow in the Saspowska Valley in the vegetation season of the year 1968. B—Cassida rubiginosa Müll., C—C. vibex L., D—C. viridis L., E—C. flaveola Thunber, 1—temperature, 2—humidity, 3—rains, 4—old imagines, 5—larvae, 6—pupae, 7—young imagines

less rapidly, already in the first half of October only single specimens being encountered. Usually in the second half of July the first specimens of young imagines of C. vibex L. appear, reaching their greatest numbers in the second half of August or in the first half of September, then a slow decrease in their number occurs in September, only few specimens being found about the middle of October. Young imagines of C. viridis L. and C. flaveola Thunba. appear in the first half of August but since very small numbers of them are found within the study area, it was very difficult to examine the dynamics of their numbers. Probably the maxima of their number occur in the second half of August, in September a slow decrease is observed in the number of specimens, and at the beginning of October they are no more noted in the valley. Climatic conditions distinctly influence the term of hatching and of maximum number of young beetles of cassids, and, moreover, decide about the beginning and course of migration of imagines for wintering in forest regions.

In comparing the results of investigations in the consecutive years considerable differences appear in the maximum numbers of development stages of cassids, particularly in the investigation seasons 1969 (fig. 8) and 1970 (fig. 9). Great number of larvae and of young beetles of the investigated species was brought about by the unusually good climatic conditions (hot summer without rains) in 1969, this consequently influencing favourable development of the population of cassids in 1970. This year was characterized by greatest numbers of old beetles, larvae, and young beetles (with the exception of *C. vibex* L.) in spite of unfavourable weather conditions (strong rains and low temperatures). In 1971 (fig. 10) in consequence of continuous rains and very low temperatures in the second half of May and especially in June significantly lower values as compared with the preceding years were noted in the numbers of development stages of cassids.

Seasonal fluctuations in the numbers of cassids are closely connected with the size of the population of these beetles. In the years 1969-1971 in order to determine and closely investigate these dependences a complete catch of old imagines of the investigated species was carried out within the study area in the period of 3-5 days of their maximum appearance. Since the imagines of cassids use to return and since the death rate of specimens is high in spring, the Lincoln's index (1930) was not applied in these studies, while the method of a complete catch carried out in a very short period of time (3-5 days) enabled considerable elimination of these two factors. The obtained data enabled the evaluation of the size of imago population of the investigated species using ZIPPIN's method (1956) of the greatest probability. To the calculated values the number of other specimens caught throughout the whole season was added and in this way the most probable number of the population was obtained (Tab. VI). The table clearly indicates that the highest values of the population numbers of beetles occur in 1970, this being influenced by favourable climatic conditions in summer 1969, while in consequence of unfavourable development conditions in summer 1970 the values of population numbers were much lower





130 min 120 min 130 mi

wilgotność humidity

18 July 18

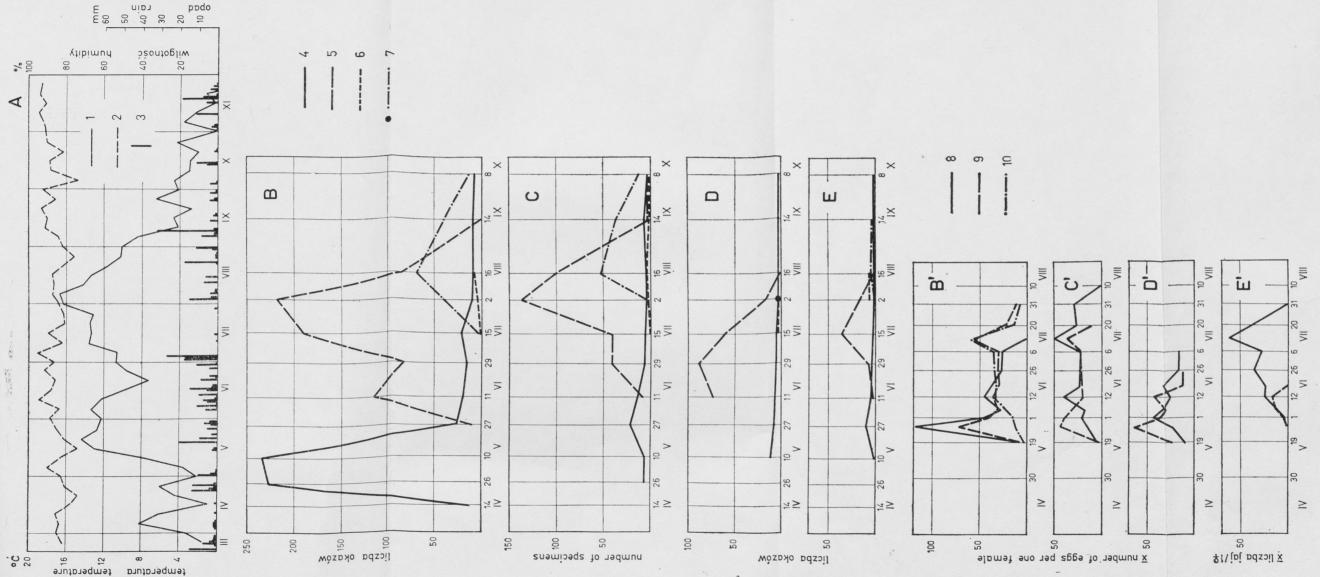


Fig. 10. Influence of climatic factors (A) on the fluctuations of quantity (B, C, D, E) and of fecundity (B', C', D', E') of Cassids in the study area on the meadow in the Saspowska Valley in the vegetation season of the year 1971. B. B' — Cassida rubiginosa Müll., C, C' — C. vibex L., D, D' — C. viridis L., E, E' — C. flaveola Thunbs, 1 — temperature, 2 — humidity, 3 — rains, 4 — old imagines, 5 — larvae, 6 — pupae, 7 — young imagines, 8 — one-year old female, 9 — two-year old female, 10 — three year old female

A. Kosior Acta Zoologica Cracoviensia X

Table VI Evaluation of the numbers of adult imagines\* of Cassidinae within the study area in the Sąspowska Valley in the Ojców National Park

Year of investiga- tions	Species	Maximal number of specimens found in the total catch	Other specimens collected throughout the vegetation season	Evaluation of numbers acc. to ZIPPIN's method	Actual number of the population (4)+(5)
1969	Cassida rubiginosa				
	MÜLL.	615	85	715.1	800.1
	Cassida vibex L.	15	38	15.9	53.9
	Cassida viridis L.		7	_	
	Cassida flaveola				
	THUNBG.		9	_	_
1970	Cassida rubiginosa		-		
	MÜLL.	3086	290	5698-1	5988-1
	Cassida vibex L.	79	112	121.5	233.5
	Cassida viridis L.	32	42	35.9	77.9
	Cassida flaveola				
	THUNBG.	24	17	25.5	42.5
1971	Cassida rubiginosa	,			
	MÜLL.	1001	285	1251.2	1536.2
	Cassida vibex L.	35	38	36.8	74.8
	Cassida viridis L.	34	15	50.0	65.0
	$Cassida\ flaveola$				
	THUNBG.	11	9	13.2	22.2

Explanations: \*—specimens which returned to the meadow from wintering in the forest.

\*\* — ZIPPIN's method of greatest probability (1956) enables relatively precise evaluation of the numbers of the population of investigated species of cassids on the basis of data obtained by complete catch of beetles and with the use of regression equations.

in 1971 than in the preceding year. Moreover, the above-mentioned table show that *C. rubiginosa* MÜLL. is the dominating and most numerous species within the study area, *C. vibex* L. and *C. viridis* L. being fairly numerous. *C. flaveola* Thunbe. was found a rarely occurring species.

## 2. Fecundity

The existence, development, and the numbers of cassids closely depend on their fecundity. In young imagines of cassids the features of maturity and fecundity appear as late as after wintering, in spring of the next year. Their

Table VII

Fecundity of females of various age classes of Cassidinae within the study area on the meadow in the Saspowska Valley of the Ojców National Park

in the vegetation season 1969

1	•					1	
	min. — max.		1970	179		1971	
laveola BG.	88 88 8		season	242		season	229
Cassida flaveola Thunbg.	egg batches		in the vegetation season 1970	151		in the vegetation season 1971	147
	eggs in a batch	*	the veg	1.6		the veg	1.7
	min. — max.		in	98		in	
ridis L	98 88 8			201			206
Cassida viridis L.	egg batches			20.5			24
) )	eggs in a batch	*		9.8			8.6
	min. — max.	112 273			57		191
bex L.	egges S	204		117	147		277
Cassida vibex L.	eggs in egg a batch batches	146		89.7	6.76		212
Cc	eggs in a batch	1.4 (13)		1.3.	1.5		1.3
z .	min.    max.	187			82 340		
biginose L.	98 88 88	285		288	199		344
Cassida rubiginosa Müll.	egg	32		34.7	29.3		37
Ca	eggs in egg a batches	8.9 (15)		8.3 (10)	6.8		9.3
Species	x number // female // Age of specimens	l-year old fe- male		l-year old fe- male	2-year old fe- male		1-year old fe- male

27	
88	
27	
1.4	
73	
175	
14.3	
12.2	
254	126
135	79
(1)	1.6**
192 — 447	208
331	262
43	34
7.7	7.7 (2)
2-year old fe- male	3-year old fe- male

Explanations: (15) — figure in bracket denotes the number of observed females.

\*—in 1969 fecundity of females of C. viridis L. and C. flaveola Thunbe. was not investigated.

\*\* — fecundity of a three-year old female of C. vibex L. was observed additionally in the vegetation season 1972.

appearance depends on several factors: temperature, length of the day, rains, and quality of food. Favourable distribution of temperatures significantly influences the activity of beetles which strongly feed on young leaves of host plants with a low L/N coefficient. The increasing length of day hastens the maturation of cassids which begin to mate and lay eggs. Considerable decreases in temperatures connected with strong rains may inhibit this process or even stop it completely.

Investigations carried out in permanent observation points on the meadow, on the fecundity of females of cassids in different age classes in 1969—1971 showed that with the investigated species the egg-laying is carried out in the period from the beginning of May to the beginning of August, thus at a long day of the length of more than 15 hours (Tab. II). In spite of distinct differences in the phenology of the emergence of separate species the term of the beginning of egg-laying by the females of *C. rubiginosa* Müll., *C. vibex* L., and *C. viridis* L. is identical, and only with *C. flaveola* Thunbg. it is a little later. The periods of egg-laying and the curves of the fecundity of females of cassids in different age classes are presented in figures 8—10.

In the years of investigation the beginning of egg-laying was recorded at different periods: in 1970 as early as on 12th May, while in 1969 as late as 23rd May, this resulting from unfavourable climatic conditions (fairly strong rains and low temperatures). Maximum fecundity of females of cassids occurs chiefly in June and in the first half of July while the maximum numbers of eggs are almost always greater with 1-year old females than with 2- and 3-year old ones. Strong depressions in the course of the fecundity curves and the occurrence of several maxima in the number of eggs are brought about by considerable decreases in temperatures and by continuous rains, this being distinctly showed in figure 10. The terms of the end of fecundity in 1-year old females and in older ones are the same (fig. 9) or show certain delay in the former (fig. 10) with the exception of C. rubiginosa Müll. The length of the day is decisive here since with the short day (below 15 hrs.) maturation of femiles and egg-laying do not occur any more. The fact of the maximum fecundity with the females of cassids observed in June and in the first half of July is supported by the investigation of Kowalska (1969) and Wegorek (1959) on the Colorado beetle and of Opyr-CHAŁOWA (1970) on other insects. They found distinct positive correlation between an increase in the length of the day and the rate of the maturation of females and an increase in the number of deposited eggs.

Observations conducted on the fecundity of females of cassids in various age classes enabled to compute the mean number of eggs laid by one female (Tab. VII). It was found that in all years of investigation the greatest number of eggs was laid by 1-year old females: C. rubiginosa Müll laid 285—344 eggs, while with the other species these numbers ranged from 200—280 eggs. The too low mean number of eggs (117) laid by 1-year old female of C. vibex L. seems somewhat doubtful as compared with 2-year old female (147 eggs). It may be supposed that the main reason of such low fecundity was the unfavourable

Feeundity of 1-year old females of Cassidinae under laboratory conditions in 1971

Substitution of the substi												
Species	Cassida r	Cassida rubiginosa Müll.	Müll.	Cassi	Cassida vibex L.	از.	Casside	Cassida viridis L.	L.	Cassida f	Cassida flaveola Thunbg.	UNBG.
$\overline{x}$ number/1 female Age of specimens	eggs in a batch	egg	eggs	eggs in egg a batch batches	egg batches	eggs	eggs in egg a batch batches	egg batches	eggs s	eggs in egg	egg batches	eggs s
1-year old female	6.0	40.6	243.6	1.3	171.3 222.7	222.7	8.1	38.3	229.5	1.3	154.0	200.2

Explanations: (5) — figure in bracket denotes the number of observed females.

influence of climatic conditions (rains, low temperatures). Statistical analysis was carried out using Student's T test for different size of samples (Gullford, 1964) in order to check the significance of differences in the fecundity of 1-year and 2-year old females of C. vibex L. in the vegatation season of 1970. It was found that at the significance level of P < 0.05 insignificant differences occur in the fecundity of females of different age classes. Moreover, it was observed that the fecundity of females distinctly decreases in the second and third year of their life (Tab. VII), this being mostly marked with the 2-year old female of C. vibex L. (a more than 5-fold decrease) and in the 3-year old female of C. vibex L. (a more than 2-fold decrease).

The available literature contains scarce data on the fecundity of female of various age classes. According to Gusev and Žuravlev (1958) the 2-year old females of the Colorado beetle lay eggs, this being supported by the observations of Miksiewicz (1948) who found that 1-year old female of the Colorado beetle laid 875 eggs and in the second year only 183 eggs, thus its fecundity was decreasing in older age. This is wholly consistent with the results of the present author, therefore, the opinion of Kowalska (1969) that 2-year old females of the Colorado beetle do not lay eggs at all seems a little doubtful.

Laboratory observations carried out in 1971 on the fecundity of 1-year old females of cassids showed (Tab. VIII) that the number of eggs laid by one female, as compared with the results obtained in field investigations, is lower with *C. rubiginosa* Müll. and *C. flaveola* Thunber. and a little higher with the other two species. However, the numbers of eggs are in the limits of the fecundity characteristic for 1-year old females of cassids.

A comparison of the fecundity of 1-year old females of cassids with that of other herbivorous insects shows that:

x fecundity of a cassid female is 201-344 eggs (author's data)

of a Colorado beetle 793—1301 eggs (Węgorek, 1957a)

832-1455 eggs (Wegorek, 1959)

of Longitarsus suturellus Dft. 85 eggs (Warchalowski, 1958)

of Ceuthorrhynchus quadridens Panz. 124 eggs (Dmoch, 1959)

of Gaurotes virginea L. 23 eggs (Starzyk, 1970).

As this list indicates the females of cassids may be classified among the insects of medium fecundity while the enormous fecundity of the Colorado beetle and a very low one of *Gaurotes virginea* L. should be stressed here.

## 3. Density

The problem of density is very closely connected with the fecundity of cassids. The degree of density changes throughout the vegetation season in accordance with the phenology of the occurrence and course of development of separate stages. The measurements of the ranges of the distribution of host plants of cassids carried out in 1966, 1968, and 1970 enabled to study both quantitative changes in the size of these ranges (figs. 2—4) and changes in the density of

beetles. It was found that the size of patches of Cirsium oleraceum (L.) Scop. and Mentha longifolia (L.) Huds. was increasing continuously while Stellaria graminea L. reached a maximum range in 1968 and afterwards its surface was slowly decreasing. Against this background the changes in the degree of the density of cassid populations (Tables IX—XI) seem interesting. In comparing the results of investigation in three different years it may be said that the degree of the density of the population of cassids increases in spite of a great increase

Table IX

Changes in the degree of density of the development stages of Cassidinae within the study area on the meadow in the Sąspowska Valley of the Ojców National Park in the vegetation season 1966 (x specimen/m²)

Species	Ca	ssida 1	rubigina	sa Mü	LL.		Cass	ida vib	ex L.	
Stage Date of investigations	AI	E	L	P	YI	AI	E	L	P	YI
20. IV 30. IV 11. V 25. V 7. VI 27. VI 15. VII 8. VIII 8. IX 5. X	0·01 0·31 0·27 0·08 0·09 0·05 0·05	0·01 0·05 0·09 0·04 0·01	0·09 0·40 0·30 0·27 0·01	0·01 0·01 0·01	0·01 0·06 0·05 0·13 0·01	0·01 0·01 0·02 0·02 0·01 0·01 0·02	0·01 0·01 0·02 0·01	0·03 0·10 0·17 0·10 0·01	0·01 0·01 0·01	0·01 0·04 0·04 0·02

Explanations: AI — adult imagines

E — eggs

L — larvae

P — pupae

YI - young imagines

in the surface of patches of their host plants. It is particularly distinct with old imagines and eggs while in other stages of development these regularities undergo changes and with young imagines of *C. rubiginosa* Müll. and *C. vibex* L. the density was even smaller. In spring 1966 maximum density of old imagines of *C. rubiginosa* Müll. and *C. vibex* L. amounting to 0·3 of specimen per 1 sq.m. and 0·02 of specimen per 1 sq.m. while in 1970 0·6 and 0·08 respectively. The degree of the density of the other two species was only investigated in 1968 and 1970 (Tables X and XI). The maximum density of adult imagines of *C. viridis* L. is greater in 1968 (a minimum range of mint) than in 1970, nevertheless, considering a great increase in the patch of mint in the period of two years, the value of 1·1 specimen/1 sq. m. was accepted as in increase in the densite

Changes in the degree of density of the development stages of Cassidinae within the study area on the meadow in the Saspowska Valley of the Ojców National Park in the vegetation season 1968 (x̄ specimen/m²)

a	YI														
Cassida flaveola Thunbg.	Ъ												1		
sida flav. Thunbg.	T														
Cassi	Œ						~7		_						
	AI						0.02		0.01	0.0					
	YI		,												
dis L.	Ъ														
Cassida viridis L.	L							0.50	1.50						
Cassie	日						22.50		00.6		4.50				
	AI				0.50	1.50		0.50							
	YI										0.01	0.01	0.03	0.01	0.01
ex L.	Ъ											0.01	0.01	0.01	
Cassida vibex L.	T								0.04	90.0	60.0	90.0	0.05		
Cass	闰						0.01	0.03	0.01	0.01					
	AI		0.03	0.05	0.03	0.05	0.03	0.02	0.05	0.01					
ÜLL.	YI									0.05	0.05	60.0	0.07	0.04	0.05
osa M	Ъ											0.01	0.01		
rubiginosa Müll.	ı						0.01	0.07	0.11	0.50	0.24	0.15	0.04	0.01	
Cassida r	田					0.01	80.0	0.05	80.0	0.12	0.05	0.01			
Ca	AI	0.01	0.22	0.32	0.28	90.0	0.05	0.05	0.04	0.01	0.01				
Species	Stage Date of investigations		17. IV												

Explanations: AI — adult imagines

E — eggs L — larvae

P — pupae YI — young imagines

Changes in the degree of density of the development stages of Cassidinae within the study area on the meadow in the Sąspowska Valley of the Ojców National Park in the vegetation season 1970 ( $\bar{\mathbf{x}}$  specimen/ $\bar{\mathbf{m}}^2$ )

NBG.		XI													0.01		0.02	0.01	
Тни		А												-	67		20	67	
veola		I											0.11				0.08	0.0	
da fla		덛							0.13	0.52	0.70		0.53	0.33	0.19	0.01			
Cassida flaveola Thunbg.		AI						0.03		0.10	0.12		0.04	0.03	0.03	!	0.03	0.03	0.05
		YI													0.19		0.05		0.05
dis L.		А												0.44	0.34				
Cassida viridis L.		T									17.40		17.60 12.20	3.74	1.65				
Cassic		Ħ					2.38	4.62			72.30		1	16.0					
		AI						0.87		1.07	1.02		0.63	0.53	0.53		0.48	0.48	0.48
		XI												0.01	0.01		0.01	0.02	0.01
x T.		А													0.01		0.01	0.01	
Cassida vihex L.		L									0.12		0.11	60.0	0.10		0.04		
Cassi		因	la la				0.05	0.58		0.73	0.05	0.01							
		AI		ý.	0.01	0.01		80.0		80.0	0.04		0.04	0.03	0.05		0.05	0.03	0.05
T.		YI											0.01	0.01	0.05		90.0	90.0	0.01
Cassida mbiainosa Mill.	200	Ъ													0.03			0.01	
hiain	na fa co	L									69.0		0.72	0.56	0.41		0.12	0.01	
ida m	man	घ				0.01	0.18	1.18		1.23	0.48		0.40	0.18	0.18		0.04		
Case	0,000	AI	0.01	60.0	0.49	0.64		0.24		0.23	0.10		0.05	0.04	0.03		0.05	0.05	0.05
Specioon	apronda	Stage Date of inve- stigations	15. IV	22. IV	27. IV	5. V	15. V	29. V	4. VI	10. VI	26. VI	7. VII	10. VII	24. VII	4. VIII	12. VIII	20. VIII	7. IX	28. IX

Explanations: AI — adult imagines

E — eggs L — larvae

P — pupae

YI - young imagines

of beetles. In case of *C. flaveola* Thunber, an increase in the degree of density was observed in all development stages but this phenomenon might havy resulted from a gradual regression in the range of distribution of the foodplant of this cassid in 1970 (fig. 4) and also since 1970 from the use of a sweep net in the study of the numbers of development stages of this species.

In comparing the degree of density of all development stages within individual species (Tables IX—XI) it should be said that *C. rubiginosa* MÜLL. is really the most numerous species on the meadow, *C. vibex* L. and *C. viridis* L. are not very numerous, *C. flaveola* Thunbg. being rare. The greatest maxima of density noted in almost all stages of the investigated species in 1970 (Tab. XI) suggest that this favourable situation was indirectly influenced by very good climatic conditions of summer 1969 (high temperatures, strong insolation, almost no rains) since the greatest density of old imagines of cassids of four investigated species was observed in spring 1970.

The reports of other workers concerning the degree of the density of various species of cassids seem a little doubtful. Palij and Klepikova (1957) report that in 1953 the numbers of beetles of  $C.\ nebulosa$  L. amounted to 200-250 imagines/1 sq.m. on specimens of pigweed, while ŠEREMET and GORBUNOV (1969) elaim that in invididual years the numbers of beetles of H. subferruginea Schrnk. amounted to 50-70 imagines per sq.m. on Convolvulus and of C. rubiginosa MÜLL. to 30-50 imagines per 1 sq.m. on Canadian thistle, in 1965 the density of larvae of the two species being 115—235 and 89—112 respectively. However the above-mentioned authors do not define whether the density of these beetles (larvae) was uniformly distributed on the whole surface of the range of their host plants or was only determined on small randomly selected patches of plants. Throughout several-year studies the author found that in the spring period on randomly selected small patches (1 sq.m.) of foodplants the density of imagines of C. rubiginosa Müll. was from several to scores of specimens per 1 sq.m. while that of larvae from a few to twenty specimens per 1 sq.m., but if the whole area of the distribution of these plants was considered, the degrees of the density of cassids reached the values given in Tables IX—XI.

## 4. Migrations

The changes in the degree of density of young imagines of cassids at the end of summer and in autumn and of adult ones in speing are connected with the phenomenon of migration. The problems of migrations and wintering of cassids were relatively comprehensively presented in another work (Kosior, Klein, 1970). Several-year studies carried out on the meadow in the Sąspowska Valley showed that direct reasons of the migration of young imagines to winter-quarters in wooded areas are physical factors: temperature, insolation, length of days, humidity; biotic factors being indirect reasons: quality of food and physiological condition of beetles.

As it was already mentioned, in September of consecutive years minimum temperatures of air almost never exceeded  $+13\cdot0^{\circ}\mathrm{C}$  on the meadow and were decisive for the term and course of the migration of beetles. It was found that the cassids were distinctly heliophilous insects and therefore the increasing degree of shading of the meadow and worse humidity conditions made them migrate in the region of the lime-hornbeam forest, situated on a slope of south exposition in the Sąspowska Valley, where they wintered in the litter under favourable conditions of temperature and insolation. Owing to the factor of the length of day the beetles which hatched late (at the end of summer) migrated after about 2 weeks to their winter-quarters while those which hatched earlier (at the beginning of summer) did it as late as after about 2 months.

The quality of food connected with the process of senescence of leaves of the host plants of cassids, inhibits the maturation of young beetles which do not reach sexual maturity and begin to sink into the state of diapause, preceded by their migrations to winter-quarters. In the period of autumn in the bodies of beetles great amounts of reserve substances (fats) are found and the content of water reaches the lowest level in their life, amounting to about 55.00 per cent in consequence of this physiological condition the beetles migrate for wintering into the forest.

It might have been observed that in the spring period adult beetles which had hibernated, returned from the forest to the meadow. As it was mentioned the period of the beginning and course of return of cassids above all depends on climatic conditions.

Among the authors who investigated the cassids only Kleine (1917) discusses in a slight measure the problem of migration. He claims that the reason of the migration of young imagines of *C. viridis* L. for wintering are low values of temperatures in the autumn period. The investigations of Kuznecov-Ugamski (1929) on the migration of ladybirds and of Chroliński (1963) on weevils showed that the reasons of the migration of young beetles to wooded areas were: a difference in air humidity between the forest and open space and the search of places most suitable for wintering. The opinions of the above-mentioned workers are in agreement with the results of the present author, however, they treat the problems of migration on a limited scale.

The courses of migrations and returns of the imagines of the investigated species of cassids are presented in figures 5—10. The wintering migration of young cassids begins in the second half of August or at the end of this month (depending on the influence of climatic conditions), is fairly intense in September and ends in the first half of October. The return of beetles from winter-quarters to the territory of the meadow occurs in spring of the next year: the earliest species being *C. rubiginosa* MÜLL. (I or II half of April) while the other species appear successively in 7—10-day intervals. A maximum return takes place in May, then in June a slow decrease and at the beginning of July an end of it are observed.

VI. THE INFLUENCE OF PHYSICAL AND BIOTIC FACTORS ON THE POPULATIONS OF CASSIDS

### A. Physical factors

# 1. Temperature, rains, and wind

Climatic conditions which considerably influence the development of the populations of cassids are: air temperature, rains, and wind; this being wholly supported by the results of the investigations of Kleine (1916, 1917) on cassids, of Miksiewicz (1948), Wilusz (1958) and Wegorek (1959) on the Colorado beetle, of Starzyk (1970, 1971) on Gaurotes virginea L. and on other beetles of the family Cerambycidae, and of Wilski (1951) on the pests of culture plants. Among these three factors the dominating role is played by the temperature. Certain minimum amount of heat is necessary for the development of the populations of the investigated cassid species. On the investigated meadow the temperature of the threshold value of  $+13.0^{\circ}\mathrm{C}$  is necessary for the beginning of the vegetation and return of beetles from wintering. Further increase in the temperature favours intense development of the vegetation and, in consequence, good living conditions are found by the coming beetles. A proper development of cassids depends on weather conditions in May, particularly in its first half, since at this time strong return of imagines occurs; soon the masses of beetles begin to mate and afterwards to lay eggs. Heavy and continuous rains connected with low temperatures and winds considerably limit the activity of feeding and mating of the investigated species, they also influence their fecundity and the period of the development of eggs. When the weather conditions improve the beetles reappear and continue their development cycle.

Investigations on the length of development and of the reduction degree of eggs and larvae of cassids were carried out on the meadow at permanent observation stations in the years 1969—1971. The influence of physical factors on the reduction of eggs is presented in Table XII. It was found that in the investigated species this degree ranged from 23.68 to as many as 72.54 per cent. The greatest reduction of eggs was noted with C. flaveola Thunbg. (59.34—72.54 per cent) and C. vibex L. (41.64—60.03 per cent), while with two other species it was lower almost by half and amounted to 23.68—53.54 per cent with C. rubiginosa Müll. and 24.72—30.86 per cent with C. viridis L. The great degree of egg reduction with C. flaveola Thunbg. and C. vibex L. in 1970—1971 is very interesting.

In both years of investigations in the spring period great decreases in the temperature and often rains were noted (figs. 9, 10). It is supposed that these two factors connected with strong winds brought about this enormous reduction of eggs. The egg batches of both species of cassids are composed of one or rarely of two eggs or more, and are a little more weakly stuck by females to the leaf surface so that strong rains and winds easily wash or thrust them to the ground,

Table XII

Influence of physical factors (temperature, rains, wind) on the degree of reduction of eggs of *Cassidinae* within the study area on the meadow in the Sąspowska Valley of the Ojców National Park

in the vegetation season 1969

a .			Number	of eggs		
Species	initial	%	reduced	%	final	%
Cassida rubiginosa MÜLL. Cassida vibex L.	4272 2652	100·00 100·00	2287 1443	53·54 54·42	1985 1209	46·46 45·58

in the vegetation season 1970

Cassida rubiginosa Müll.	4872	100.00	1154	23.68	3718	76.32
Cassida vibex L.	2223	100.00	1334	60.03	889	39.97
Cassida viridis L.	2009	100.00	497	24.72	1512	75.28
Cassida flaveola THUNBG.	1933	100.00	1147	59.34	786	40.66

in the vegetation season 1971

Cassida rubiginosa Müll.	2855	100.00	867	30.36	1988	69.64
Cassida vibex L.	808	100.00	336	41.64	472	58.36
Cassida viridis L.	731	100.00	226	30.86	505	69.14
Cassida flaveola Thunbg.	304	100.00	221	72.54	83	27.46

while the egg batches of *C. rubiginosa* MÜLL. and *C. viridis* L. are usually composed of a greater number of eggs and are more strongly stuck to leaves or stems of foodplants. It should be also stressed that among the batches thrown down by winds or rains many were surely attacked by egg parasites (biotic factors) but unfortunately it was not possible to determine it.

The course of weather conditions greatly influences the development and death rate of cassid larvae. In the summer period high temperatures and the lack of rains greatly affect their development, distinctly shortening the development cycle (Tab. IV), while low temperatures, long periods of rains and winds (which blow in the Sąspowska Valley from SW, W, and NW directions for a great part of the year; personal communication of Dr. J. Klein) strongly inhibit the development and considerably reduce the larvae. The observations of the author showed that strong rains and winds threw down great amounts of larvae in the first and second instar from the plants, this being also supported by the results of the studies of Kleine (1915) and Rammer (1934) on cassids and of Kaczmarek (1955) and Miksiewicz (1957) on the Colorado beetle. The degree of reduction of separate stages of development of cassids under field conditions in the years 1969—1971 are presented in Table XIII. Since it was not possible to determine precise numbers of larvae reduced as well by physical as by biotic

Table XIII

Degree of reduction of individual development stages of Cassidinae within the study area on the meadow in the Saspowska Valley of the Ojców National Park

in the vegetation season 1969

	Percentage of the hatch of imagines	1.86
•	$\sum \overline{\mathbf{x}}(\%)$	98·14 98·76
	Ъ	-
	PP	92.0
	L5	1.86
(%)	L4	3.02 4.96
$\overline{\mathbf{x}}(\%)$	L3 ,	4.48 8.69
	L2	13·50 14·31
	L1	63.08
	된	11.44
Reduction	Species	Cassida rubiginosa Müll Cassida vibex I

in the vegetation season 1970

Jassida rubiginosa Müll.	26.06	48.87	13.64	4.79	2.88	1.99	0.11	0.48	98.82	1.18
$\exists assida\ vibex\ L.$	40.38	37.46	29.6	6.30	3.49	1.35	1	1	98.65	1.35
Jassida viridis L.	51.39	15.54	8.40	7.54	5.56	8.60	1.39	0.99	99.41	0.59
Jassida flaveola Thunbe.	49.24	40.46	5.47	2.54	0.51	×	68.0	1	99.11	68.0

in the vegetation season 1971

Jassida rubiginosa Müll.	23.74	56.85	10.76	2.52	2.16	1.46	0.70	0.35	98.54	1.46
Jassida vibex L.	23.94	47.67	11.65	66.9	4.66	4.03		1	98.94	1.06
Jassida viridis L.	46.73	31.88	7.52	3.17	2.18	4.36	2.18	0.99	10.66	0.99
Cassida flaveola Thunbb.	33.74	43.38	12.05	4.82	3.61	×	1.20	-	08.86	1.20

 $\Sigma \overline{x}$  — total degree of reduction with relation to the initial number of eggs Explanations:

E — eggs

 $\begin{array}{c} {\rm L1-\!L5-successive~larval~instars} \\ {\rm PP--prepupae} \end{array}$ 

P—pupae

× - with O. flaveola Thunbe. only 4 larval instars were found.

Table XIV

Mortality of young imagines of Cassidinae throughout the wintering in the litter of the lime-hornbeam forest on a slope of southern exposition in the Sąspowska Valley of the Ojców National Park

Species	Cassida rubig	rubiginosa Müll.	Cassida	Cassida vibex L.	Cassida	Cassida viridis L.	Cassida flav	Cassida flaveola Thunbg.
Specimens	dead	living	dead	living	dead	living	dead	living
Date of investigation	number %	number %	number %	number % number % number %	number %	number %	number %	number %
X. 1968—V. 1969 X. 1969—V. 1970 X. 1970—V. 1971 X. 1971—V. 1972	321 34·30 23 31·99 29 35·80 47 39·17	615 65·70 49 68·01 52 64·20 73 60·83	36 54·55 42 58·33 15 53·57 47 51·09	30 45.45 30 41.67 13 46.43 45 48.91	15 23.08 8 23.53 16 26.23	50 76.92 26 76.47 45 73.77	5 20.83 19 29.23 10 21.28	19 79.17 46 70.77 37 78.72

Life table of imagines of Cassidinae

75	өх	13.4	12.9	11.9	6.01	6.6	8.9	6.7	7.3	9.9	6.5	5.5	5.9	5.3	6.5	9.4	9.9	9.9	4.6	3.6	2.6	2.0	1.3	8.0	0.5			
HUNB	100qx			0.00			0.00	4.17	4.35	3.64	0.00	1.05	29.9	8.57	0.00	0.00	0.00	0.00	0.00	0.00	4.28	29.9	0.00	29.9	0.00			
ola T	dx ]	40				0	0	40		120 1	0		40			0	0	0	0	0	40 1		80 4		40.10			
flave	X	0001	096	096	096	096	096	096	920	880	094					280	280	280	280	280	280	240	200	120	40	0		
Cassida flaveola Thunba.	м	0—1	1-2	2—3	3—4	45	5—6	2—9	2—8	8—8	9—10	10—11	11-12	12 - 13	13—14	14—15	15—16	16—17	17—18	18 - 19	19-20	20-21	21 - 22	22—23	23-24	24-25	25-26	26—27
	өх	12.3	11.5	10.5	9.5	8.5	2.2	6.5	5.8	5.4	4.9	4.8	8.4	9.9	4.6	8.4	7.4	6.4	5.4	4.4	3.8	3.1	3.5	3.1	3.8	4.4	7.5	6.5
L.**	100qx			0.00	0.00	0.00	0.00	4.62	89.6	0.81	00.9	9.05	14.6	0.00	54.17	0.00	0.00	0.00	0.00	60.6	00.0	3.33	19.9	00.01	33.33	50.00	0.00	00.00
iridis	dx			0		0	0	46	91	91 1			151 2			0	0	0	0	15	15 1		15 1	30 4	15 3	16 8	0	0
Cassida viridis L.**	lx	1000	985	985	985	985	985	985	939	848	757	636	515	364	364	167	167	167	167	167	152	137	91	94	46	31	15	15
Cas	×	0—1	1—2	2-3	3-4	4-5	2—6	2—9	2—8	8—8	9—10	10—11	11 - 12	12 - 13	13 - 14	14-15	15 - 16	16—17	17—18	18—19	19-20	20-21	21 - 22	22 - 23	23 - 24	24 - 25	25 - 26	26-27
	жә	13.2	12.4	11.4	10.4	9.4	8.4	7.4	7.5	8.7	11.2	10.2	10.5	6.01	11.5	12.5	11.5	0.5	9.5	8.5	7.5	6.5	6.3	5.3	5.5	6.1	8.9	8.9
L.*	100qx			0.00		0.00							14.81							0.00	0.00	11.76	0.00	20.00	25.00	2.23	14.28	0.00
vibex	фх	15		0	0	0		134 1				45 1	60 1		45 1	0		0	0	0	0	30 1	0	45 2	44 2	30 2	15 1	0
ıssida	Ix	1000	985	985	985	985	985	985	851	717	448	448	403	343	862	253	253	253	253	253	253	253	223	223	178	134	104	88
Ö	м	0-1	1—2	2—3	3—4	45	5—6	2—9	2—8	6—8	9—10	10-11	11 - 12	12 - 13	13—14	14—15	15—16	16—17	17—18	18—19	19—20	20-21	21 - 22	22—23	23—24	24 - 25	25—26	
L.	ех	6.8	6.2	6.9	0.9	5.0	4.2	3.3	5.6	1.9	1:1	6.4	8.6	11.4	11.4	13.4	12.4	11.4	10-4	9.4	8.4	8.4	9.2	8.2	8.5	8.4	9.4	8.4
osa Müll. Cassida v	100qx			0.21									23.33														00.00	
iginosa	dx	6.1	4	01	0		44				612 9	4 1	7 2	67		0					2 1	3		2 1			0	1 1
la rub	lx	1000	866	994	893	992	950	906	821	736		36	32	25	23	18	18	18	18	18	18	16	13	13	11	10	00	00
Cassid	×	0—1	1—2	2—3	3—4	45	5—6	2—9	2—8	6—8	9—10	10-11	11 - 12	12—13	13 - 14	14—15	15 - 16	16—17	17—18	18—19	19—20	20—21	21 - 22	22 - 23	23—24		25—26	26—27

													-					
27—28	28—29	29—30	30—31	31—32	32—33	33—34	34—35	35—36	36—37	37—38	38—39	39—40	40—41	41—42	42—43	43—44	44—45	45—46
5.2	4.5	3.5	2.5	1.5	0.5													
0.00	00.00	0.00	0.00	0.00	00.00													
0	0	0	0	0	1510													
15	15	15	15	15	15	0												
27—28	28—29	29—30	30—31	31—32	32—33	33—34	34-35	35-36	36—37	37—38	38-39	39-40	40—41	41—42	42—43	43—44	44—45	45—46
5.8	4.8	3.8	2.8	1.8	1.5	1.5	1.5	0.5										
0.00	00.00	00.0	0.00	33.33	50.00	20.00	0.00	00.00		1								
88	89	88	88	89	59	29	15	15	0									
27—28	28—29	29—30	30—31	31—32	32—33	33—34	34—35	35—36	36-37	37—38	38—39	39—40	40-41	41—42	42-43	43—44	44-45	45-46
8.5	2.2	6.5	5.5	4.5	0.9	11.5	10.5	9.5	8.5	7.5	6.5	5.5	4.5	3.5	2.5	1.5	0.5	
	0.00																	
0	0	0				0				0		0			0	0	210	
7	7	7	7	7	4	2	67	23	67	23	23	2	67	67	6.1	63	63	0
27—28	28—29	29—30	30-31	31—32	32—33	33-34	34-35	35—36	36-37	37—38	38—39	39—40	40-41	41—42	42—43	43-44	44-45	45—46
-				100000						_								

Explanations: x — age of specimens in successive months

lx — number of specimens living at the beginning of each month given in column x

dx — number of specimens dying within each month given in column x

qx — number of specimens dying within each month divided by the number of specimens living at the beginning of a given month (death rate)

expected length of life; average length of life left for each specimen living at the beginning of a given month

\* — observations were begun on 1st August 1968

\*\* — observations were begun on 1st August 1969

factors, it was accepted on the basis of author's own field observations that larvae of the first and second instar are reduced to 1/3 of their number by the first group of factors, while in the next instars the decisive role was played by biotic factors.

In the years 1969—1972 four controlled winterings of young imagines of four cassid species were carried out in the lime-hornbeam forest on a slope of south exposition in the Sąspowska Valley (pl. XXI, A). The obtained results enabled to determine the death rate of beetles in the periods of wintering (Tab. XIV). In four winter seasons the highest death rate was found among the imagines of C. vibex L. (51·09—58·33 per cent), while the lowest one (with one exception) among C. flaveola Thunber. (20·83—29·23 per cent); the two other species had medium places in this classification. In the literature only one information was found with regard to the death rate of beetles wintering in forest litter. Vasiley (1963) found that in Gastrolina thoracica Baly (Col. Chrysom.) wintering in a more or less dry forest litter in low riverine terraces, the death rate amounted to 15 per cent, while in more humid places to 25—30 per cent. The results obtained in the present work (Tab. XIV) are very similar to the data of Vasiley, but in case of C. vibex L. they seem to suggest that the litter in which the beetles wintered was very humid.

The problem of the course of mortality throughout the wintering of beetles should be briefly discussed. According to Kowalska (1960) and Łarczenko (1957) the physiological condition of the imagines of Colorado beetle greatly influences the whole course of wintering and is the reason of their variable winter mortality. The late the stage of diapause occurs in autumn, the greater is the resistance of insects in the period of wintering. In diapause the beetles are resistant to low temperature, high humidity, and fungal infection.

Investigations on the mortality of the imagines of cassids in autumn, winter, and spring showed that the highest death-rate occurs in spring (50—70 per cent of the total number of beetles dead throughout wintering). It is supported by the investigation of Kowalska (1960) on winter mortality of the imagines of the Colorado beetle. According to Wegorek (1957) and Kowalska (1960) meteorological factors do not play any role in the mortality of beetles in winter but they do in spring. The greatest mortality occurs in spring period because the diapause is finished in a part of beetles but unfavourable climatic conditions prevent them to return to the regions of feeding. Climatic conditions of the end of April and the first half of May play decisive role with the imagines of cassids. In consequence of low temperatures, often rains, and winds for a long period of time many beetles perish on account of starvation in the period before the return on the meadow.

Parallel to the study on four wintering of young beetles (new specimens were observed every year) observations were carried out on the winter death rate and the lifetime of the same specimens of four cassids species (Tab. XV). Obviously, the initial numbers of beetles observed from every species were much smaller, but according to the rule of the elaboration of life tables, these values

were calculated for 1000 specimens. The problem of the lifetime of separate species is very interesting. The average length of life (e<sub>0</sub>) of beetles in a population at the moment of hatching (August 1968 with C. rubiginosa MÜLL. and C. vibex L. and August 1969 with C. viridis L. and C. flaveola Thunbe.) amounts to highest values with C. flaveola Thunbel: 13.4 months and with C. rubiginosa Müll. only 8.9 months, this resulting from a very high death rate of the imagines of this species in spring of the first year of their life. The two other species show medium values with regard to eo. In this table fairly regular periods of greatintensity in the death rate of beetles may be seen separated with periods of the death-rate equal to zero. They illustrate winter mortality in successive years. particularly increasing at the turn of winter. In the present study a maximum life length was almost 4 years with C. rubiginosa Müll., 3 years with C. vibex L., almost 3 years with C. viridis L., and 2 years with C. flaveola Thunba. With all species males lived shorter than females, with the two sexes the differences ranging from 2 months with C. flaveola Thunbg. to almost 2 years with C. rubiginosa Müll. (cf. Tab. III). The anticipated life length (e<sub>x</sub>) of imagines which reached these maximum age classes was only half a month (Tab. XV).

#### 2. Insolation

Besides the three factors discussed above, insolation is another one playing an extremely important role decisive for the occurrence and development of the population of the investigated cassid species within the study area on the meadow. The situation of the meadow on the bottom of the Saspowska Valley between the mountains Chełmowa and Złota (pl. XXI, B) causes that in connection with a constant change in the solar declination the amount of energy from the direct solar radiation reaching the surface of the meadow as well as the degreeof its shading are also subject to essential changes. The dependences between the occurrence of cassid populations within the patches of their foodplants on the meadow and the changes in the degree of its shading throughout the vegetation season 1970 are presented in figures 11-17. At the end of March in spite of the fact that a greater part of the meadow was already insolated (fig. 11), no appearance of any cassid imagines was observed yet. In this period unfavourable climatic conditions occur on the meadow (Klein, unpublished) therefore the development of vegetation and, in consequence the appearance of beetles: are not yet possible. In April at maximum temperatures of +13.0°C and more, intense development of the vegetation is observed on the meadow and then more and more numerous beetles appear there (fig. 12); in May they begin toreproduce, the development of new populations of cassids being thus originated.

The degree of shading of the meadow distinctly decreases in April (fig. 12) and May (fig. 13) reaching its lowest level in June (fig. 14); afterwards it slowly increases in July (fig. 15), more rapidly in August and September (figs. 16, 17), and in October (an additional observation) almost the whole area of the meadow is in the zone of shade of the Chełmowa Góra Mt. In December (also an additional

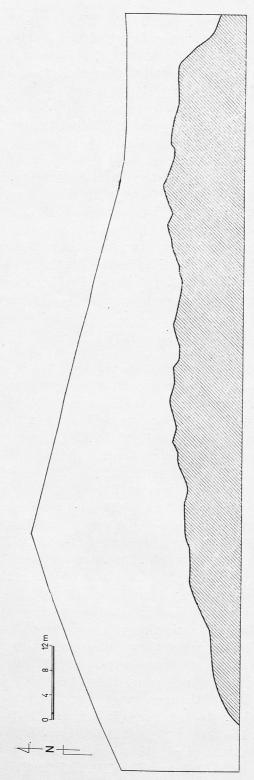


Fig. 11. Degree of shading in the study area on the meadow in the Sąspowska Valley of the Ojców National Park on March 21. 1970

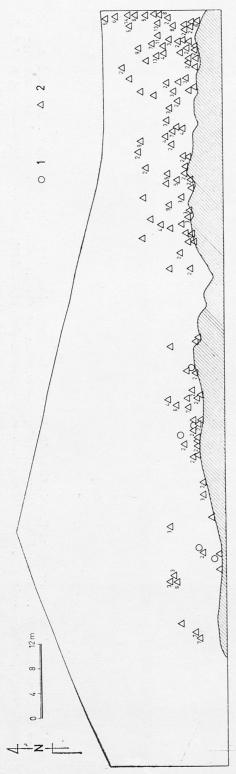
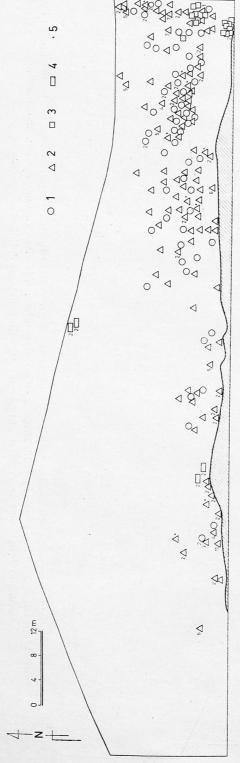


Fig. 12. Dependence of the occurrence of Cassids (April 27. 1970) on the degree of shading in the study area on the meadow in the Sąspowska Valley of the Ojców National Park (April 20. 1970). 1—imagines of Cassida vibex L. one-year old, 2—imagines of C. rubiginosa Müll. one-year old. Figure beside signature denotes number of specimens



Saspowska Valley of the Ojców National Park (May 21. 1970). 1—imagines of Cassida vibex L. one-year old and two-year old, 2—imagines of C. vividis L. one-year old, 4—imagines of C. vividis L. one-year old, 4—imagines of C. fla-Fig. 13. Dependence of the occurrence of Cassids (May 29. 1970) on the degree of shading in the study area on the meadow in the veola Thunbe. one-year old, 5 — a dead specimen. Figure beside signature denotes number of specimens

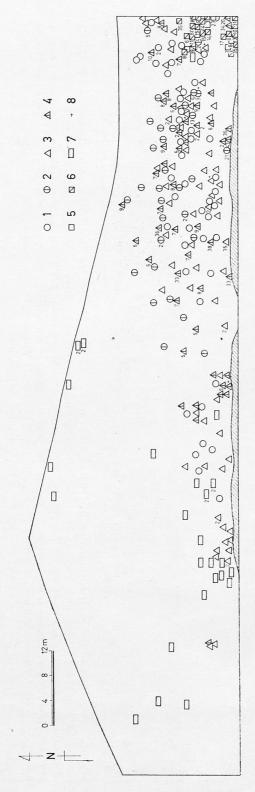


Fig. 14. Dependence of the occurrence of Cassids (Juni 27. 1970) on the degree of shading in the study area on the meadow in the Saspowska Valley of the Ojców National Park (Juni 22. 1970). 1 — imagines of Cassida vibex L. one-year old and two-year old, 2 — larvae of C. vibex L., 3—imagines of C. rubiginosa Müll. one-year old and two-year old, 4—larvae of C. rubiginosa Müll., 5—imagines of C. viridis L. one-year old, 6 — larvae of C. viridis L., 7 — imagines of C. flaveola Thunbe. one year old, 8 — a dead specimen. Figure beside signature denotes number of specimens

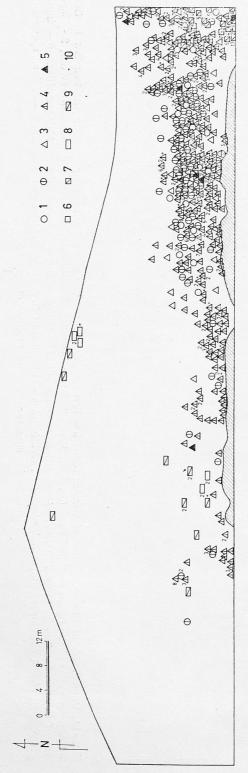
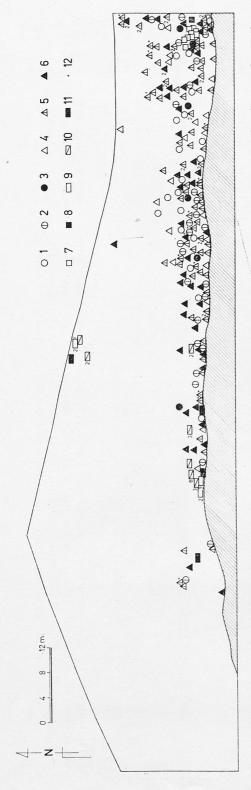


Fig. 15. Dependence of the occurrence of Cassids (Juli 24. 1970) on the degree of shading in the study area on the meadow in the Sąspowska Valley of the Ojców National Park (Juli 21. 1970). 1 -- imagines of Cassida vibex L. one-year old and two-year old, 2 -- larvae of C. vibex L., 3—imagines of C. rubiginosa Müll. one-year old and two-year old, 4—larvae of C. rubiginosa Müll., 5—imagines of C. rubiginosa Müll. hatched in summer of the year 1970, 6—imagines of C. viridis L. one-year old, 7—larvae of C. viridis L., 8 — imagines of C. flaveola Thunbg. one-year old, 9 — larvae of C. flaveola Thunbg., 10 — a dead specimen. Figure beside signature denotes number of specimens



of the Ojców National Park (August 20. 1970). 1— imagines of Cassida vibex L. one-year old and two-year old, 2—larvae of C. vibex L., 3 — imagines of C. vibex L. hatched in summer of the year 1970, 4 — imagines of C. rubiginosa Müll. one-year old and two-year old, 5-larvae of C. rubiginosa Müll., 6-imagines of C. rubiginosa Müll. hatched in summer of the year 1970, 7-imagines of C. viridis L. one-year old, 8 — imagines of C. wiridis L. hatched in summer of the year 1970, 9 — imagines of C. flaveola Thunbs. oneyear old, 10 — larvae of C. flaveola Thunbe., 11 — imagines of C. flaveola Thunbe. hatched in summer of the year 1970, 12 — a dead Fig. 16. Dependence of the occurrence of Cassids on the degree of shading in the study area on the meadow in the Saspowska Valley specimen. Figure beside signature denotes number of specimens

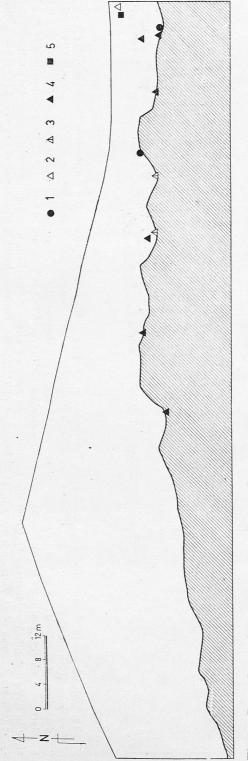


Fig. 17. Dependence of the occurrence of Cassids (September 28. 1970) on the degree of shading in the study area on the meadow in the Sąspowska Valley of the Ojców National Park (September 21. 1970). 1 — imagines of Cassida vibex L. hatched in summer of the year 1970, 2—imagines of C. rubiginosa Müll. two year old, 3—larvae of C. rubiginosa Müll., 4—imagines of C. rubiginosa Müll. hatched in summer of the year 1970, 5 - imagines of C. viridis L. hatched in summer of the year 1970

observation) its shade covers the whole meadow together with slopes of the Złota Góra Mt. near the valley bottom.

A doubtless conclusion may be drawn on the basis of the included figures that a distinct positive correlation exists between the size of insolation on the surface of the meadow and the appearance of individual development stages of cassids there, which are almost never encountered in the zone of constant shading where the direct solar radiation does not reach. This fact indicates that the cassids are distinctly heliophilous insects and their development also depends on insolation. It distinctly influences the course of return and maturation of beetles in spring, stimulates the development of larvae, and contributes to the phenomenon of wintering migration of young beetles.

The occurrence of various development stages of cassids within the patches of their host plants considerably changes in consecutive months of investigations. It may be observed that in April (fig. 12) and in May (fig. 13) the appearance of imagines of C. rubiginosa Müll. and C. vibex L. is not uniform since as well small as larger groups of specimens are observed, places with no beetles at all being also noted. In June (fig. 14) in connection with the emergence of great numbers of larvae, the appearance of specimens of four species is more uniform, this being most distinct with C. viridis L., probably because its foodplant is not much distributed. The most even occurrence of the development stages of cassids is noted in July (fig. 15), August (fig. 16), and September (fig. 17). Figures 13—16 showed that almost throughout the whole season on the south side, just at the line of permanent shade, patches of foodplants occurred on which almost no specimens of cassids were encountered. At these places (cf. fig. 4) a compact spread of stinging nettle Urtica dioica L. occurs stifling the foodplants of cassids and bringing about secondary shading of these patches.

#### B. Biotic factors

Biotic factors play an essential role in modelling the size of insect populations. According to Galecka (1953) they are a link in the chain of mutual dependences while the physical factors are acting at random. The influence of meteorological conditions is independent from the quantitative state of a population controlled since as well numerous as not numerous populations may suffer catastrophic declines, being limited to similarly low numbers, while the action of limiting biotic factors is modulated by the size of the population. This dependence is brought about by the phenomenon of attracting predators by their prays, which is the more intense the greater is the density of the prays. The above-quoted author ascribes a destructive role to physical factors as opposed to the controlling role played by the biotic ones.

The biotic factors reducing the number of cassid populations are: parasites (endoparasites, oophagous animals), predators, and microorganisms. Table XVI Presents their qualitative composition (with exception of microorganisms)

Parasites and predators attacking the development stages of Cassidinae (according to other authors)

Authors	Parasites	Cassida rubiginosa Müll.	Cassida vibex L.	Cassida viridis L.	Cassida nebulosa L.	Cassida nobilis L.
		E L P I	ELPI	ELPI	E L P'I	ELPI
KAUFMANN (1933)	Nematodes			1 1		+++++
	Hymenoptera	   +   +   +			   +   +   +	-   -   -
Matis (1968)	Chalcidoidea	  -  -  -  -  -	1	1	   +   +   +	1 1 1
I	F. Tetracampidae					
KLEINE (1918)	Tetracampa flavipes FÖRST. $= Svn.$ Foersterella flavi-					
	pes (Förster)				1.	
JOLIVET (1946)	Tetracampe gallerucae					
	Forse.	1   +				-
MANOLACHE (1938)	Tetracampe gallerucae					
	Fonsc.			       		1 1 1
	F. Trichogrammatidae					
STEINHAUSEN (1950)	Centrobia sp.		1 1	       +		
Menozzi (1938)	•			     	     + +	
JOLIVET (1946)	Trichogramma evanescens					
•	Westw.					     +
MANOLACHE (1936)	Trichogramma evanescens					
	Westw.		The same of the sa			
MATIS (1971)	Rrichogramma sp.	       				
	F. Chalcididae					
KAUFMANN (1933)	Brachisycha pungens. =					
	MAYR. Brachista pungens					
	Syn. (MAYR.)		-			
Menozzi (1938)	Chalcis vitripennis Först. = Svn Reachameria vitrimennis	ris 1				
	(FÖRST.)	       	1 + +	    -  -		
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11	-we		ES.																				TZ.										
Chalcis vitripennis Först. =	Brachymeria vitripen- Först.)		Eulophus dimidiatus Nees.				is		is		sis		iis		unu		uni		un.		so		Entedon cassidarum RATZ.					;			χ · .	rıa	
nis F	ria v		iatus				Tetrastichus bruzzonis		Tetrastichus bruzzonis		Tetrastichus bruzzonis		Tetrastichus bruzzonis		Tetrastichus cassidarum		Tetrastichus cassidarum		Tetrastichus cassidarum		Tetrastichus rhosaces		x				9	Pimpla turionella L.			Pseudoptilops nitida v.	Syn. <i>Dufouria</i> Rön	
ipen	yme.	a sp	imid	.ds	ds s	ds s	n.iqs		s pro		s pro		s pro		s ca		s ca		s ca		y s.		isside	dae	s sp.	dea	nida	rione		. 91	sdo	m. L Rön	TOO.
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0	Sy	Brachymeria F. Eulophidae	En	En	Pl	$T\epsilon$	$T\epsilon$	M	$T\epsilon$	M	T	M	T	M	$T_{\epsilon}$	(F	T	(F	T	(I	T	×	E	F. 1	P	Ichn	F. 1	P	Dip	Œ.	P	<b>4</b> 8	100
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1946		971)	1946	(193)	(193	971)	N (1		1946		(193)		(193)		1918		(1) NJ		HE (		HE (		932)		3 (18			HE (			IN (		
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TOLIVET (1946)		Matis (1971)	JELIVET (1946)	Menozzi (1938)	Menozzi (1938)	MATIS (1971)	KAUFMANN (1933)		JOLIVET (1946)		Menozzi (1938)		NIETZKE (1939)		KLEINE (1918)		KAUFMANN (1933)		MANOLACHE (1938)		MANOLACHE (1938)		ENGEL (1932)		BRISCHKE (1883)			MANOLACHE (1938)			KAUFMANN (1933)		
		-	-	H	-	H					-		-				_		-		-				Α,			-					

Cassida nobilis L.	E L P I	+								
Cassida nebulosa L.	ELPI					       				
Cassida viridis L.	E L P I	-		-       			-	- -		       
Cassida vibex L.	E L P I	,								
Cassida rubiginosa Müll.	E L P I			1						
Parasites		Pseudoptilops nitida v. Röd. = Syn. Dufouria nitida v. Röd.	$\frac{\text{Predators}}{Heteroptera}$	F. Pentatomidae Troilus luridus F.	Picromerus bidens L.	Piesma quadratum FIEB.	F. Thomisidae Xysticus cristatus Ct.	F. Lycosidae Dolomedes nlantarius	HAHN.	Lycosidae gen. sp.
Authors		JOLIVET (1946)		MANOLACHE (1938)		Вкізснкв (1883)	Engel (1932)			

Explanations: E - eggs L - larvae P - pupae I - imagines

identified by various workers for the species of cassids investigated by the present author as well as the species which were additionally observed. A complete lack of data was found with regard to C. flaveola Thunber, and very scarce data were noted with regard to C. vibex L. The relatively greatest number of informations was found on the parasites of eggs, larvae, and pupae of C. rubiginosa Müll, and C. viridis L., as well as of C. nebulosa L. and C. nobilis L. With regard to the parasites of the imago stage no data are found, with the exception of C. nobilis L. The influence of predators on the population of cassids was observed and investigated in a very limited degree with C. viridis L. only.

The qualitative composition of the reducers of development stages determined by the present author with regard to *C. rubiginosa* MÜLL., *C. vibex* L., *C. viridis* L., and *C. flaveola* Thunber. is presented in Table XVII. Individual predators and parasites and their influence on the number of cassid populations will be separately reviewed with each development stage.

### 1. Enemies of eggs

The reducers of eggs of the investigated cassid species are (in the order of their percentage share): parasitic hymenoptera of the superfamily Chalcidoidea (Stresemann, 1964), mortality caused by the disturbances in the development, predatory harvestmen (Opiliones), and mites (Acari) (Table XVII). The evaluation of the influence of biotic factors on the degree of reduction of eggs was carried out under field conditions in 1969—1971, and then in the laboratory, showing that this degree was variable (Table XIII) and in separate years amounted to 11.44—26.06 per cent with C. rubiginosa Müll., 10.92—40.38 per cent with C. vibex L., 46·73—51·39 per cent with C. viridis L., and 33·74—49·24 per cent with C. flaveola Thunbg. A comparison of the resultes of the investigations carried out in three successive years showed that the egg batches of C. flaveola THUNBG. and C. viridis L. were most strongly reduced, while those of the two other species were reduced in a much less degree (sometimes even half as much). Extreme degrees of reduction of eggs are identical with those found with the Colorado beetle and amounted to 11.20 per cent (according to KARG and TROJAN, 1968) and to 56.00 per cent (according to Wegorek, 1950).

In the years of the investigation among the three above-mentioned biotic factors of egg reduction the decisive role was played by parasitic hymenoptera. In successive years the degree of the egg reduction effected by them (Table XVIII) ranged from 8·26—23·32 per cent with *C. rubiginosa* MÜLL., 4·80—37·91 per cent with *C. vibex* L., 41·58—49·34 per cent with *C. viridis* L., and 31·33—34·48 per cent with *C. flaveola* Thunb. The table showed that the eggs of cassids were reduced by hymenoptera in the strongest measure in 1970, and then in 1971. It seems that it was in a great degree brought about by unfavourable climatic conditions (low temperatures and rains) which prevailed in the spring period in both years of investigations, while in spring 1969 the weather conditions

Parasites and predators attacking the development stages of Cassidinae (author's own observations)

Parasites   Cassida rubiginasa   Cassida rubez L.   Cassida oiridis L.   Cassida rubez L.   Cassida rubez L.   Cassida rubez L.   Cassida rubez L.   Cassida rubez L.   Thropas Thropas Egg Larva Pupa Imago   Egg Larva Pupa Imago					
Egg Larva Pupa Imago   Egg Larva Pupa Imago	Parasites	Cassida rubiginosa WÜLL.	Cassida vibex L.	Cassida viridis L.	Cassida flaveola Thunbe
P.— -larvae sp.— + + + + + + +		Egg Larva Pupa Imago	Egg Larva Pupa Image	Egg Larva Pupa Imago	Egg Larva Pupa Imago
sp. –           -larvae           sp. –           -larvae           sp. –           - + + + +           + + + +           + + + +           + + + +           + + + +           + + +           + + + +           + + + +           + + + + +           + + + + + +           + + + + + + + + + + + + + + + +	Nematodes				
ap.—         ++++++++++++++++++++++++++++++++++++	F. Mermithidae				
Saryae	Hexamermis sp. —				
-larvae	larvae	+		     	1
sp.—       + + + +	Mermis sp. — larvae	+	1 1		
ve         awipes         the sest Bčx.       + + + + + + + + + + + + + +	Agamomermis sp. —				
averages + + + + +	larvae	 	1 1	-	    -
lae         'Tavipes       +       -       +       -       +       - <t< th=""><th>Hymenoptera</th><th></th><th></th><th></th><th></th></t<>	Hymenoptera				
davipes       +       -       +       -       -       +       - </th <th>F. Tetracampidae</th> <th></th> <th></th> <th></th> <th></th>	F. Tetracampidae				
idarum       + <th>Foersterella flavipes</th> <th></th> <th></th> <th></th> <th></th>	Foersterella flavipes				
idarum       +       +       +       +       +       +       +       - <th>(FÖRSTER)</th> <th>        +</th> <th>                                       </th> <th>      +</th> <th>   </th>	(FÖRSTER)	+		+	 
	Foersterella erdoesi Bčk.	     +		+	
+       +					
idarum     + <td< th=""><th>F. Eulophidae</th><th></th><th></th><th></th><th></th></td<>	F. Eulophidae				
idarum + + + + + + + + + + + + + + + + + + +	Pediobius sp.		+		1 1 1
cassidarum       + + + + + + + + + + + + + + + + + + +	Entedon cassidarum				
cassidarum       - + + + + + + + + +	RATZ.	+		+	
s sp. — + + + — — — + + + — — — — — — — — —	Tetrastichus cassidarum				
s sp	(RATZ.)		     		
sp.       -       -       +       -	Achrysocharis sp.		+		
1).	Sphenolepis sp.	1 1 1		     +	
1) + + + + +	F. Mymaridae				
llybeata	Ferrierella sp.		+	+	     +
llybeata +	Diptera				
öb	F. Tachinidae				
ia nitida V. Röp.	Dufouria chalybeata		i i		
	MEIG.	+			
	Dufouria nitida V. Röd.			1 1 1	+

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Predators Heteroptera F. Miridae	Deraeocoris ruber L. F. Anthocoridae	Orius sp.	Anthocoris nemorum L.	" sp. — larvae	F. Nabidae	Nabis apterus F.	", limbatus Dahlb.	F. Pentatomidae Picromerus bidens L. —	larvae	imago	Coleoptera	F. Camendarade larvae	F. Theridionidae	Theridion ovatum	(CLERCK.)	(L.)	F. Linyphiidae Linnmhia triamanlamic	(CLERCK.)	Linyphia peltata	(WIDER)	Linyphiidae gen. sp. Bathyphantes nigrinus	(Westr.)	F. Araneidae	Araneus sp.	r. Tetragnatnaae Pachygnatha degeeri	Sund.

Parasites	Cassida rubiginosa Müll.	Cassida vibex L.	Cassida viridis L.	Cassida flaveola Thunba.
	Egg Larva Pupa Imago	Egg Larva Pupa Imago	Egg Larva Pupa Imago	Egg Larva Pupa Imago
F. Lycosidae				
F. Thomisidae				
Xysticus bifasciatus				
C. L. Koch	    + 	     	     	1
Misumena tricuspidata	-			
(F.) F. Salticidae	   	    -		· 
Evarcha arcuata				
(Clerck.)	+	     	 	1
Opiliones				
F. Fratangraae Phalangium sp.	  -  -		-	+
Acari				
F. Parasitidae				
Poecilochirus necrophori			•	
VITZ. Peraamasus sententrio-	    - 	-	+	+
	    + 	+	     	+
F. Trombiculidae				
Trombicula sp.	     			
F. Trombidudae	- -	-	 	+
F. Eruthraeidae				
Leptus sp.				+
Erythraeus sp.	1 1 1			+
F. Anystidae				
Anystis sp.	    + 		 	+

were good and consequently a low degree of egg reduction by hymenoptera was observed.

Six genera and species of parasitic hymenoptera were found in the eggs of investigated cassids (Table XVII) and among them only Foersterella flavipes Förster is a species common with those quoted by other workers (Table XVI); five others were indicated for the first time, among them Foersterella erdoesi Bčk. is a species new to fauna of Poland. Table XIX presents the percentage share of individual genera and species of hymenoptera in the reduction of cassid eggs in the years 1968—1971. Foersterella flavipes Förster is a decisively dominating species in the constant of

Hymenoptera usually lay one egg to the cassid eggs, two specimens of parasites in one egg of C. rubiginosa Müll. and C. viridis L., and even four specimens in one egg of C. flaveola Thunbg. being sporadically found. It was interesting to compare the length of cassid egg development (Table IV) with that of parasitic hymenoptera (Table XX). The results of observations carried out in 1969-1971 showed that the development of a parasite was always longer than the period of embrional development of cassid eggs, this difference ranging from 1 day in the eggs of C. flaveola Thunbe. to 13 days in those of C. vibex L. These observations in a measure agree with the results of Bilewicz (1960) who claims that the development of a parasitic hymenoptera took almost twice as long as the embrional development of a bug. It was also found that in 1970— 1971 the emergence of the first specimens of hatched hymenoptera occurred in the last days of June, a maximum of hatching was observed in the first half of July, in the second half a slight decrease was noted in the numbers, and about the middle of August the last specimens of the parasite were already hatched. In 1969 under the influence of strong drought in spring and summer (Budzi-SZEWSKA, PRZEDPEŁSKA, 1970) their emergence was noted as late as the end of July and occurred only up to the middle of August.

As it was already mentioned another biotic factor which played a role in the reduction of eggs was mortality brought about by the disturbances in the development (Table XVIII). Probably, these disturbances were effected by low temperatures, and rains in spring 1970 and 1971 (figs. 9, 10). In 1970 mortality of eggs ranged from 0.36 per cent with C. viridis L. to 14.00 per cent with C. flaveola Thunber. In the next year these values were higher (with the exception of C. flaveola Thunber.) under the influence of a cold and rainy month of June. According to Miksiewicz (1957) also with the Colorado beetle a great number of specimens dies in consequence of uneven development of eggs in the batches.

The third factor reducing the number of eggs of cassids are oophagous

Table XVIII

in the vegetation season 1969

Influence of biotic factors on the degree of reduction of eggs of Cassidinae within the study area on the meadow in the Sąspowska Valley of the Ojców National Park

	Number	Number of eggs		Nu	Number of reduced	e peonpe	eggs		Number of eggs	of eggs
Species	initial	%	damaged	%	dead	%	parasi- tized	%%	final (larvae)	%
Cassida rubiginosa Müll Cassida vibex L.	1985 1209	100.00	56 74	2.82 6.12	7	0.36	164 58	8.26	1758 1077	88.56

Cassida rubiginosa Müll.	3718	100.00	1	-	102	2.74	867	23.32	2749	73.94
Cassida vibex L.	688	100.001	1	1	22	2.47	337	37.91	530	59.65
Cassida viridis L.	1512	100.001	12	62.0	19	1.26	746	49.34	735	48.61
Cassida flaveola Thunbg.	1786	100.001	9	92.0	110	14.00	271	34.48	399	50.76

Cassida rubiginosa Müll.	1988	100.00	54	2.72	77	3.87	341	17.15	1516	76.26
Cassida vibex L.	472	100.00	1	1	37	7.84	92	16.10	359	90.92
Cassida viridis L.	505	100.00		1	26	5.15	210	41.58	569	53.27
Cassida flaveola Thunbg.	83	100.001	-	1	<b>c</b> 1	2.41	26	31.33	55	66.26

Table XIX

Percentage share of individual genera and species of parasitic Hymenoptera in the reduction of eggs, larvae and pupae of Cassidinae, collected within the study area and outside it on the meadow in the Saspowska Valley of the Ojców National Park, in the years 1968-1971

	Cassida flaveola Thunbg.			1	1	1	100.001				1	1
pae			_		1	_	82		87		)4	
Larvae and Pupae	Cassida viridis L.		-				ò	,	10.28	:	80.94	
Larvae	Cassida vibex L.		1		1		18.18		1	81.82	1	
	Cassida rubiginosa Müll.		1	.	1		2.07		94.93	1	1	
	Cassida flaveola Thunbg.	1	07.0	1.50	1	1	0.75				1	97.00
Eggs	Cas <b>sid</b> a viridis L.	1	37.06	47.98	7.83		7.04			-	1	60.0
· 图	Cassida vibex L.		72.46	23.19	1	1.45	1.45		1	1	1	1.45
	Cassida rubiginosa Müll.		84.20	13.16		1.32	1.32		1	-	1	
Stages	Species of the cassid Parasite		Foersterella flavipes (FÖRSTER)	Foersterella erdoesi Bok.	Foersterella sp.	Pedobius sn.	Entedon cassidarum RATZ.	Tetrastichus cassidarum	(RATZ.)	Achrusocharis sp.	Subenolenis sn.	Ferrierella sp.

Development of parasitic Hymenoptera in egg batches of Cassidinae within the study area on the meadow in the Sąspowska Valley in the Ojców National Park

Sp	oecies	Committee of the same of	a rubi Müll.	ginosa	Cassi	da vib	ex L.	Cassid	la viri	dis L.	Cassio Ti	da fla	
of			min.	max.	_ X	min.	max.	x	min.	max.	x	min.	max.
VV	III. 1969 III. 1970 III. 1971	28·0 31·4 31·3	22 19 19	41 54 43	$34 \cdot 2 \\ 34 \cdot 9 \\ 31 \cdot 2$	.26	42 49 43	34·8 34·1	23 26	49 39	22·0 19·0		30

animals namely *Microtrombidium* sp. and *Phalangium* sp. (Table XVII). The specimens of both genera were fairly often encountered on the leaves of foodplants of cassids among egg batches and in a few cases destruction of eggs by them was observed. The observations of Miksiewicz (1957) also showed that certain species of genus *Phalangium* damaged the eggs of the Colorado beetle. It is supposed that the activity of feeding of these oophagous animals increases at favourable weather since it is indicated by percentage values of damaged eggs of *C. rubiginosa* Müll. (2·82 per cent) and *C. vibex* L. (6·12 per cent) in 1969 and *C. rubiginosa* Müll. (2·72 per cent) in 1971 as compared with relatively low values with *C. viridis* L. (0·79 per cent) and *C. flaveola* Thunber. (0·76 per cent) in 1970 (Table XVIII).

# 2. Enemies of larvae and pupae

The most numerous group of reducers have the larvae of cassids while the pupae are attacked in a less degree. The following systematic composition of these reducers (Table XVII) was found: parasitic hymenoptera of the superfamily Chalcidoidea and nematodes of the family Mermithidae, predatory bugs (Hemiptera), beetles (Coleoptera), spiders (Araneida), and mites (Acari), and moreover a quite separate group-microorganisms. The list elaborated by other authors (Table XVI) differs from the above-mentioned one with the absence of Coleoptera and Acari as predatory reducers of cassids.

The evaluation of the degree of the reduction of larval instars and of pupae of cassids was carried out in 1969—1971 within the study area on the meadow. It was found (Table XIII) that the strongest reduction basically occurred in the first larval instar or sometimes in the stage of egg. The reduction was constantly

Table XXI

Evaluation of the degree of reduction of cassid larvae\* by the biotic factors under laboratory conditions (specimens collected outside the study area on the meadow in the Saspowska Valley of the Ojców National Park)

Species		Cas	ssida rubig	jinosa Mü	LL.				Cassida	vibex L.					Cassida	viridis L.				Ca	ssida flave	eola Thun	BG.	
Date of	Larvae obser-		Redu	icers		Imagi- nes	Larvae obser-		Red	ucers		Imagi- nes	Larvae obser-		Red	ucers		Imagi- nes	Larvae obser-		Red	ucers		Imagi
investi-	ved	N	M	Ρ .	Н	hatched	ved	N	M	P	Н	hatched	ved	N	M	P	Н	hatched	ved	N	M	P	Н	hatched
gations	Number	Number	Number	Number	Number	Number	Number	Number	Number	Number	Number	Number	Number	Number	Number	Number	Number	Number	Number	Number	Number	Number		Numbe
	%	%	%	%	%	1 /0	%	%	%	%	%	%	%	%	%	1 %	%	%	%	%	%	%	%	%
VI—IX.	147	55 37·41	10 6·80	3 2.04	33 22·45	46 31·30	61 100·00	$\frac{14}{22.95}$	5 8·20	3 4·92	20 32·79	19 31·14	39 100·00	8	6 15·38	4	16	5	_				_	_
1968	100.00	37.41	0.90		$\frac{2243}{20}$	121	38		8.20	4.92	32.19			20.51	19.38	10.26	41.03	12.82						
VI—IX. 1969	181 100·00	3.87	1.66	30 16·57	11.05	66.85	100.00	2.63	7.89	23.68	8 21·06	17 44·74	35 100·00	2.86	8.57	6 17·14	20 57·14	14.29			_	_	_	-
VI—IX.	264	58	44	9	60	93	108	10	12	3	40	43	114	5	12	4	84	9	15	1	8	1	4	1
1970	100.00	21.97	16.66	3.41	22.73	35.23	100.00	9.26	11.11	2.78	37.04	39.81	100.00	4.39	10.53	3.51	73.68	7.89	100.00	6.67	53.33	6.67	26.66	6.67
VI—IX.	168	12	1	11	32	112 66-66	75	2	1	8	22	42	108	2	5	13	78	10	6	_	2	_	3	1
1971	100.00	7.14	0.60	6.55	19.05	. 00.00	100.00	2.67	1.33	10.67	29.33	56.60	100.00	1.85	4.63	12.04	72.22	9.26	100.00	_	33.33	_	50.00	16.67

Explanations: \* - evaluation of reduction of larvae and pupae (which developed from them) was carried out together

N — Nematodes

M — microorganisms

P — predators (concerns the larvae damaged by them under field conditions)

H — Hymenoptera

A. Kosior Acta Zoologica Cracoviensia XX/9 much higher with the larvae: C. rubiginosa Müll. (48·87—63·08 per cent) and C. vibex L. (37·46—56·08 per cent) (with one exception); with C. flaveola Thunbg. this arrangement changed in successive years, while with C. viridis L. the reduction of eggs always exceeded that of the larvae. In consecutive larval instars the percentage reduction constantly decreased, showing some increase with C. viridis L. in the fifth larval instar. The investigations on the Colorado beetle by Kaczmarek (1955) also showed that there was an extreme dominance of damages to eggs and larvae of the first instar in the general picture of reduction. The degrees of reduction of separate development stages found by Karg and Trojan (1968) with the Colorado beetle showed the values very similar to those obtained with cassids.

In 1969—1971 the curve of the reduction of development stages of cassids shows the shape of the capital L (fig. 18). This shape is a little changed by the prevalence of the reduction of eggs over that of larvae especially with C. viridis L. KARG and TROJAN (1968) explain this course of the courve with the Colorado beetle by irregular intensity of reduction in separate stages of the development of this beetle. The complete reduction of development stages of cassids with regard to the initial number of egg which remained healthy on the leaves of foodplants, was very high and with the investigated species ranged from 98.00-99.50 per cent. The highest values of reduction were found with cassids in 1970 (with the exception of C. vibex L.) when the summer period was particularly unfavourable for the development of these insects (strong and frequent rains, low temperatures). Very similar and high values of the reduction were also found by Karg and Trojan (1968): 93.00 per cent and by Kaczmarek (1955) 96.40 per cent in their studies on the development of the Colorado beetle. In the case of cassids this high degree of reduction was most likely brought about by the fact that the meadow was not mown for a few years and owing to a rich dense layer of vegetation favourable conditions prevailed for the development of reducers of cassids. It was found that seasonal changes occurred in the reduction of cassids since in the vegetation season the space structure of larvae of these beetles changed from a concentrated to dispersed (accidental) one, and owing to this fact connected with a considerable increase in the density of larvae (cf. Tables IX-XI) their contacts with the reducers and consequently the degree of reduction also increased. This phenomenon is also stressed by WE-GOREK and SZMIDT (1966) in their studies on the Colorado beetle.

Observations and laboratory cultures of development stages of cassids carried out in the years 1969—1971 with specimens collected on the meadow in the Sąspowska Valley (outside the study area) enabled the determination of the percentage share of individual groups of reducers in the reduction of larvae and pupae of these beetles (Table XXI). These relations are surely different within the unmown study area but no other way of studying this problem was available. It was found that in the reduction of these development stages the greatest role is played by parasitic hymenoptera. In the years of investigation the degree of the reduction of larvae of *C. rubiginosa* Müll. ranged from 11·05—

22·73 per cent, of *C. vibex* L. from 21·06—37·04 per cent, of *C. viriāis* L. from 41·03—73·68 per cent, and of *C. flaveola* Thunbg. from 26·66—50·90 per cent. It was observed that out of the four species the larvae of *C. viriāis* L. were most strongly parasitized throughout the years of the investigations.

In the larvae and papue of cassids in laboratory cultures representatives of four genera and species of hymenoptera were found (Table XVII). Among them only two: Entedon cassidarum RATZ. and Tetrastichus cassidarum RATZ. were also found by other workers (Table XVI), while Achrysocharis sp. and Sphenolepis sp. were noted for the first time. The percentage share of these individual genera and species of hymenoptera in the reduction of larvae and pupae is presented in Table XIX. Tetrastichus cassidarum RATZ. decisively dominates with C. rubiginosa Müll. (94.93 per cent), Achrysocharis sp. with C. vibex L. (81.82 per cent), Sphenolepis sp. with C. viridis L. (80.94 per cent), and Entedon cassidarum RATZ. with C. flaveola Thunbg. (100.00 per cent). Entedon cassidarum RATZ. with C. rubiginosa Müll. and C. viridis L., Achrysocharis sp. only with C. vibex L., and Sphenolepis sp. only with C. viridis L.

The above-mentioned parasitic hymenoptera deposit 1—23 eggs in the bodies of the larvae of *C. rubiginosa* Müll., 3—65 eggs in those of *C. vibex* L., 1—28 eggs in *C. viridis* L., and 5—9 eggs in *C. flaveola* Thunbg. The mean number of 9·1, 18·6, 17·4, and 7·0 eggs respectively falls to one larva of cassids. Therefore, the report of Kleine (1918) that in one larva of *C. nebulosa* L. on the average 4—5 hymenoptera develop, seems strongly doubtful. The data of the present author agree with the observations of Kościelska (1966) who (for insects in general) reports that parasitic hymenoptera lay one to some scores of eggs in the bodies of host animals.

In the course of 4-year investigations it was found that hymenoptera hatched and left the bodies of larvae and pupae of cassids 3—5 weeks after the moment of egg laying. The behaviour of parasitic larvae of cassids in the period before the hatching of hymenoptera is worth noting. Their motion and feeding activity gradually declines, they strongly stick with the ventral side to the surface of leaves, become motionless, and their bodies grow brown (pl. XXXII, A). Similar symptoms were also found by Bilewicz-Pawińska (1969) in the larvae of bugs occurring on rye. The emergence of first hymenoptera is usually observed in the second half of July and the maximum appearance in August; about the middle of September last specimens of the parasite are noted. The present results are essentially consistent with the observations of Kleine (1918) on the phenology of the emergence of parasitic hymenoptera from the larvae of C. rubiginosa Müll and C. nebulosa L. and with those of Bilewicz-Pawińska (1969) on hymenoptera from the larvae of bugs occurring on rye.

It should be also stressed that a part of hymenoptera hatches in summer (they have two generations in a year) and only a part as late as in spring of the next year (after an almost 10-month diapause, only one generation). The spring emergence, contrary to that in summer, had the character of mass appearance.

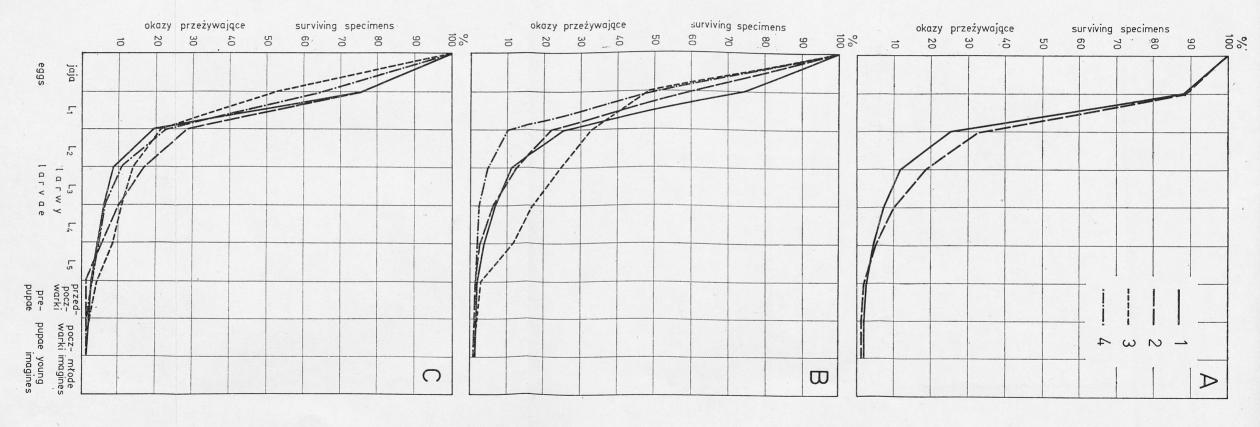


Fig. 18. Reduction of the development stages of Cassids in the study area on the meadow in the Sąspowska Valley of the Ojców National Park: A — in the vegetation season of the year 1969, B — in the vegetation season of the year 1970, C — in the vegetation season of the year 1971, 1 — Cassida rubiginosa Müll., 2 — C. vibex L., 3 — C. viridis L., 4 — C. flaveola Thunba.

BILEWICZ-PAWIŃSKA (1969) obtained a similar result in the study on *Lygus* rugulipennis Popp. Moreover, she found that on the average 30 per cent or even more bugs of this species occurring on a rye field, dies parasitized by hymenoptera of the genus *Leiophron* Nees. This result is highly consistent with the results of the present author, obtained in his study on the degree of parasitization of larvae and pupae of cassids (Table XXI).

Parasitic nematodes of the family Mermithidae play an important role in the reduction of development stages of cassids. In the period of investigations the degree of reduction of larvae and pupae brought about by these nematodes (Table XXI) ranged from 3·87—37·41 per cent with C. rubiginosa Müll., 2·63—22·95 per cent with C. vibex L., 1·85—20·51 per cent with C. viridis L. and in 1970 6·67 per cent with C. flaveola Thunbg. The table shows that the development stages of C. rubiginosa Müll. were attacked most seriously. With regard to the parasitic nematodes of cassids a short reference was only found in the work of Kaufmann (1933), who observed their presence in the development stages of C. nobilis L. (Table XVI) Moreover, it should be mentioned that Mermithidae are also frequent parasites of other beetles: eg. of Longitarsus Latr. (Warchałowski, 1959), Colorado beetle (Węgorek, 1959, Sandner, Stanuszek, 1970, Koval, 1969), and of Gaurotes virginea L. (Starzyk, 1970).

A comparision of the results of the present author with the data of some workers on the Colorado beetle indicates that according to Wegorek (1959) mortality of the larvae of this beetles amounts to as many as 70 per cent, while Sandner and Stanuszek (1970) report that the mean value of reduction is 30.6 per cent, in some regions amounting to 50 per cent (Kraków province). On the other hand Charčenko (1968) found that the degree of the infection of some insects is usually about 40 per cent. This comparison shows that the results of the author (Table XXI) are to some extent consistent with the data

of SANDNER, STANUSZEK, and CHARČENKO.

Laboratory cultures showed that the larvae and pupae of cassids are parasitized by three genera of nematodes: Hexamermis Stein., Mermis Duj., Agamomermis Stein. (Table XVII). Their percentage share in the reduction of cassids is presented in Table XXII. It was found that Hexamermis sp. (pl. XXXII, B, C) dominates with C. rubiginosa Müll., C. vibex L., and C. viridis L., while Agamomermis sp. with C. flaveola Thunbg. The observations of Wegorek (1959), Charčenko (1968), and Koval (1969) also support the fact of the dominance of Hexamermis sp. over other nematodes. In one larva of C. rubiginosa Müll. 1.7 nematodes are found on the average, with C. vibex L. 1.6, with C. viridis L. 3.4, and with C. flaveola Thunbg. 4.0 nematodes. The total number of nematodes per 1 larva ranges from 1 to 9. It was observed that body length of parasites depended on their number in the body of larvae of host insects. It is supported by the observations of Koval (1968) who also found this dependence: if 1—4 nematodes developed in a larva their body length was 70—90 mm, while if 1 nematode was found, its body length was 170—200 mm.

The life cycle of nematodes is synchronized with the development of host

Percentage share of individual genera of parasitic Nematodes in the reduction of larvae and pupae and of imagines of Cassidinae, collected within the study area and outside it on the meadow in the Sąspowska Valley of the Ojców National Park in the years 1968—1971

Development stages		Larvae a	and Pupas	)		Imag	gines	
Species of the cassid Parasite	Cassida rubigino- sa Müll.	Cassida vibex L.	Cassida viridis L.		Cassida rubigino- sa Müll.	Cassida vibex L.	Cassida viridis L.	Cassida flaveola Thunbg.
Hexamermis								
sp.	96.00	100.00	100.00	_	14.29	a		
Mermis sp. Agamomer-	2.00	_	_		85.71	_	=	_
mis sp.	2.00	_		100.00		<u> </u>	_	<u> </u>

animals and as it is fairly interesting, it should be shortly discussed. The development cycle of Hexamermis sp. and Mermis sp. to a certain degree differ from each other and their course was very particularly described by Charčenko (1968). The life-cycle of Hexamermis sp. takes 1 year and shows 5 stages: embrional, pre-parasitic (invading), parasitic, post-parasitic larval, and the stage of sexual maturity. Larvae hatch (for the most part in May and June) from eggs deposited by females in the soil, get on the leaves of foodplants, and attack host insects. The body length of larvae is usually 1-2 mm. They usually pierce the integument of the body of host larvae on the line of contact of segments since the cuticula is thin there. Host animals are usually attacked by nematodes in younger larval instars though the attack may also happen with older larvae. Field observations and laboratory cultures showed that the attack on cassid larvae took chiefly place in the second and third instar, while in the fourth and fifth ones it was very rare. The invasion may also occur through the mouth or anus. Nematodes get through to the haemocoele and feed endoosmotically with fat substances of the host. As the parasites grow they completely fill the haemocoele of the larvae whose body weigth considerably decreases. Owing to increasing body length the nematodes curl up in balls or coils and so they remain up to the moment of leaving the body of host animals.

The development of parasitic larvae of eelworms in the bodies of cassid larvae occurred in about one month or sometimes longer and principally was as long as the development of the latter (cf. Table IV). The emergence of nematodes in wet years (1968, 1970) was noted from the beginning of July, a maximum being observed in the first decade of August, and a decline at the end of this month. In dry years (1969, 1971) the appearance of first eelworms was observed as late as at the beginning of August, maximum numbers in the second half of this month, the last specimens of the parasite being observed at the first days

of September. A distinct agreement occurs between the results of the author and those obtained by Charčenko (1968) and Koval (1969) who found that a mass appearance of post-parasitic nematode larvae was observed in July and August. The nematodes usually leave the body of host animals during rain or at morning dew. They get out piercing the integument of the host or through mouth or anus. Almost 100 per cent of cassid larvae die in the course of the emergence of nematodes; the majority of them die because of nutritive crisis and the remaining ones in consequence of secondary microbiological infection of wounds. The nematodes go down to the soil, moult, and develop into sexually mature specimens.

Mermis sp. shows a characteristic way of egg-laying. In the periods of increased air humidity females get out of the soil on plants and lay eggs under the influence of light incitement. Unlike other Mermithidae the eggs of Mermis sp. have egg sheds with ramifying processes which stretch out and stick to leaf surface. They are the so-called invading eggs, containing larvae which attack host animals. The latter eat eggs with food and when the shed is digested in their intestines the larva gets out and pierces through to haemocoele. Its further development is identical with that of Hexamermis sp. It is supposed that the development of Agamomermis sp. is similar to that of both eelworms mentioned above.

The group of predators includes a very great number of species and considerably contributes to the reduction of larvae of the investigated species of cassids. In the period of investigation the degree of reduction (Table XXI) amounted to 2.04—16.57 per cent with C. rubiginosa Müll., 2.78—23.68 per cent with C. ribex L., 3.51—17.14 per cent with C. riridis L., and 6.67 per cent with C. flaveola Thunber. In the opinion of the present author these results are strongly lowered since the larvae collected on the meadow with the aim of the evaluation of their reduction by biotic factors (under laboratory conditions) were chiefly in the third, fourth, and fifth instar, therefore, in the period when they were not so violently attacked by predators as they were in the first and second instar. Moreover, a great number of larvae killed by predators fell down from foodplants to the ground and therefore were not collected.

Among the predators the bugs bring about the greatest reduction of cassid larvae. They damage the larvae by sucking out the content of their bodies and throwing away empty integuments. The occurrence of 7 genera and species of bugs was noted within the study area, they all contributing to the reduction in the number of cassid larvae (Table XVII). Particular activity of feeding was observed with Anthocoris nemorum L., Nabis apterus F., Nabis limbatus Dahlb., and Picromerus bidens L. (pl. XXXII, B). The last species, unlike the first ones, mainly attacks the larvae from the third to fifth instar.

Picromerus bidens L. deserves special attention. At the end of June 1967 the meadow was invaded by the larvae of this species which to a very great degree influenced the number of cassid larvae in July. Beginning from the end of July the emergence of imagines of bugs was observed and in August they

strongly reduced the larvae of the investigated species. It was distinctly visible by an unusual course of the curve of numbers of larvae, especially of C. rubiginosa MÜLL. (fig. 6). In summer the number of bugs ranged from 200 specimens at the beginning of summer to about 50 at the end of August. Thus additional observations were carried out on the meadow and in the laboratory with the aim of the determination of the average number of cassid larvae daily killed by a nymph and imago of Picromerus bidens L. The observations showed that under laboratory conditions one nymph sucked out on the average 2.5 larvae in 24 hours and on the meadow only 1.2 larvae on the average. Similarly, the imago of this bug sucks out as many as 3 larvae in the laboratory and 1.3 larvae under field conditions. The total number of larvae sucked out by a nymph was 1 to 4 specimens in 24 hrs. and by an imago 1 to 6 specimens. Very similar result was obtained by Schumacher (1910) who found that 1 bug sucks out on the average 1 caterpillar of Symphyta in 24 hrs. He calculated that 20 specimens of bugs may consume as many as 180 caterpillars in 3 months. Therefore, it is clear that the considerable number of bugs of Picromerus bidens L. brought about an enormous reduction of cassid larvae on the meadow in Ojców in 1967.

In the period of investigation it was found that from the number of net spiders 8 genera and species reduced the cassid larvae while from the wandering spiders only 4 genera and species (Table XXXVII). The share of the former group in the reduction of larvae is by far greater, such species as Theridion ovatum Clerck., Th. bimaculatum L., and Linyphia triangularis Clerck. being particularly important. Out of the latter group the greatest share in the reduction of larvae had Evarcha arcuata Clerck. The spiders of the first group attacked the larvae in the second, third, and fourth instar, while those of the second group chiefly the fifth instar. After being sucked out the prey of net spiders remained in the net while the wandering spiders threw it away.

Unlike bugs and spiders predatory larvae of beetles of the family Cantharidae as well as mites (Acari) (Table XVII) do not suck out their pray but eat it. They chiefly attack the larvae of cassids in the first and second instar, and only exceptionally in the third and fourth instar. Out of seven genera and species of predatory mites Poecilochirus necrophori VITZ., Pergamasus septentrionalis Oud., Microtrombidium sp., and Anystis sp. deserve particular attention. The report of Kaczmarek (1969) should be mentioned in discussing the share of predatory beetles in the reduction of cassids: this worker claims that ladybirds also among others feed on the larvae of these beetles. But this fact was not supported by field observations carried out by the present author.

Microorganisms form a quite separate group of reducers of the larvae and pupae of cassids. Their percentage share in the reduction of development stages depend to a great degree on weather conditions in successive years of investigations. Often rains and fairly low temperatures unfavourably influence the development of larvae and pupae bringing about its lengthening. Owing to such unfavourable situation the larvae and pupae become less resistant to infection by microorganisms and consequently to fungi. The degree of their reduction

brought about by microorganisms (Table XXI) amounted to 0.60—16.66 per cent with *C. rubiginosa* MÜLL., 1.33—11.11 per cent with *C. vibex* L., 4.63—15.38 per cent with *C. viridis* L., and 33.33—53.33 per cent with *C. flaveola* Thunber. The last values are very high since a very small numbers of larvae of this species were observed (it was extremely difficult to find them under field conditions).

The evaluation of the degree of reduction in the larvae and pupae of cassids by biotic factors, carried out under laboratory conditions in the years 1968—1971 showed a distinct dependence between the value of the percentage share of separate factors of this reduction (Table XXI) and the weather conditions of a given year (figs. 7—10). It was found that in years with a considerable number of rains and frequent decreases in the temperature (1968 and 1970) the percentage share of parasitic nematodes, hymenoptera (with the exception of *C. viridis* L. in 1968 and *C. flaveola* Thunber. in 1970), and microorganisms were much higher than those found in years with dry weather (1969 and 1971), while in case of the percentage share of predators a reverse situation was noted.

Moreover, it was found that nematodes and hymenoptera attacked most strongly the fifth instar and pre-pupae, microorganisms pre-pupae and pupae, and the predators the cassid larvae of the first and second instar.

## 3. Enemies of imagines

It was found in the period of investigation (1966—1971) carried out within the study area on the meadow that the imagines of cassids are reduced by the following biotic factors: parasitic diptera of the family *Tachinidae*, nematodes of the family *Mermithidae* (Table XVII), and, after the return on the meadow, by natural mortality in consequence of emaciation connected with wintering.

The parasite Dufouria chalybeata Meig. (Diptera) (pl. XXXII, B) plays the greatest role in modulating the number of the population of imagines C. rubiginosa Müll. Table XXIII presents the degree of the reduction of beetles brought about by this parasite in 1967-1970. It was found that this reduction was relatively high ranging from 62.57-85.00 per cent. The development of the larvae of this parasite is exceptionally interesting. It deposits eggs into the body of the larvae of C. rubiginosa Müll. in their fourth or fifth instar. Afterwards the development stages of the fly pass through the pupae of the beetles to the imagines and leave them as adult larvae in spring. In the period of that final development the larvae devour almost all internal organs of beetles. Laboratory observations showed that a mass emergence of diptera larvae from empty abdomens of imagines occurs every year regularly in the first half of May. It is also supported by the fact that in the period of 6-year investigations a strong and rapid decrease in the number of adult beetles was always noted in the first half of May (cf. figs. 5-10). The emergence of larvae in the period of increased air humidity (after rain, with morning dew). The emergence from the abdomens of beetles takes several to some scores of seconds, then the larvae pass on the under surface of leaves where they pupate within 1-3 hrs. After 2-3 weeks

Natural mortality and reduction of adult imagines <sup>1</sup> of Cassida rubiginosa Müll. by parasitic larvae of Dufouria chalybeata Meig. and of Cassida flaveola Thunbeg. by those of Dufouria nitida von Röd. (Diptera) in the spring period within the study area on the meadow in the Saspowska Valley of the Ojców National Park

Species		Cassida rubiginosa Müll.					Cassida flaveola Thunbg.			
Specimens		ural tality	Paras	itized	Hea	lthy	Paras	sitized	Hea	lthy
Period of investigations	Numb	er %	Numbe	er %	Numb	er %	Numb	er %	Numb	er %
26. IV—19. V. 1967	4	4.00	85	85.00	11	11.00	_	_		_
25. IV—9. V. 1968	18	18.00	67	67.00	15	15.00	-	_	-	_
6—20. V. 1969	139	22.60	445	$72 \cdot 36$	31	5.04	_			
5—26. V. 1970	727	23.56	1931	62.57	428	13.87	4	20.00	16	80.00

Explanations: 1 — young specimens which have wintered

imagines of diptera hatch from cocoons. Parasitized beetles die immediately after the emergence of larvae or after a few hours (pl. XXXII, B). The sex ratio in these beetles is 1:1.

In 1970 also the presence of the parasite *Dufouria nitida* v. Röd. (*Diptera*) was found in four specimens of beetles of *C. flaveola* Thunbg. (Table XXIII). Because of the small number of all beetles collected, the degree of the reduction amounted to as many as 20.00 per cent. The course of development of this parasite is identical with that discussed above. The presence og this parasite was found by Kaufmann (1933) and Jolivet (1946) in the development stages of *C. nobilis* L. (Table XVI).

In the period of investigations only several instances of the emergences of parasitic nematodes from the imagines of *C. rubiginosa* Müll. were noted. Three nematodes hatched from two adult imagines in spring, this showing the possibility of invading beetles during wintering. This is unquestionably supported by the results of investigations of Koval (1969) on the Colorado beetle and of Warchalowski (1959) on *Longitarsus* Late. Moreover, two nematodes hatched from two young imagines in summer, thus the invasion of cassid larvae by the larvae of the parasite surely occurred very late, this being also found by Charčenko (1968) in his study on the parasites of insects.

The percentage share of parasitic nematodes in the reduction of imagines of *C. rubiginosa* Müll. is presented in Table XXII. It was found that contrary to larvae and pupae *Mermis* sp. (85·71 per cent) dominates in imagines, the share of *Hexamermis* sp. amounting to about 15·00 per cent only.

Table XXIII presents natural mortality of imagines of *C. rubiginosa* MÜLL. brought about by the emaciation after the too long period of diapause in the years 1967—1970, registered after the return of beetles from wintering. In the period of investigations this mortality amounted to 4·00—23·56 per cent.

The highest one (23.56 per cent) occurred in spring 1970 and was probably effected by the too long winter period and unfavourable weather conditions prevailing on the meadow in the month of May (cf. fig. 9). On account of the high rate of mortality of the imagines of *C. rubiginosa* Müll. brought about the invasion of diptera, connected with natural mortality due to the emaciation, the degree of survival of adult imagines was very low ranging from 5.00 to 15.00 per cent in the years 1967—1970 (Table XXIII).

VII. BIOENERGETICS OF DEVELOPMENT STAGES OF C. RUBIGINOSA MÜLL. AND C. VIBEX L.

### 1. Consumption, excreting facces, and assimilation

On the basis of investigations carried out on the development of larvae and young imagines of *C. rubiginosa* MÜLL. and *C. vibex* L. under laboratory conditions, the amount of consumed food and excreted faeces as well as the increase in their body weight were evaluated.

It was found (Tab'e XXIV) that in the whole period of development a larva of *C. rubiginosa* MÜLL. consumes 110·1 mg of leaf biomass, i.e. 13·0 mg of dry matter, this corresponding to 58·9 cal while a larva of *C. vibex* L. consumes 103·2 mg of biomass, 12·2 mg of dry matter, and 55·2 cal. Thus the size of consumption is very similar with both species. Similar nutritive cultures carried out by KLEINE (1915, 1920) with the larvae of *C. nebulosa* L. showed that the value of total consumption, necessary for their development, was 95·5—136·2 mg of leaf biomass, a result consistent with that of the present author.

The share of individual larval instars in the total food consumption is: C. rubiginosa Müll. I — 1·38 per cent, II — 3·12 per cent, III — 7·58 per cent, IV — 22·46 per cent, V — 65·40 per cent; C. vibex L. I — 1·68 per cent, II — 3·06 per cent, III — 8·63 per cent, IV — 20·79 per cent, V — 65·84 per cent. The above data indicate that the rate of food consumption doubles in the successive instars. A maximum degree of consumption and of time of the development was observed in the last larval instar, this being also stressed by Rammner (1934) in his study on C. murraea L. and by Chłodny (1967) on the Colorado beetle. It should be mentioned here that the rate of food consumption is inhibited in the periods of moulting. With an adult larva a strong inhibition and at last a lack of consumption occurs before the pupation. With young imagines of C. rubiginosa Müll. during the first 45 days of their life the consumption amounts to 305·6 mg of leaf biomass, this corresponding to 35·3 mg of dry mass and 157·9 cal, with C. vibex L. these values being 292·3 mg, 33·7 mg, and 151·0 cal respectively.

Since it was not possible to determine the fresh matter of excreted faeces, these values were calculated in dry matter and in calories (Table XXIV). In the course of its development a *C. rubiginosa* MÜLL larva excretes 23.6 cal in the form

Consumption and utilization of food by the larval instars and young imagines (from hatch to the 45th day of life) of cassids

Cassida rubiginosa Müll.

		Consumption		Excre	Assimilation	
Instar mg biomass/	mg dry matter/spe- cimen	cal/speci- men	mg dry matter/spe- cimen	cal/speci- men	cal/speci- men	
		i.			0.00	0.44
L1	1.52	0.20	0.80	0.09	0.36	0.44
L2	3.43	0.41	1.84	0.14	0.63	1.21
L3	8.35	0.98	4.47	0.39	1.57	2.90
L4	24.72	2.91	13.24	1.04	4.30	8.94
L5	72.06	8.48	38.58	3.35	16.72	21.86
Total	110.08	12.98	58.93	5.01	23.58	35.35
YI after 45	305.64	35.26	157.93	11.37	32.97	124.96

### Cassida vibex L.

Ll	1.73	0.23	0.91	0.09	0.32	0.59
L2	3.16	0.37	1.69	0.15	0.51	1.18
L3	8.90	1.05	4.76	0.38	1.86	2.90
L4	21.45	2.53	11.49	1.14	4.24	7.25
L5	67.92	8.00	36.36	3.97	14.81	21.55
Total	103-16	12.18	55.21	5.73	21.74	33.47
YI after 45	292.34	33.73	151.05	10.04	29.43	121.62

Explanations: L1—L5 — successive larval instars YI — young imagines

of excrements and  $C.\ vibex\ L.\ 21\cdot7$  cal. The data in Table XXIV indicate that the amount of excrements increases and almost doubles with the age of larvae. The percentage share of larval instars in the total excretion was:  $C.\ rubiginosa\ M\"{u}LL.\ I - 1\cdot53$  per cent, II - 2·67 per cent, III - 6·66 per cent, IV - 18·24 per cent, V - 70·90 per cent;  $C.\ vibex\ L.\ I - 1\cdot47$  per cent, II - 2·34 per cent, III - 8·56 per cent, IV - 19·50 per cent, V - 68·13 per cent. Young imagines of  $C.\ rubiginosa\ M\ddot{u}LL.$  excreted about 33·0 cal in the period of 45 days, and those od  $C.\ vibex\ L.\ 29\cdot4$  cal.

The food assimilation (A) was calculated using the following formula:

$$A = C - FU$$

where: A — assimilated energy in cal,

C - value of consumed food in cal,

FU — value of excrements in cal.

The total assimilation necessary for the complete larval development of C.rubiginosa Müll. was 35.4 cal and of C.vibex L. 33.5 cal (Table XXIV). The assimilation value increases with an increase in larval biomass, the percentage share of individual instars being: C.vibiginosa Müll. I — 1.24 per cent, II — 3.42 per cent, III — 8.20 per cent, IV — 25.29 per cent, V — 61.85 per cent; C.vibex L. I — 1.76 per cent, II — 3.52 per cent, III — 8.66 per cent, IV — 21.66 per cent, and V — 64.39 per cent. Great values of the assimilation of energy amounting to almost 125.9 cal, with young imagines of C.vibiginosa Müll. and to 121.6 cal with C.vibex L. are remarkable. They are four times greater than the values of excreted faeces.

## 2. Production of the body

Increases in body weight of larvae and young imagines of *C. rubiginosa* MÜLL. and *C. vibex* L. were determined not only in units of biomass but also in dry mass and in calories. It was found (fig. 19) that the content of water in the development

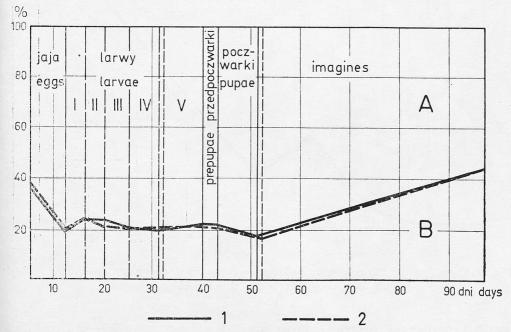


Fig. 19. Content of water (A) and of dry mass (B) in the development stages of the Cassids.

1—Cassida rubiginosa Müll., 2—C. vibex L.

Stages of *C. rubiginosa* Müll. and *C. vibex* L. was very similar. It amounted to 63.58 per cent in eggs of cassids, increased to 81.00 per cent with newly hatched larvae, and decreased to 76.50 per cent in the second instar, and then in the next instars (including the pupa) was within 76.00—80.50 per cent. The highest water content (82.00—83.00 per cent) was noted in newly hatched imagines of cassids. Similar values were also found by Wegorek (1959) in young imagines of the

Colorado beetle. Throughout 45 days of life of young imagines of *C. rubiginosa* Müll. and *C. vibex* L. the water content considerably decreased and after this period was 55.59 per cent and 57.57 per cent respectively.

The calorific value of one specimen of *C. rubiginosa* Müll. and *C. vibex* L. in the course of their development was presented in figure 20. As it shows minimal differences were noted with both species up to the IV larval instar. This value

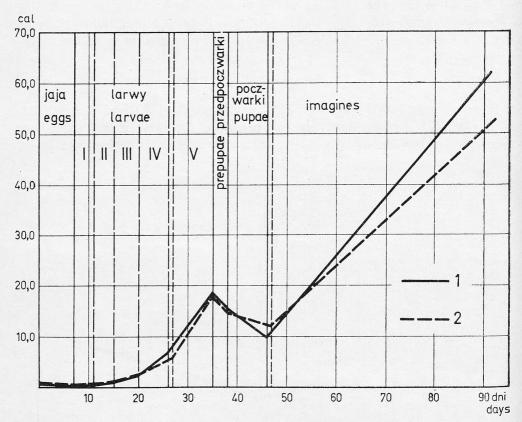


Fig. 20. Calorific value of one specimen of Cassids during its development. 1 — Cassida rubiginosa Müll., 2 — C. vibex L.

was 0.5 cal in eggs, decreased in freshly hatched larvae to 0.1—0.2 cal, then gradually increased, and in the pre-pupae stage was 18.4—19.1 cal. Afterwards a distinct decrease in the calorific value of the pupa and a further one in newly hatched imagines (10.3—12.5 cal/were observed. Throughout the 45 days of life of young imagines their calorific value rapidly increased and amounted to 62.3 cal with *C. rubiginosa* MÜLL. and to 53.3 cal with *C. vibex* L. The course of changes in the calorific value throughout the development of one specimen of *Tribolium castaneum* HBST., presented by KLEKOWSKI, PRUS, and ŻYROMSKA-RUDZKA (1967), is in a measure similar to that in cassids, a distinct difference occurring as late as in young imagines.

Table XXV

Values of body production of the larval instars and young imagines (from hatch to the 45th day of life) of cassids

Species	Casside	a rubiginosa ]	Müll.	Cassida vibex L.			
Instar	mg biomass/	mg dry matter/spe- cimen	cal/speci- men	mg biomass/	mg dry matter/spe- cimen	cal/speci- men	
L1	0.28	0.08	0.40	0.33	0.10	0.52	
L2	0.68	0.19	0.82	0.61	0.14	0.64	
L3	1.50	0.32	1.52	1.57	0.36	1.75	
L4	3.92	0.86	4.84	3.54	0.81	4.13	
$L_5$	11.45	2.85	12.90	12.38	2.81	12.60	
Total	17.83	4.30	20.48	18.43	4.22	19.64	
	* 5.68	6.57	52.02	* 4.17	6.07	40.72	
YI after 45	ΣΔ 8.27			ΣΔ 7.50			

Explanations: L1-L5 — successive larval instars

YI - young imagines

\* — body production calculated from the difference between the final and initial value of the biomass

 $\Sigma\Delta$  — body production calculated from the sum of all increases in biomass within 45 days of investigations.

In a newly hatched larva of C. rubiginosa Müll. mean biomass amounted to 0.2 mg and with C. ribex L. to 0.3 mg, while in the last larval instar to 18.0 mg and 18.7 mg respectively. The initial period of the pre-pupa stage was regarded as a maximum in the development of a larva. The production of biomass (P) was calculated by substracting the initial value of newly hatched larvae  $(P_0)$  from the initial value of pre-pupa biomass  $(P_m)$ , this being expressed in the formula:

$$P = P_m - P_o$$

The biomass of moults (from successive instars) was added to the calculated production value of separate instars and thus the final production of biomass was obtained. It was found (Table XXV) that the larva of C. rubiginosa Müll. Produced 17.8 mg of body biomass in the course of its development, this being 4.3 mg of dry matter and corresponding to 20.5 cal; for a larva of C. ribex L. the respective values were -18.4 mg, 4.2 mg, and 19.6 cal. The following percentage distribution of the total biomass production in successive instars was recorded: C. rubiginosa Müll. I -1.57 per cent, II -3.81 per cent, III -8.41 per cent, IV -21.99 per cent, V -64.22 per cent; C. ribex L. I -1.79 per cent, II -3.31 per cent, III -8.52 per cent, IV -19.21 per cent, V -67.17 per cent. The results obtained for the larvae of both species are very similar, the greatest difference not even exceeding 3.00 per cent. The above data also indicate that the increase in body biomass in separate instars distinctly increases with the age of larvae.

The results obtained in the study on the production of body biomass in young imagines of cassids are fairly striking and need an explanation (Table XXV). The production of biomass calculated according to the above-quoted formula is 5.7 mg with the beetles of *C. rubiginosa* MÜLL. and 4.2 mg with *C. vibex* L.; while its value obtained from the sum of all increases in biomass in the period of 45 days is 8.3 mg and 7.5 mg respectively. As compared with these results

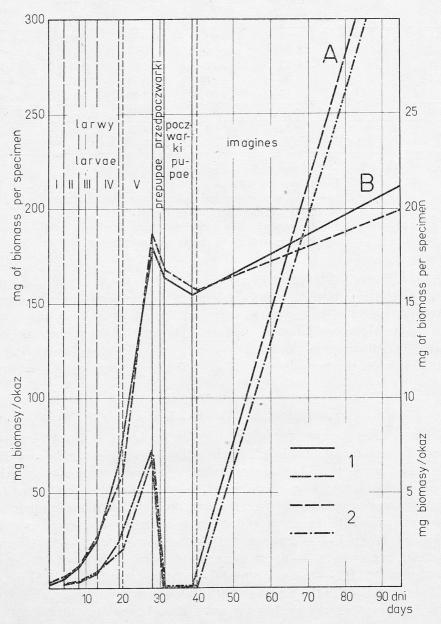


Fig. 21. Consumption (A) and increase in body weight (B) in the development stages of the Cassids. 1—Cassida rubiginosa MÜLL., 2—C. vibex L.

(in miligrams of biomass) the value of body production in miligrams of dry matter is very high in both species. It was observed (cf. fig. 19) that the content of dry matter in the bodies of young imagines increases by 26·00 per cent with *C. rubiginosa* Müll. and 27·00 per cent with *C. ribex* L. throughout 45 days of their life. In consequence, the content of water decreases from 82·64 to 56·30 per cent and from 83·00 to 55·98 per cent respectively. The changes in the value of body biomass of young imagines, observed in the successive days of their life are probably connected with smaller or greater consumption of strongly hydrated food (fresh young leaves of *Cirsium oleraceum* (L.) Scop. being always fed) in which the water content was always 87·00—88·50 per cent. The value of body production measured with energy units was 52·0 cal with the imagines of *C. rubiginosa* Müll. and only 40·7 cal with *C. vibex* L. Contrary to larvae a fairly great difference was found in the value of body production of imagines.

A comparison of the curve of food consumption with the curve of increase in body weight in the development stages of both cassid species is fairly interesting (fig. 21). A distinct positive correlation was found in the course of the curves especially throughout the whole larval stage. It may be observed that an increase in food consumption results in an increase in body weight, their maxima occurring for the body weight at the beginning of the pre-pupal stage and for the consumption a little earlier. In rest periods (pre-pupa, pupa) when the value of food consumption is 0 a distinct decrease in body weight of specimens was also noted. From the moment of hatch of young imagines a very great increase in the food consumption may be observed though it is not connected with an increase in body biomass, which only increases by a few miligrams after 45 days of life of the beetles (cf. Table XXV). It should be also stressed that as it was already mentioned the values of the food consumption and of the increase in body weight are very similar in the development stages of both species. Also a complete development of the investigated species at the constant temperature of 20°C+2·0 observed from the moment of the hatch of larvae to the emergence of young imagines is almost identical and amounts to 39 days with C. rubiginosa Müll. and to 40 days with C. vibex L. According to Gromadzka (1968) at the temperature of 20°C for the Colorado beetle this period was 34 days from the hatch of larvae to the emergence of imagines, this being fairly consistent with the data of the present author.

# 3. Energy budget of the development of cassids

The parameters of the energy budget of larvae and young imagines of C. rubiginosa Müll. and C. vibex L. were calculated on the basis of results of laboratory investigations, and the study of the budget was carried out on the formula (Cheodny, Gromadzka, Trojan, 1967):

$$C = P + R + FU$$

where: C — food consumption,

> P - body production.

 $\mathbf{R}$ - respiration, FU — excrements.

The respiration (R) was calculated from the differences between the assimilation (A) and production (P). The values of parameters of the energy budget expressed in cal/specimen are presented in Table XXVI. It was found with both

Table XXVI

Energy budget of the larval instars and young imagines (from hatch to the 45th day of life) of cassids, calculated from nutritive experiments (cal/specimen)

Cassida rubiginosa MÜLL.

Instar	C	P	R	FU	A
Lı	0.80	0.40	0.04	0.36	0.44
L2	1.84	0.82	0.39	0.63	1.21
L3	4.47	1.52	1.38	1.57	2.90
L4	13.24	4.84	4.10	4.30	8.94
L5	38.58	12.90	8.96	16.72	21.86
Total	58.93	20.48	14.87	23.58	35.35
YI after 45	157.93	52.02	72.94	32.97	124.96

#### Cassida vibex L.

Ll	0.91	0.52	0.07	0.32	0.59
L2	1.69	0.64	0.54	0.51	1.18
L3	4.76	1.75	1.15	1.86	2.90
L4	11.49	4.13	3.12	4.24	7.25
L5	36.36	12.60	8.95	14.81	21.55
Total	55.21	19.64	13.83	21.74	33.47
YI after 45	151.05	40.72	80.90	29.43	121.62

Explanations: L1-L5 - successive larval instars

YI - young imagines

C - food consumption

P - body production

R — respiration

A — assimilation

FU - excrements

species that all elements of the equation showed the lowest values in the firstlarval instar and the highest ones in the last instar, this supporting the opinion that they were connected with the growth of the organism. The values of the respiration are extremely low in the first larval instar and amount to 0.04 cal/specimen with C. rubiginosa Müll and to 0.07 cal/specimen with C. ribex L., indicating remarkably intense increase in their body weight. It should be also stressed that with both species production (P) slightly (5·0 cal) dominates over respiration (R) in the development of larval instars, this being the basic condition of the proper course of this development, while a contrary situation is observed with young imagines since the respiration (R) distinctly prevails over the production (P), the difference between them being  $23\cdot0$  cal with C. rubiginosa MÜLL. and as many as  $40\cdot0$  cal with C. ribex L.

# 4. Coefficients of energy efficiency

The obtained results enabled to calculate the coefficients of energy efficiency (Petrusewicz, 1966). They are presented in Table XXVII. Among them the coefficient of production efficiency (P/C) is most important from the ecological point of view, since it determines the percentage of energy used for the growth of body. The highest coefficient was found with the larvae of the I instar amounting to 50.80 per cent with C. rubiginosa Müll. and to as many as 57.02 per cent with C. vibex L. In the subsequent instars (with an exception of the fourth instar of C. rubiginosa Müll.) it gradually declines reaching the lowest value in the fifth instar: 33.44 and 34.68 per cent respectively. With the larvae of cassids the mean value of this coefficient was 39.97—40.44 per cent, thus being very high as compared with that of the Colorado beetle - 27.70 per cent (Chlodny, Gro-MADZKA, TROJAN, 1967). The present author's results considerably differ from those of CHŁODNY (1967) who claims that with the Colorado beetle the production efficiency increases from the first to third larval instar, than distinctly decreases in the fourth one. He explains this decreased efficiency of production in the last larval instar of the Colorado beetle with intense accumulation of fats in the bodies of the larvae, which are later used as a source of energy during the metamorphosis. On the other hand the efficiency of production is considerably lower with young imagines of cassids amounting to 32.94 per cent with C. rubiginosa MÜLL. and to 26.96 per cent with C. vibex L.

Another highly important coefficient of energy efficiency is that of assimilation (A/C) (Table XXVII) which denotes the percentage of the utilization of consumed energy. It is very high with the larvae of both species and ranges 55·65—67·51 per cent for C. rubiginosa Müll. and 59·28—69·58 per cent for C. vibex L., the mean values being 62·17 and 63·47 per cent respectively. A comparison with the larvae of other insects is very favourable for cassids. Chlodny (1967) found that with Colorado beetle A/C coefficient amounted to 45·40 per cent while Wiegert (1964) claimed that this value was 15·80 per cent with the larvae of Philaenus spumarius L. As compared with the larvae of cassids this coefficient is only slightly higher with the caterpillars of cabbage butterfly amounting to 66·00 per cent (Chlodny, 1967). In the case of young imagines of cassids remarkable high values of the A/C coefficient are observed 79·13 per cent with C. rubiginosa Müll. and 80·52 per cent with C. ribex L. Such great

Utilization of consumed energy by the larval instars and young imagines (from hatch to the 45th day of life) of cassids (per cent)

Cassida rubiginosa Müll.

Instar	$\frac{\mathrm{P}}{\mathrm{C}} \cdot 100$	$\frac{\mathrm{R}}{\mathrm{C}} \cdot 100$	$\frac{\mathrm{FU}}{\mathrm{C}} \cdot 100$	$\frac{\mathrm{A}}{\mathrm{C}} \cdot 100$
L1	50.80	4.85	44.35	55.65
L2	44.90	21.12	33.98	66.02
L3	34.11	30.88	35.01	64.99
L4	36.60	30.91	$32 \cdot 49$	67.51
L5	33.44	23.22	43.34	$56 \cdot 66$
$\overline{\mathbf{x}}$	39.97	22.20	37.83	62.17
YI after 45	32.94	46.19	20.87	79.13

Cassida vibex L.

		1		
L1	57.02	7.46	35.52	64.48
L2	37.76	31.82	30.42	69.58
L3	36.82	24.09	39.09	60.91
L4	35.92	27.18	36.90	63.10
L5	34.68	24.60	40.72	59.28
, <b>x</b> ,	40.44	23.03	36.53	63.47
YI after 45	26.96	53.56	19.48	80.52

Explanations:

 $\frac{P}{C}$  — efficiency of production (percentage of energy used for body growth)

A — assimilation coefficient (percentage of utilization of consumed energy)

 $rac{FU}{C}$  — assimilation coefficient (percentage of released energy)

 $\frac{R}{C}$  — respiration coefficient (percentage of metabolic losses connected with growth)

L1—L5 — successive larval instars

YI - young imagines

values of this coefficient indicate unusual efficiency of these beetles with regard to the utilization of consumed energy.

Also the FU/C coefficient (Table XXVII) is in principle an assimilation coefficient, but contrary to the former one it determines the percentage of energy released by larvae and young imagines, derived by them from a determined amount of consumed energy.

The R/C coefficient (Table XXVII) calculated from the amount of energy consumed by larvae and young imagines of both species determines the percentage value of metabolic losses connected with the growth of specimens. In the

larvae of these species it in principle shows an increase tendency with the exception of some disturbances in the fifth instar with  $C.\ rubiginosa\ M\"ull$  and in the second and fifth instar with  $C.\ rubex\ L$ . The mean value of this coefficient was  $22\cdot20$  per cent with the former and  $23\cdot03$  per cent with the latter. With young imagines of  $C.\ rubiginosa\ M\"ull$  and  $C.\ ribex\ L$  the values of this coefficient are very high, amounting to  $46\cdot19$  and  $53\cdot56$  per cent respectively, thus they twice exceeded the respiration losses calculated for the whole larval stage of both species.

## 5. Respiration metabolism of cassids

One of the parameters included in the study of the productivity was respiraation (R), i.e. the losses of energy connected with metabolism. For a precise evaluation of the amount of energy required for the maintenance of an indivual the knowledge of the respiration quotient (RQ), i.e. the ratio of produced  $CO_2$  to the consumed  $O_2$  is necessary. Its value changes with the growth of a specimen and depends on the quality of combusted food (carbohydrates, fats, proteins). The larvae and young imagines of both species of cassids were continually fed with fresh young leaves of Cirsium oleraceum (L.) Scop. in whose biochemical composition mainly carbohydrates were found (according to dr Myrcha) and hence they showed very high value of RQ. Therefore, in the calculations of the consumed  $O_2$  to energy units, the value of RQ = 0.95, with which 1 ml  $O_2$  corresponds to 4.895 Kcal was taken, according to Myrcha and Stelgwillo-Laudańska (1970).

The highest oxygen consumption per a unit of body biomass (Table XXVIII) was found in the I larval instar amounting to 27.7 mm<sup>3</sup> O<sub>2</sub>/mg/h with C. rubiginosa Müll. and to 25.1 mm<sup>3</sup> O<sub>2</sub>/mg/h with C. vibex L., then its value gradually decreased with an increase in body weight of specimens, its lowest value being found in rest stages: with C. rubiginosa Müll. in the pupa stage (2.8 mm<sup>3</sup> O<sub>2</sub>/mg/h) and with C. vibex L. in the pre-pupa stage (2.4 mm<sup>3</sup> O<sub>2</sub>/mg/h). The value of oxygen consumption increased to 5.5 mm<sup>3</sup> O<sub>2</sub>/mg/h in newly hatched imagines of C. rubiginosa Müll. and to 6.1 mm<sup>3</sup> O<sub>2</sub>/mg/h with C. vibex L., slightly decreasing after 45 days of the life of beetles (to 3.44 and 4.9 mm<sup>3</sup> O<sub>2</sub>/mg/h respectively). Figure 22 gives a graphic illustration of these changes. It was found that the oxygen consumption in successive development stages was very similar with both species, the differences between them (in the third larval instar, in the pre-pupa stage, and with young imagines) being statistically insignificant. The course of the curve of oxygen consumption in separate development stages of cassids is somehow similar to that calculated by Gromadzka (1966) for the Colorado beetle likewise at the temperature of 20.0°C).

The amount of energy used by one specimen in the metabolic processes in 24 hrs. (Table XXVIII) distinctly (with some exceptions) increases with an increase in body weight. In the first larval instar of C. rubiginosa MÜLL. it amounts to 0.6 cal/specimen/24 hrs. while with C. vibex L. to 0.8 cal/speci-

Metabolism expressed in oxygen consumption in the development stages of cassids (at 20.0°C)

\* Cassida rubiginosa MÜLL.

Stage	Number of speci- mens	Body weight in mg of bio- mass/speci- men	$mm^3O_2/mg/h$ $\bar{x}\pm SE$	Cal/speci- men/24hrs.	$ m mm^3O_2/spe-$ cimen/stage	Cal/speci- men/stage
L1	308	0.1857	$27.7 \pm 4.9$	0.6043	493.44	$2 \cdot 42$
L2	214	0.4657	$18.4 \pm 1.6$	1.0067	822.72	4.03
L3	111	1.1491	$17.1 \pm 1.5$	$2 \cdot 3084$	2,358.00	11.54
L4	61	2.6489	$10.8 \pm 0.9$	3.3609	4,119.84	20.17
L5	40	6.5722	$7.4 \pm 1.6$	5.7136	10,504.08	51.42
PP	22	18.0182	$3.0 \pm 0.2$	6.3503	3,891.60	19.05
P	40	16.3667	$2.8 \pm 0.4$	5.3837	8,801.28	43.07
NHI	23	15.4917	5.5 + 0.3	10.0098	30,990.96	151.70
YI after 45	18	21.1700	$3.4 \pm 0.3$	8.5554	78,645.60	384.90

### Cassida vibex L.

Ll	183	0.2828	$25 \cdot 1 \pm 2 \cdot 9$	0.8339	681.60	3.34
L2	87	0.6088	$18.1 \pm 1.6$	1.2945	1,057.92	5.18
L3	60	1.2161	$15.0 \pm 1.4$	2.1430	2,188.80	10.72
L4	38	2.7816	$10.7 \pm 0.6$	3.4966	4,999.68	24.48
L5	34	6.3226	7.9 + 0.7	5.8680	9,590.40	46.94
PP	22	18.7000	$2 \cdot 4 + 0 \cdot 2$	5.2725	3,231.36	15.82
P	31	16.8250	$2.8 \pm 0.3$	5.5345	10,175.76	49.81
NHI	21	15.6857	6.1 + 0.9	11.2408	31,925.52	156.29
YI after 45	15	19.8571	$4.9 \pm 1.1$	11.4308	105,084.00	514.39

Explanations:

L1-L5 - successive larval instars

PP — prepupae

P — pupae

NHI — newly hatched young imagines

YI after 45 — young imagines after 45 days of life

SE — standard error of the measurements of oxygen consumption.

men/24 hrs. Its highest value was noted at the beginning of the pre-pupa stage (this moment being regarded as the maximum of larval development) with the former species (6·4 cal/specimen/24 hrs.) and in the fifth larval instar (5·9 cal/specimen/24 hrs.) with the latter, this being not consistent with the course of the discussed dependences. In the rest stages of both species a decrease in body weight connected with lower energy losses are observed. With newly hatched and 45-day old imagines of *C. rubiginosa* MÜLL. a quite reverse situation was found with regard to the discussed dependence, while with *C. vibex* L. a distinct accordance occurred in this problem. In 24 hrs. almost twofold energy losses were

noted in the imagines as compared with maximal losses of the larvae, amounting to  $10\cdot0$  cal/specimens/24 hrs. with C. rubiginosa MÜLL. and to  $11\cdot4$  cal/specimen/24 hrs. with C. vibex L.

Throughout the development from the hatch from eggs to the emergence of imago a specimen of C. rubiginosa Müll. consumes 30,990.96 mm³  $O_2$ , this

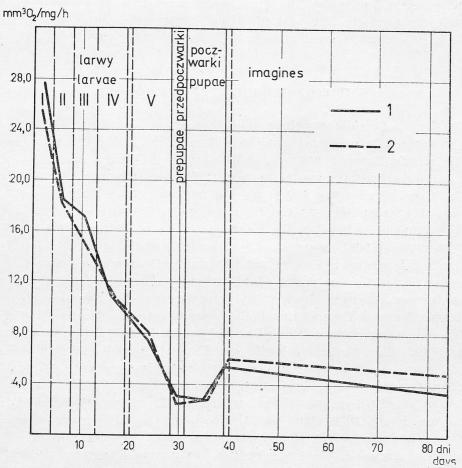


Fig. 22. Oxygen consumption in the successive development stages of the Cassids at the temperature of 20°C. 1 — Cassida rubiginosa Müll., 2 — C. vibex L.

corresponding to  $151\cdot7$  cal, and C. vibex L.  $31,925\cdot52$  mm³  $O_2=156\cdot3$  cal. The obtained results are very similar with both species of cassids and also very similar to the results obtained by Gromadzka (1968) in her study on the development of the Colorado beetle. The energy losses of young imagines throughout 45 days of life amount to  $385\cdot0$  cal with C. vibiginosa Müll. and as many as  $514\cdot4$  cal with C. vibex L.

Great differences between the experimental R value (Table XXVIII) and that calculated from the budget (Table XXVI) should be also shortly discussed. They can partly result from the differences in the conditions of nutritive and respiro-

metric experiments. In the respirometers larvae were kept on the substratum of the blotting paper and did not receive any food, this greatly increasing their motion activity. Moreover, they could be affected by light since in the culture they were kept in a weakly lighted room and in the course of experiments the respirometric chambers were strongly lighted because of technical reasons (readings every 5 minutes). The influence of temperature may be also suspected since it was precisely  $20^{\circ}\text{C} \pm 0.1$  when the oxygen consumption was controlled and in the culture it greatly fluctuated and was  $20^{\circ}\text{C} \pm 2.0$ .

#### VIII. ECONOMIC IMPORTANCE OF CASSIDS

Subfamily Cassidinae include a number of species which play a serious role in controlling weeds occurring in culture fields. It is distinctly supported by the results of investigations of many workers. According to Kleine (1917), Matis (1968), Šeremet and Gorbunov (1969), and Gorbunov and Šeremet (1968) Cassida rubiginosa Müll. plays a positive role in controlling Cirsium arvense (L.) Scop.; Deceaux (quoted according to Steinhausen, 1950) reports that it damages artichokes Cynara Scolymus L. in France, while Zwölfer and Eichhorn (1966) claim that if feeds on these plants only under laboratory conditions. According to Zwölfer and Eichhorn (1966) Cassida vibex L. is also a serious pest of Cirsium arvense (L.) Scop. and of Centaurea jacea L. but under laboratory conditions it also strongly damages artichokes Cynara Scolymus L. In connection with the fact that both species of cassids may attack artichokes which are an important culture plant in Western Europe Zwölfer and Eich-HORN (1966) claim that these beetles should not be recommended in biological weed control. A similar opinion is expressed by Steinhausen (1950) and Matis (1968) with regard to Cassida viridis L. which is supposed to attack valuable medicinal plants of the genera Salvia L. and Mentha L.; on the other hand Kleine (1917) and Palij (1959) claim that this cassid plays an important role in controlling Mentha arvensis L. Hypocassida subferruginea Schrnk. strongly attacks Convolvulus arvensis L. this being supported by Palij and Klepikova (1957), Palij (1959), MATIS (1968), ŠEREMET and GORBUNOV (1969), and GORBUNOV and ŠEREMET (1968).

Discrepant opinions prevail with regard to Cassida nebulosa L. and C. nobilis L. Several workers maintain that these cassids are serious pests of Beta vulgaris L. (Wilke, 1923, Menozzi, 1938, Simm, 1948, Lopatin, 1960, Ogloblin and Medvedev, 1971) while others report Chenopodium album L. as their main foodplant and the Beta vulgaris L. as a supplementary one (Kleine, 1914, 1915, Steinhausen, 1950, Palij and Klepikova, 1957, Palij, 1959, and Matis, 1968). If any or even considerable damages to beet leaves are encountered, they may result from wrong cultivation of root crops as well as from neglects in the timely and efficient weed control (Chenopodium sp.) in these crops.

In a situation that depending on circumstances the same species of cassids

may be pests or not, it should be stressed that very distinct adaptation to thermic and moisture conditions of the environment is observed with the species of this subfamily. According to Matis (1968) uncertainty in the problem of the economic importance of cassids is limited by the environment and by the nutritive and ecologic properties of species.

In the years 1966—1971 in the territory of the Ojców National Park and outside this territory observations and studies were carried out on the economic importance of the following species of cassids: Cassida rubiginosa Müll, C. vibex L., C. viridis L., C. flaveola Thunbg., and, additionally C. nebulosa L., C. nobilis L. and Hypocassida subferruginea Schrnk. In the result of the conducted investigations it was found (pl. XXXIII) that C. rubiginosa Müll and C. vibex L. strongly and spontaneously attack Cirsium arvense (L.) Scop.; C. viridis attacks Mentha arvensis L., Stachys palustris L., Galeopsis pubescens Bess.; and C. flaveola Thunbg. damages Stellaria media Vill. Moreover, it was found that C. nebulosa L. and C. nobilis L. above all attack Chenopodium album L., and only slightly Beta vulgaris L.; while H. subferruginea Schrnk. damages Convolvulus arvensis L.

The investigated species of cassids pass their whole development cycle on the leaves of weeds, greatest damages to these plants being caused by adult beetles in the period of complementary feeding in spring and later by the larvae of the fifth instar and by young imagines. With the density of cassids amounting from several to scores of specimens per 1 m² of plant surface the injuries on weed leaves were so strong that the growth of these plants was stunted and retarded by 1 to 2 months, they usually did not yield seeds, and most often wholy wilted.

It was found that the cassids *C. rubiginosa* MÜLL., *C. vibex* L., *C. viridis* L., and *C. flaveola* Thunbe. develop in very great numbers under favourable laboratory conditions, their complete development taking about 30 days, hence a very real possibility occurs of using beetles and larvae of these species in the control of most troublesome weeds. In connection with the increasing chemization of the environment this fact may be of essential importance in preserving the biocenotic equilibrium of agrocenoses and, indirectly, in the protection of health of man.

### IX. DISCUSSION AND CONCLUSIONS

In the course of the investigations conducted in the years 1966—1971 the occurrence of 11 species of cassids was found in the territory of the Ojców National Park; eight of them were identified by the present author, 3 were caught by other persons. A systematic list of the species collected is given below:

Cassida rubiginosa Müll.

- C. vibex L.
- C. viridis L.
- C. flaveola Thunbg.

- C. hemisphaerica HBST.
- C. nobilis L.
- C. nebulosa L.
- C. prasina Illig.
- C. rufovirens Suffr.
- C. vittata VILL.
- C. sanguinolenta Müll.

Out of that number 6 species were included in the investigations: C. rubiginosa Müll, C. vibex L., C. viridis L., C. flaveola Thunber, C. hemisphaerica Hest., and C. prasina Ill., mereover, additional observations were carried out on C. nebulosa L. and C. nobilis L. The least number of observations was made with regard to C. hemisphaerica Hest. and C. prasina Ill., since they were extremely rare in the territory of the Park. Therefore, further additional observations on the biology and ecology of these species are necessary, while from the results obtained in the course of the investigation the following conclusions may be drawn:

- 1) With regard to the environmental moisture requirements the investigated species of cassids may be classified to the mezo- and hygrophilous group, *C. viridis* L., *C. prasina* Ill., and *C. flaveola* Thunbg. showing greater tendency to hygrophilousness and *C. hemisphaerica* Hbst. to xerophilousness.
- 2) C. rubiginosa Müll. is a species encountered very frequently and in very great numbers, C. vibex L. and C. viridis L. are fairly frequent but occur in less numbers, C. flaveola Thunber. is rarely found and in small numbers, and C. hemisphaerica Hbst. and C. prasina Ill. are very rarely found and as single specimens.
- 3) Return of cassids from wintering to the meadow, their maturation and course of development above all depend on climatic factors (temperature, insolation, rains, wind).
- 4) C. rubiginosa Müll. appears on the meadow at the earliest period, the other species appearing one after another at weekly intervals. Maximum number occurs with the first species in the first half of the month of May, and with the other species in the second half of May or in June, already in July a slow decrease in the numbers is observed, only single specimens of old beetles being encountered at the end of the season.
- 5) The investigated species of cassids are very narrow oligophagous animals, C. rubiginosa Müll, C. vibex L., and C. prasina Ill. being closely connected with the plants of the family Compositae, C. viridis L. with the family Labiatae, C. flaveola Thunbg. and C. hemisphaerica Hbst. with the family Caryophyllaceae. The species additionally observed (C. nebulosa L. and C. nobilis L.) are connected with the plants of the family Chenopodiaceae; Hypocassida subferruginea Schrnk. being a decided monophagous animal feeds on Convolvulus arvensis L. (family Convolvulaceae).
- 6) The measurements of the distribution on foodplants of cassids showed in 1966, 1968, and 1970 that under the influence of the fact that the meadow was not mown quantitative changes occurred among the plants.

- 7) The so-called complementary feeding, necessary for the maturation of beetles was observed with the investigated species in the spring season.
- 8) The pictures of feeding of the beetles and larvae of cassids on the leaves of host plants are very characteristic for separate species.
- 9) The eggs of cassids are in a great majority of cases deposited on the lower leaf surface of host plants, to protect them from the unfavourable influence of physical factors and partly also of biotic ones.
- 10) The average length of life of the investigated species is about 1 year or a little more, the minimal length being 1 month, the maximum one almost 4 years with C. rubiginosa Müll., 3 years with C. ribex L., almost 3 years with C. viridis L., and 2 years with C. flaveola Thunbb. With all species males live shorter than females, the differences between the two sexes being from 2 months with C. flaveola Thunbb. to almost 2 years with C. rubiginosa Müll.
  - 11) The sex ratio of cassids shows a slight prevalence of females.
- 12) The cassids belong to the group of insects of the day rhythm of activity, showing particular preference for sun light and a distinct positive phototaxis.
- 13) The course and length of the development of eggs, larvae, and pupae of cassids decisively depend on climatic conditions (temperature, insolation, rains).
- 14) The so-called sociability of feeding is observed with newly hatched larvae of cassids and maintained only as late as the end of the second instar, and moreover, in this period of life the larvae always feed on the lower leaf surface of foodplants.
- 15) The emergence of the larvae of cassids usually occurs in June, the maximum numbers occurring in July or in the first half of August, single specimens being only encountered at the beginning of September.
- 16) A coat of exuviae and excrements carried by the larvae on their bodies is among others a characteristic feature of the subfamily of cassids.
- 17) Only one generation in a year is noted with the investigated species of cassids.
- 18) In the newly hatched imagines of cassids a change in the coloration of the cuticula of prothorax and elytrae occurs in the first day of their life, their full coloration being observed after wintering in spring of the next year, before the mating period.
- 19) The emergence of young imagines of *C. rubiginosa* MÜLL. is observed in the first or second half of July, of *C. vibex* L. usually in the second half of July, of the two other species at the beginning of August; maximum numbers occur in August or in the first half of September, the last specimens being encountered as late as the first half of October.
- 20) Young imagines of cassids do not attain sexual maturity in the year of hatch and they fall into diapause whose origin and course are very complicated phenomena and depend on physical (temperature, length of day, humidity) and biotic factors (quality of food, physiological state of beetles).
- 21) The activity of young imagines depends on the period of hatch. Specimens which hatched earlier (at long day) fed and stayed on the meadow for about

- 2 months, while those which hatched later (at short day) stayed there for only 2 weeks.
- 22) At the end of summer and in autumn young imagines of the investigated species migrate to the lime-hornbeam forest, on the slope of south exposition in the Sąspowska Valley, where they winter in the state of diapause in the litter at the depth of 5—8 cm. Migrations of beetles are brought about by physical factors (temperature, insolation, length of day, humidity) and also partly by biotic factors (quality of food, physiological state of beetles).
- 23) In the period of migration for wintering the content of free water decreases in the bodies of cassids from over 80·00 per cent to about 50·00 per cent. In the bodies of wintering beetles its amount gradually increases (chiefly owing to the combustion of fats) and in spring reaches the value of 60·00—70·00 per cent, at that value spring activation of beetles and then their maturation being observed.
- 24) The size of the populations of investigated species of cassids changes in successive years and depends on the influence of climatic factors (temperature, rains, wind).
- 25) The fecundity of cassid females depends on temperature, length of day, rains, and on the quality of food. Maximum fecundity chiefly occurs in June and in the first half of July, i.e. in the periods of longest days (about 17 hours). The highest fecundity is found with 1-year old females and gradually decreases with 2- and 3-year old ones.
- 26) The degree of density of separate development stages of cassids changes throughout the vegetation season and depends on the size of patches of foodplants.
- 27) Physical factors greatly influence the reduction of eggs and larvae in the first and second instar as well as the rate of winter mortality of young cassid imagines (20·83—58·33 per cent). From the total number of dead beetles the greatest number of specimens dies at the end of winter.
- 28) A distinct positive correlation occurs between the degree of insolation of the surface of the meadow throughout the consecutive months of the vegetation season and the appearance of separate development stages of cassids.
- 29) In the reduction of all development stages of cassids the decisive role is played by biotic factors: parasites (endoparasites, oophagous animals), predators, and microorganisms. In separate years the percentage share of these factors in the reduction of cassids chiefly depends on physical factors: temperature, rains. The total reduction of development stages of cassids was very high with relation to the initial number of eggs which remained healthy on the leaves of plants and with the investigated species ranged from 98·00—99·50 per cent.
- 30) In the whole period of development a larva of *C. rubiginosa* MÜLL. consumes 110·1 mg of leaf biomass (58·9 cal) and *C. ribex* L. 103.2 mg of leaf biomass (55·2 cal). The rate of feeding doubles in the successive instars of development, maximum consumption occurring in the fifth larval instar. A young

imago of C. rubiginosa Müll. consumes 305·6 mg of leaf biomass (157·9 cal) and of C. ribex L. 292·3 mg of leaf biomass (151·0 cal) throughout 45 days of life.

- 31) The total energy assimilation required for the whole development cycle of a larva amounts to 35.4 cal with *C. rubiginosa* Müll. and to 33.5 cal with *C. vibex* L., while the values of energy assimilation are very high with young imagines amounting to 125.0 and 121.6 cal respectively.
- 32) The total production of body biomass is 17.8 mg (20.5 cal) with *C. rubiginosa* Müll. and 18.4 mg (19.6 cal) with *C. ribex* L. In separate instars an increase in biomass is distinctly greater with the age of a larva; the highest increase is noted at the beginning of the pre-pupa stage and therefore this moment is regarded as a maximum in the development of larvae. With young imagines the production of body biomass is 5.7 mg or 8.3 mg (depending on the method of calculation) with *C. rubiginosa* Müll. and 4.2 mg or 7.5 mg with *C. vibex* L. The values of the body production calculated as dry matter amount to 6.6 mg (52.0 cal) and 6.1 mg (40.7 cal) respectively.
- 33) With both species the highest production efficiency (P/C) is observed in the first larval instar, then it decreases, reaching the lowest level in the fifth instar. The mean value of this coefficient is 39·97 per cent with *C. rubiginosa* Müll larvae and 40·44 per cent with *C. vibex* L. With young imagines these values are even lower and amount to 32·94 and 26·96 per cent respectively.
- 34) The mean value of the assimilation coefficient (A/C) is very high, amounting to 62·17 per cent with the larvae of *C. rubiginosa* MÜLL. and to 63·47 per cent with *C. vibex* L. With young imagines even higher values were noted: 79·13 and 80·52 per cent respectively. Such high values of this coefficient indicate unusual efficiency of larvae and imagines of both species with regard to the utilization of food.
- 35) The mean values of respiration losses (R/C) in larvae amount to 22·20 per cent (C. rubiginosa MÜLL.) and 23·03 per cent (C. vibex L.) while with young imagines to 46·19 per cent and 53·56 per cent respectively. It should be stressed that in the larvae of both species the values of production efficiency are higher than the respiration losses and in young imagines vice versa. Moreover, the respiration losses of young imagines are two times greater than those of the larvae.
- 36) The oxygen consumption per a unit of body biomass distinctly decreases with an increase in biomass in the successive development stages of both species of cassids.
- 37) From the moment of hatch of larvae to the emergence of an imago the energy losses are 151·7 cal with *C. rubiginosa* Müll. and 156·3 cal with *C. vibex* L., while in the 45 days of life of young imagines they are 385·0 cal and 514·4 cal respectively.
- 38) Great differences are noted between the experimental R value and that calculated from the budget. They can result from the differences in the conditions of nutritive and respirometric experiments.

39) It was found that as well the investigated species as those additionally observed play a serious role in controlling weeds in agricultural crops, with the reservation that under certain circumstances *C. nebulosa* L. and *C. nobilis* L. may be secondary pests of sugar beet.

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#### REFERENCES

- Balli A. 1943. Ricerche biologici in *Melasoma populi* L. Atti Soc. nat. mat. Modena, 74: 138—150.
- BECKER G. 1940. Beobachtungen über Schädlichkeit, Frass und Entwicklungsdauer von Anobium punctatum DE GEER. Zs. Pflanzenkr. Pflanzenschutz, 50: 159—172.
- BILEWICZ T. 1957. Wstępne obserwacje nad ilościowym występowaniem i rozmieszczeniem przestrzennym populacji Aelia acuminata L. i A. rostrata Boh. Ekol. Pol., S. A, 5 (5): 165—185.
- BILEWICZ T. 1960. Uwagi o ekologii i biologii Eurydema ornata L. Ekol. Pol., S. B., 6 (1): 51—55
- BILEWICZ-PAWIŃSKA T. 1969. Natural limitation of Lygus rugulipennis Popp, by a group of Leiophron pallipes Curtis on the rye crop fields. Ekol. Pol., S. A, 17 (41): 811—825.
- Brischke C. G. A. 1883. Beschreibung der forst-, garten- und landwirtschaftlichen Feinde und Freunde unter den Insekten. Schrift. Natur. Ges., n. F., 5 (4): 97—125.
- Budziszewska E., Przedpełska W. 1970. Susza w roku 1969 na tle analogicznych zjawisk w okresie wieloletnim. I Ogólna charakterystyka suszy w 1969 roku. Przegl. Geofiz., 15 (1): 37—56.
- Burgess A. F., Collins C. W. 1917. The Genus Calosoma. Bull. U. S. Dep. Agric.: 417.
- Charčenko N. A. 1968. O biologii mermitid (Mermithidae, Nematodes) polostnych parazitov bespozvonočnych. Zool. Žurn., 47 (8): 1142—1150.
- Cheodny J. 1967. The amount of food consumed and production output of larvae of the Colorado beetle (*Leptinotarsa decemlineata* Say). Ekol. Pol., S. A, 15 (25): 531—541.
- CHEODNY J. 1967. The energetics of the development of cabbage white *Pieris brassicae* (L.). Ekol. Pol. S. A, 15 (27): 553—561.
- CHŁODNY J., GROMADZKA J., TROJAN P. 1967. Energetic budget of development of the Colorado beetle Leptinotarsa decembineata (SAY) (Col. Chrysom.). Bull. Acad. Pol. Sci. Cl. II, 15 (12): 743—747.
- Chroliński L. 1963. Sezonowe wędrówki ryjkowców (Curculionidae) z rodzaju Apion Herbst w warunkach przyrodniczych obwodu czerniowieckiego. Przegl. Zool., 7 (2): 139—142.
- CZECZUGA B. 1971. Assimilation of carotenoids with food by the Colorado beetle, Leptinotarsa decembineata SAY. J. Insect Physiol., 17 (10): 2017—2025.
- DMOCH J. 1959. Badania nad chowaczem czterozębnym Ceuthorrhynchus quadridens PANZ. Morfologia, biologia, ekologia oraz znaczenie dla rzepaku. Prace Nauk. IOR, 1 (3): 37—74.
- Dubeško L. N. 1970. Ob èkologii listoedov (Col. Chrysom.) poberežja Bajkala. Zool. Žurn., 49 (10): 1526—1533.
- EICHLER W. 1914. Przyczynek do tęgopokrywych Ojcowa. Pam. Fizjogr., 22 (3): 138—149. EMDEN VAN H. F. 1962. Key to species of British Cassidinae larvae (Col. Chrysom.). Ent. monthly Mag., 98: 33—36.
- ENGEL H. 1932. Beiträge zur Kenntnis der Biologie von Cassida viridis L. (Col. Chrysom. Cassidinae). Dtsch. ent. Z., 1: 195—207.

- ENGEL H. 1935. Biologie und Ökologie von Cassida viridis L. Zs. Morph. Ökol., 30: 41—96. GALECKA B. 1953. Obserwacje nad czynnikami redukującymi populacje mszyc w środowiskach naturalnych. Ekol. Pol., S. A, 1 (2): 49—68.
- Gorbunov N. N., Šeremet V. G. 1968. Ščitonoski uničtožajut sornjaki. Zašč. Rast., 13 (2): 54.
- Gromadzka J. 1968. Respiratory metabolism of the Colorado beetle (Leptinotarsa decembineata Say). Ekol. Pol., S. A, 16 (17): 375—383.
- Gusev G. V., Žuravlev V. N. 1958. Biologičeskie osobennosti koloradskogo žuka. Zašč. Rast., 3: 46—47.
- Guilford J. P. 1964. Podstawowe metody statystyczne w psychologii i pedagogice. PWN, Warszawa.
- Jankowska K. 1967. Sezonowe zmiany roślinności i produkcja pierwotna netto w płacie łąki. Arrhenatheretum elatioris. Studia Naturae, S. A, 1: 153—173.
- Jankowska K. 1971. Net primary production during a three-year succession on an unmoved meadow of the *Arrhenatheretum elatioris* plant association. Bull. Acad. Pol. Sc., Cl. II, 19 (12): 789—794.
- Jolivet P. 1946. Les parasites des Chrysomelides françaises. Miscell. Entom., 43: 87—92. Kaczmarek W. 1955. Z badań nad naturalną redukcją populacji Leptinotarsa decemlineata Say w warunkach polowych. Ekol. Pol., S. A, 3 (6): 109—179.
- KARG J., TROJAN P. 1968. Fluctuations in numbers and reduction of the Colorado beetle (Leptinotarsa decembineata SAY) in natural conditions. Ekol. Pol., S. A, 16 (5): 147—169.
- Karkanis D. 1967. Warunki glebowe lasu bukowego Fagetum carpaticum i łąki Arrhenatheretum elatioris. Studia ekosystemów lasu bukowego i łąki w Ojcowskim Parku Narodowym. Studia Naturae, S. A, 1: 49—60.
- Kaufmann O. 1933. Der glanzstreifige Schildkäfer Cassida nobilis L. nebst einigen Bemerkungen über den nebeligen Schildkäfer Cassida nebulosa L. Arb. Biol. Reichsanst., Abt. Land. u. Forstw., 20: 457—516.
- Klein J. 1967. Charakterystyka fitoklimatu badanych powierzchni na tle warunków mezoklimatycznych Ojcowa. Studia Naturae, S. A, 1: 25—47.
- Klein J. 1974. Mezo- i mikroklimat Ojcowskiego Parku Narodowego. Studia naturae, S. A., 8: 1—105.
- Klein J., Niedźwiedź T., Sztyler A. 1965. Badania mikroklimatyczne na terenie Ojcowskiego Parku Narodowego. Ochr. Przyr., 31: 189—201.
- KLEIN-KRAUTHEIM F. 1950. Über die Überwinterung des Kartoffelkäfers (Leptinotarsa decemlineata SAY) und sein Erscheinen im Frühling in seinen Beziehungen zu meteorologischen Faktoren. Nachrichtenblatt Deutsch. Pflanzenschutzdients, 11: 161.
- KLEINE R. 1914. Cassida nebulosa L. Ein Beitrag zur Kenntnis ihrer Biologie und ihrer Bedeutung für die Landwirtschaft. Ent. Bl., 10 (14/15): 321—331.
- KLEINE R. 1915. Cassida nebulosa L. Ein Beitrag zur Kenntnis ihrer Biologie und ihrer Bedeutung für die Landwirtschaft. Zs. wiss. Insektenbiol., 11 (1/2): 27—32, (3/4): 65—70, (5/6): 113—117, (7/8): 180—186.
- KLEINE R. 1916. Über die Generationsfrage von Cassida nebulosa L. (Der Einfluss der Wetterlage in den Jahren 1915—1916). Ent. Bl., 12 (10—12): 245—258.
- K<sub>LEINE</sub> R. 1917. Cassidenstudien II. Cassida murraea L. (Ein Beitrag zur Kenntnis ihrer Biologie und ihrer Standpflanzen). Ent. Bl., 13 (—13): 24—43.
- K<sub>LEINE</sub> R. 1917. Cassidenstudien III. Über Cassida rubiginosa Müll. Ent. Bl., 13 (4—6): 63—73.
- Kleine R. 1917. Cassidenstudien V. Über Cassida flaveola Thunbg. Ent. Bl., 13 (4—6): 91—97.
- K<sub>LEINE</sub> R. 1917. Cassidenstudien VI. Die Entwicklung des Larwenfrassbildes von Cassida viridis L. Ent. Bl., 13 (7—9): 163—178.
- K<sub>LEINE</sub> R. 1917. Cassidenstudien VII. Das diesjährige Erscheinen von Cassida viridis L. (Ein Beitrag zur Bewertung der meterologischen Faktoren, namentlich der Bodentemperaturen). Ent. Bl., 143 (10—12): 269—277.

- KLEINE R. 1918. Cassidenstudien VIII. Die Entwicklung der Cassida nebulosa L. Larve unter Einfluss verschiedenfarbigen Lichtes. Ent. Bl., 14 (1—3): 27—36, (4—6): 103—122.
- KLEINE R. 1918. Kleine coleopterologische Mitteilungen. Tetrastichus cassidarum (RATZ.), ein Parasit von Cassida rubiginosa MÜLL. Ent. Bl., 14 (7—9): 248—249.
- Kleine R. 1919. Cassidenstudien IX. Cassida nobilis L. Cassida subferruginea Schrnk. Cassida lineola Creutz. Ent. Bl., 15 (10/12): 221—228.
- KLEINE R. 1920. Cassidenstudien X. Der Einfluss thermischer Faktoren auf die Entwicklung der Praeimaginal- und Imaginalstadien von Cassida nebulosa L. Ent. Bl., 16 (4—9): 178—186
- KLEKOWSKI R., PRUS T., ZYROMSKA-RUDZKA H. 1967. Elements of energetic balance of *Tribolium castaneum* (HBST.) in its developmental cycle. In: Secondary productivity of terrestrial ecosystems. (Principles and Methods), 2: 859—865.
- Kosior A., Klein J. 1970. Migrations and wintering of Cassids (Col. Chrysom. Cassidinae) under the climatic conditions of the Ojców National Park. Acta Zool. Cracov., 15 (7): 315—340.
- Kościelska M. K. 1966. Metodyka badań ilościowych owadów pasożytniczych. Ekol. Pol., S. B, 12 (3): 291—294.
- KOVAL Ju. V. 1969. Parazit koloradskogo žuka. Zašč. Rast., 14 (9): 49-50.
- Kowalska T. 1960. Badania nad wpływem niektórych czynników na diapauzę i zimowanie stonki ziemniaczanej (*Leptinotarsa decemlineata* Say). Prace Nauk. IOR, **2** (2): 109—158.
- Kowalska T. 1969. Fecundity of the Colorado beetle in relation to ecological factors. Ekol. Pol., S. A, 17 (10): 167—184.
- Kuznecov-Ugamskij N. N. 1929. Masovye skoplenija nasekomych v mestach zimovok i biologičeskoe značenie etogo javlenija. Russk. zool. Žurn., 9 (2): 111—123.
- LINCOLN F. C. 1930. Calculating waterfowl abundance on the basis of banding returns. U.S.D.A. Circ., 118: 1—4.
- LINDROTH C. H. 1945. Die Fennoskandischen Carabidae. Sjätte Följden, S. B, 4 (1): 7—709. LOPATIN I. K. 1960. Materialy po faune i èkologii žukov-listoedov (Col. Chrysom.) južnogo Zadneprov'ja. Ent. Obozr., 39 (3): 629—642.
- Łarczenko K. 1957. Odżywianie i diapauza stonki ziemniaczanej (Leptinotarsa decemlineata Say). Roczn. Nauk Roln., 74 A (2): 287—314.
- Łarczenko K. 1958. Długość rozwoju stonki ziemniaczanej (*Leptinotarsa decemlineata* Say) w zależności od temperatur. Roczn. Nauk Roln., **78** A (1): 27—41.
- Łomnicki A., Kosior A., Kaźmierczak T. 1965. Ocena suchej masy uszkodzeń, dokonanych przez roślinożerców w runie lasu bukowego (*Fagetum carpaticum*). Ekol. Pol., S. B, 11 (1): 61—67.
- Manolache C. J., Dobreanu E., Dimitru F. 1936. Contributiuni la biologia insectei Cassida nebulosa L. in România. Ann. Inst. Cerc. Agron. Român., 8: 477—500.
- Manolache C. J., Dobreanu E., Manolache F. 1938. Cercetôri a supra biologiei insecti Cassida viridis L. Ann. Inst. Cerc. Agron. Român., 10: 345—457.
- MARKIEWICZ E. 1948. Przyczynek do badań nad zimowaniem w podłożu leśnym niektórych zwierząt bezkręgowych, ze specjalnym uwzględnieniem chrząszczy. Studia Soc. Scien. Torun., S. E, 1 (6): 1—29.
- Matis È. G. 1968. Èkologo-chozjajstvennaja charakteristika ščitonosok (Col. Chrysom. Cassidinae) fauny juznogo Zaural'ja i severnogo Kazachstana. Entomologičeskie issledovanija v Kirgizii: 41—45.
- Matis È. G. 1971. Estestvennye vragi žukov ščitonosok (Col. Chrysom. Cassidinae). Trudy Vsesojuzn. NII Zašč. Rast., 1: 76—84.
- Medwecka-Kornaś A., Kornaś J. 1963. Mapa zbiorowisk roślinnych Ojcowskiego Parku Narodowego. Ochr. Przyr., 29: 17—87.

- Menozzi C. 1938. Osservatione sugli insetti dannosi alla Barbabietola e lotta contro si essi divante la campagna saccarifera 1937. Industr. Sacc. Ital., 31, 8 pp.
- Miksiewicz M. 1948. Materiały do poznania bioekologii stonki ziemniaczanej (*Leptinotarsa decemlineata* SAY) w Polsce. Pol. Pis. ent., 18 (2/4): 276—311.
- MOORE H. B. 1970. Incubation time of eggs of Xyletinus peltatus (HARRIS) (Col. Anobiidae) under constant temperatures and humidities. Ann. Entom. Soc. Amer., 63 (2): 617—618.
- Myrcha A., Stejgwiłlo-Laudańska B. 1970. Metabolism of the sucking insect Cicadella viridis L. (Homoptera-Auchenorrhyncha). Bull. Acad. Pol. Sci., Cl. II, 18 (4): 197—199.
- NIETZKE G. 1939. Aus dem Leben des nebeligen Schildkäfers Cassida nebulosa L. Natur u. Volk, 49: 355—360.
- Ogloblin D. A., Medvedev L. N. 1971. Ličinki žukov-listoedov (Col. Chrysom.) evropejskoj časti SSSR. Opredeliteli po faune SSSR, 106: 3—122.
- OPYRCHAŁOWA J. 1970. Fotoperiodyzm a owady. Ochr. Rośl., nr 10: 18—20.
- Opyrchałowa J. 1970. Termiczne progi życia owadów. Cz. II. Wytrzymałość na gorąco. Ochr. Rośl., nr 12: 15—17.
- OPYRCHAŁOWA J. 1972. Pokarm owadów. Ochr. Rośl., nr 2: 9—11.
- Palij V. F. 1959. Opisanie ličinok žukov-ščitonosok (*Col. Chrysom. Cassidinae*) evropejskoj časti SSSR i nekotorye čerty ich biologii i èkologii. Ent. Obozr., **38** (4): 805—818.
- Palij V. F., Klepikova P. I. 1957. Èkologija ščitonosok (*Col. Chrysom. Cassidinae*) centralnocernozemnoj polosy RSFSR s opisaniem kukolok naibolee rasprostranennych vidov. Ent. Obozr., **36** (1): 75—95.
- Petrusewicz K. 1966. Niektóre pojęcia w badaniach produktywności wtórnej. Kosmos, S. A, 15 (6): 581—599.
- RABAUD E. 1915. Notes sommaires sur la biologie des Cassides. Bull. Soc. Entom. France, 20: 173—174.
- RAMMNER W. 1932. Zur Biologie und Entwicklungsgeschichte der Schildkäfer. Cassida murraea L. Zs. wiss. Insektenbiol., 27 (1/2): 1—11.
- RAMMNER W. 1934. Zur Biologie des Schildkäfers Cassida murraea L. Zs. wiss. Insektenbiol., 27 (5/6): 71—82.
- RAMMNER W. 1937. Zur Biologie des Schildkäfers Cassida murraea L. Zs. wiss. Insektenbiol., 27 (7/10): 116—123.
- Reitter E. 1912. Fauna Germanica. Käfer. Stuttgart 4: 1—236.
- Ruszkowska J., Opyrchałowa J. 1969. Wybrane działy ekologii owadów. Czynniki abiotyczne. Skrypty WSR, Wrocław, 54: 1—151.
- Sandner H., Stanuszek S. 1970. Nematodes-parasites of the Colorado beetle. Zesz. Probl. Post. Nauk Roln., 92: 349—353.
- SIMM K. 1948. Zoologia dla przyrodników i rolników., 1: 3-584.
- Starzyk J. R. 1970. Sichrawa górska Gaurotes virginea (L.) (Col. Cerambycidae) wtórny szkodnik świerka pospolitego. Cz. I. Morfologia, biologia, ekologia. Acta Agr. Silv., 10: 39—96.
- Starzyk J. R. 1970. Sichrawa górska Gaurotes virginea (L.) (Col. Cerambycidae) wtórny szkodnik świerka pospolitego. Cz. II. Ekologia populacji imago, czynniki ograniczające rozród i znaczenie gospodarcze. Acta Agr. Silv., 10: 97—126.
- Starzyk J. R. 1971. Wstępne badania nad ekologią populacji antofilnych Cerambycidae (Col.) w Tatrzańskim Parku Narodowym. Acta Agr. Silv., 11: 47—71.
- Steinhausen W. 1950. Vergleichende Morphologie, Biologie und Ökologie der Entwicklungsstadien der in Niedersachsen heimischen Schildkäfer (Cassidinae, Chrysom. Col.) und deren Bedeutung für die Landwirtschaft. Dissert. Techn. Hochsch., pp. 5—69.
- STRESEMANN E. 1964. Exkursionsfauna von Deutschland. Wirbellose, II/1. Berlin.
- SZAFER W., KULCZYŃSKI S., PAWŁOWSKI B. 1967. Rośliny Polskie. Warszawa, PWN.
- Šapiro D. S., Černyšenko N. N. 1963. K faune i ekologii listoedov (*Col. Chrysom. Halticinae*, *Cassidinae*, *Hispinae*) severo-vostoka lesostepi i Poles'ja Ukrainy. Ent. Obozr., **42** (3): 576—581.
- 9 Acta Zoologica Cracoviensia XX/9

- ŠEREMET V. G., GORBUNOV N. N. 1969. Možno li ispol'zovat' nasekomych v bor'be s v'junkom polevym i osotom rozovym. Zern. maslič. Kult., 4 (2): 25—27.
- Szujecki A. 1966. O biologii stonkowatych (*Col. Chrysom.*) występujących na drzewach i krzewach leśnych w Polsce oraz ich drapieżcach i pasożytach. Zesz. Nauk. SGGW Leśn., 9: 113—132.
- Schumacher F. 1910. Beiträge zur Kenntnis der Biologie der Asopiden. Zs. wiss. Insektenbiol., 6: 263, 376, 430.
- TROUVELOT B. 1935. Le Doryphore de la pomme de terre (Leptinotarsa decembineata SAY) en Amerique du Nord. Ann. Epith. Phytog., 1: 277—336.
- VILDE J. DE, 1954. Aspect of diapause in adult insects with special regard to the Colorado beetle (Leptinotarsa decembineata SAY). Neerl. Zool., 10 (4): 375—384.
- Warchałowski A. 1958. Z biologii i fenologii długostopki (Longitarsus suturellus Dft.) (Col. Chrysom.). Pol. Pis. ent., 28 (11): 157—165.
- Warchałowski A. 1959. Rola insolacji w procesie rozmnażania niektórych gatunków rodzaju Longitarsus Latr. (Col. Chrysom.). Przegl. zool., 3 (2): 90—99.
- Warchalowski A. 1960. Ein interessanter Zusammenhang zwischen der Zeitdauer der Eiablage und dem Körpergewicht bei den Weibehen von Longitarsus gracilis Kutsch. (Col. Chrysom.). Zoologica Poloniae, 10 (4): 295—307.
- Vasil'ev R. A. 1963. K biologii orechovogo ploskogo listoeda Gastrolina thoracica Baly (Col. Chrysom.). Ent. Obozr., 42 (2): 264—272.
- Węgorek W. 1950. Obserwacje biologiczne nad stonką ziemniaczaną (Leptinotarsa decemlineata SAY) w 1948 roku w Irenie koło Dęblina. Pol. Pis. ent., 19 (3/4): 208—212.
- Węgorek W. 1957. Badania nad zimowaniem stonki ziemniaczanej (*Leptinotarsa decemlineata* Say) na tle jej fizjologii. Roczn. Nauk Roln., **74** A (2): 315—338.
- Węgorek W. 1957a. Badania nad biologią i ekologią stonki ziemniaczanej (Leptinotarsa decemlineata Say). Roczn. Nauk Roln., 74 A (2): 135—185.
- Węgorek W. 1959. Stonka ziemniaczana (Leptinotarsa decemlineata Say). Prace Nauk. IOR, 1 (2): 1—178.
- WĘGOREK W., SZMIDT A. 1966. Zagadnienia populacyjne w układzie *Perillus bioculatus* (FABR.) (*Pentatomidae*) *Leptinotarsa decemlineata* SAY (*Chrysomelidae*). Ekol. Pol., S. B, 12 (2): 147—151.
- WIEGERT R. G. 1964. Population energetics of meadow spittlebugs (*Philaenus spumarius* L.) as affected by migration and habitat. Ecol. Monogr., 34: 217—241.
- WILKE S. 1923. Der nebelige Schildkäfer. Nachr. Bl. Deutsch. Pflanzenschutz, pp. 9—10.
  WILSKI A. 1951. Wpływ czynników klimatycznych na występowanie owadów szkodników roślin. Gaz. Obser. PIHM, 4 (8): 8—10.
- Wilusz Z. 1958. Z badań nad wiosennym rozlotem stonki ziemniaczanej (Leptinotarsa decemlineata Say). Roczn. Nauk Roln., 78 A (1): 79—94.
- Wilusz Z., Górny M., Narkiewicz-Jodko J., Pacanowski A. 1958. Dalsze badania nad mikromigracjami stonki ziemniaczanej (*Leptinotarsa decemlineata* Say). Roczn. Nauk Roln., 78 A (1): 95—122.
- Wradatsch G. 1919. Ein Beitrag zur Lebensgeschichte der Cassida splendidula Suffr. Zs. Biol. System. Käfer, 15 (1/3)b: 1—11.
- ZIPPIN C. 1956. An evaluation of the removal method of estimating animal populations. Biometrics, 12: 163—189.
- Zwölfer H., Eichhorn O. 1966. The host ranges of Cassida spp. (Col. Chrysom.) attacking Cynareae (Compositae) in Europe. Zs. angew. Entomol., 58 (4): 384—397.
- ZADIN W. J., 1966. Metody badań hydrobiologicznych. 293 pp. PWN, Warszawa.
- ŻURAŃSKA I. 1959. Materiały do fauny stonkowatych (*Chrysomelidae*) roślin motylkowych, uprawianych w województwie olsztyńskim. Zesz. Nauk. WSR Olsztyn, 9 (78): 315—318.
- ŻURAŃSKA I. 1968. Wpływ warunków ekologicznych na przebieg dynamiki liczebności chrząszczy, szkodników roślin uprawnych. Zesz. Nauk. WSR Olsztyn, **24** (2): 379—401.

Badania przeprowadzono w latach 1966—1971 w obrębie powierzchni na łące Arrhenatheretum elatioris alchemilletosum w Dolinie Sąspowskiej w Ojcowskim Parku Narodowym. W kolejnych latach od kwietnia do października, w odstępach 7—30-dniowych obserwowano i badano 6 gatunków tarczyków: Cassida rubiginosa Müll. i C. vibex L. na liściach Cirsium oleraceum (L.) Scop., C. viridis L. na liściach Mentha longifolia (L.) Huds., C. flaveola Thunbg. na liściach Stellaria graminea L., oraz poza powierzchnią C. hemisphaerica Hbst. na liściach Silene nutans L. i C. prasina Ill. na liściach Achillea millefolium L. Ponadto przeprowadzano dodatkowe obserwacje nad biologią C. nebulosa L. i C. nobilis L. w uprawach roślin okopowych na terenie Parku oraz nad Hypocassida subferruginea Schrnk. poza jego granicami. W kolejnych terminach badan przeglądano liście roślin pokarmowych tarczyków w obrębie powierzchni i notowano pojaw oraz liczebność okazów z kolejnych stadiów rozwojowych badanych gatunków.

W wyniku przeprowadzonych badań poznano fenologię pojawu oraz okresy występowania stadiów rozwojowych tarczyków (ryc. 1). Stwierdzono, że C. rubiginosa Müll. jest gatunkiem najwcześniej pojawiającym się na łące, a C. vibex L., C. viridis L. i C. flaveola Thunba. przylatują kolejno w odstępach tygodniowych. Nasilenie pojawu chrząszczy obserwuje się w maju i czerwcu, a od lipca następuje wolny spadek ich liczebności. Pojaw chrząszczy na łące zależy od czynników klimatycznych (temperatura, nasłonecznienie) i następuje, gdy temperatury maksymalne są wyższe od +13,0°C. W wyniku przeprowadzonych pomiarów zasięgów roślin pokarmowych tarczyków w obrębie powierzchni w latach 1966, 1968 i 1970, stwierdzono wyraźne zmiany ilościowe u tych roślin (ryc. 2—4), spowodowane faktem niekoszenia łąki. Wykaz roślin pokarmowych tarczyków, cytowanych przez różnych badaczy oraz ustalonych przez autora pracy przedstawia tabela I. U chrząszczy stwierdzono występowanie na wiosnę tzw. żeru uzupełniającego, który trwa 8-40 dni i warunkuje dojrzewanie chrząszczy. Obrazy zerów starych chrząszczy C. rubiginosa Müll. i C. vibex L. na liściach ich roślin pokarmowych przedstawia tablica XXV, a C. viridis i C. flaveola THUNBG. tablica XXVI.

Kopulacja u tarczyków rozpoczyna się przy temperaturze wyższej od 18,0°C, trwa od kilku do kilkunastu godzin, natomiast cały okres kopulacji — podczas którego owady bardzo silnie żerują — u badanych gatunków wynosi od 4 do 8 tygodni. Składanie jaj w terenie odbywa się po 3—7 dniach od zakończenia kopulacji oraz po 2—5 w laboratorium, przebiega przy temperaturach wyższych od 18,0°C, a optimum temperatur wynosi 20,0—25,0°C. Okres składania jaj przez samice tarczyków rozpoczyna się przy dniu dłuższym od 15 godzin (tab. II), wynosi od 8 do 12 tygodni i trwa od maja aż do połowy sierpnia (ryc. 1), z wyjątkiem C. viridis L. Dojrzewanie chrząszczy i składanie jaj są zależne od czynników klimatycznych, a w wypadku ich pogorszenia następuje zahamowanie czynności życiowych tarczyków.

Badania nad długością życia imagines, płodnością samic różnowiekowych,

długością rozwoju i śmiertelnością jaj oraz larw prowadzono w stałych punktach obserwacyjnych na łące. Średnia długość życia chrząszczy tarczyków (tab. III) wynosi około 1 roku, minimalna około 1 miesiąca, maksymalna natomiast — prawie 4 lata u *C. rubiginosa* Müll, 3 lata u *C. vibex* L., prawie 3 lata u *C. viridis* L., 2 lata u *C. flaveola* Thunbg. Samce żyją krócej od samie, a różnice u obu płei wahają się od 2 miesięcy u *C. flaveola* Thunbg. do niemal 2 lat u *C. rubiginosa* Müll. U badanych gatunków zaznacza się dymorfizm płciowy. Stosunek płei wykazuje w większości wypadków nieznaczną przewagę samic. Badane gatunki tarczyków — ze względu na wymagania wilgotnościowe siedliska — należą do grupy mezo- i higrofilnych. Tarczyki są owadami o dziennej rytmice aktywności, wykazują szczególne upodobania do światła słonecznego oraz wyraźny fototaktyzm dodatni.

Jaja tarczyków są składane głównie na dolnej stronie liści roślin pokarmowych, a ich liczba w złożu wynosi u *C. rubiginosa* Müll. 2—17 sztuk, ú *C. vibex* L. i *C. flaveola* Thunbg. 1—3 sztuk, u *C. viridis* L. 5—16 sztuk. Rozwój embrionalny jaj w terenie zależy od temperatury, wilgotności, opadów i trwa 11—33 dni (tab. IV), a w laboratorium 7—17,5 dni (tab. V).

Pierwsze okazy larw spotyka się z końcem maja lub na początku czerwca, nasilenie pojawu obserwuje się w lipcu oraz w I połowie sierpnia, a ostatnie okazy znajdowano na początku września (ryc. 1), a więc długość okresu ich występowania na łące wynosi 1,5 do 3,5 miesiąca. Żer świeżo wylęgłych larw przebiega głównie na dolnej stronie liści reślin pokarmowych, ponadto występuje u nich tzw. towarzyskość żerowania, która trwa do końca II stadium, a potem larwy rozchodza sie po całej roślinie. Obrazy żerów larw C. rubiginosa MÜLL. na liściach roślin pokarmowych przedstawia tablica XXVIII, C. vibex L. tablica XXVIII, C. viridis L. i C. flaveola Thungg, tablica XXIX. Larwy trzech pierwszych gatunków linieją w ciągu swego życia 5 razy (piąte linienie do poczwarki), a C. flaveola THUNBG. tylko 4 razy. W rozwoju larw odgrywają rolę temperatura, wilgotność i opady. W warunkach terenowych trwał on średnie 21,4—37,7 dni (tab. IV), w laboratorium 14-31 dni (tab. V). Przepoczwarczenie odbywa się głównie na dolnej stronie liści. Okres przedpoczwarki trwa w terenie 2-4,5 dni (tab. IV), w laboratorium 2-3 dni (tab. V). Długość występowania przedpoczwarek i poczwarek tarczyków wynosi 1,0-2,5 miesiąca (ryc. 1). Poczwarki badanych gatunków są bardzo wrażliwe na spadki temperatur i opady, które wyraźnie przedłużają ich rozwój. W terenie wahał się on od 7 do 11 dni (tab. IV), w laboratorium od 5 do 9 dni (tab. V). Decydujący wpływ na rozwój generacji wywierają temperatura, wilgotność oraz opady. Cały cykl rozwojowy trwał w terenie średnio od 50,6 do 73,6 dni (tab. IV), w laboratorium 28,0-60,8 dni (tab. V). U badanych gatunków występuje tylko jedno pokolenie w roku.

Pierwsze okazy młodych imagines *C. rubiginosa* Müll. spotyka się w I lub II połowie lipca, *C. vibex* L. przeważnie w II połowie lipca, a pozostałych gatunków na początku sierpnia; nasilenie pojawu obserwuje się w sierpniu oraz w I połowie września, a około połowy października znajdowano tylko nieliczne okazy (ryc. 1). U świeżo wylęgłych imagines następuje w ciągu pierwszej doby

ich życia zmiana barwy kutikuli przedplecza i pokryw, a pełne wybarwienie obserwuje się dopiero po przezimowaniu, tuż przed okresem godowym. Zmiana barwy zależy od karotenoidów, obecnych w liściach roślin pokarmowych. Młode imagines żerują bardzo intensywnie w pierwszych 2-3 tygodniach życia, po czym natężenie ich żeru słabnie. Obrazy żerów młodych chrząszczy C. rubiginosa Müll. i C. vibex L. na liściach roślin pokarmowych przedstawia tablica XXX, a C. viridis L. i C. flaveola Thunbg. tablica XXXI. Budowa obrazów żeru jest bardzo charakterystyczna dla każdego gatunku. U młodych imagines, nie dojrzewających płciowo w roku wylęgu, występuje zjawisko diapauzy. Charakteryzują ją: ogólny spadek metabolizmu, zmniejszenie ilości wody wolnej w ustroju, spadek intensywności oddychania, zmniejszenie aktywności fermentów, zwiększenie ciśnienia osmotycznego oraz duża ilość substancji zapasowych (tłuszczowych). Przyczyną powstawania diapauzy są zmiany długości dnia oraz jakości pokarmu; natomiast o terminie jej następowania, połączonego ściśle z migracją na zimowanie, decydują temperatura, wilgotność i długość dnia. Przed zapadnięciem w ten stan chrząszcze migrują z terenu łąki w rejony leśne, gdzie wyszukują odpowiednie miejsca do przezimowania. Zimujące chrząszcze, będące w stanie diapauzy właściwej, wykazują dużą odporność na niską temperaturę, wysoką wilgotność oraz infekcje grzybkowe. Ilość wody wolnej wzrasta stopniowo w ieh ciele i osiąga na wiosnę wartość 60,00—70,00 %, przy której zachodzi wiosenna reaktywizacja chrząszczy, a następnie ich dojrzewanie.

Sezonowe wahania liczebności stadiów rozwojowych tarczyków w latach 1966—1971, w zależności od czynników klimatycznych, przedstawiono na rycinach 5—10. Terminy i przebieg pojawu poszczególnych stadiów, maksima ich liczebności, długość okresu występowania i rozwoju zależą w istotny sposób od czynników klimatycznych (temperatura, opady, wiatr). Niskie temperatury, połączone z opadami i wiatrami, powodują silne załamania w liczebności poszczególnych stadiów i spadek ich aktywności. Sezonowe wahania liczebności pozostają w ścisłym związku z wielkością populacji tych chrząszczy. Metoda wyłowu zupełnego starych chrząszczy, zastosowana w latach 1969—1971, umożliwiła ocenę wielkości populacji badanych gatunków (tab. VI). Stwierdzono, że C. rubiginosa Müll. jest gatunkiem dominującym i najbardziej licznym na łące, C. vibex L. i C. viridis L. są niezbyt liczne, a C. flaveola Thunbg. rzadki.

Czasokresy składania jaj oraz przebiegi krzywych płodności samic różnowiekowych przedstawiono na rycinach 8—10. Maksymalna płodność u samic tarczyków występuje głównie w czerwcu i w połowie lipca, a więc w okresie najdłuższych dni (tab. II), przy czym szczyty liczebności jaj u samic jednorocznych są niemal zawsze wyższe niż u samic różnowiekowych. Niskie temperatury i silne opady powodują załamania w przebiegu krzywych płodności (ryc. 10). Liczby jaj składanych średnio przez jedną samicę tarczyków w terenie przedstawia tab. VII, w laboratorium — tab. VIII. Największą liczbę jaj składają samice C. rubiginosa Müll.: od 285—344 sztuk, u pozostałych gatunków liczby te wahają się od 200 do 280 sztuk. Płodność samic maleje w drugim i trzecim roku ich życia (tab. VII), przy czym najsilniej zaznacza się to u 2-letniej samicy

C. flaveola Thunbg. (spadek ponad 5-krotny) oraz u 3-letniej samicy C. vibex L. (spadek ponad 2-krotny). Zmiany stopnia zagęszczenia stadiów rozwojowych tarczyków badano w latach 1966, 1968 i 1970 (tab. IX—XI), równolegle z badaniami ilościowych zmian u roślin pokarmowych tych chrząszczy (por. ryc. 2—4). Stwierdzono, że średni stopień zagęszczenia populacji tarczyków wzrasta mimo znacznego zwiększenia się powierzchni płatów ich roślin pokarmowych, co szczególnie wyraźnie zaznacza się u starych chrząszczy. Maksymalne zagęszczenie imagines C. rubiginosa Müll. i C. vibex L. wynosiło na wiosnę 1966 roku średnio 0,3 okazu/m² i 0,02 okazu/m², a w 1970 roku odpowiednio 0,6 okazu/m² i 0,08 okazu/m². Stopień zagęszczenia u dwóch pozostałych gatunków badano tylko w latach 1968 i 1970. Maksymalne zagęszczenie starych imagines C. viridis L. w 1970 roku wynosiło średnio 1,1 okazu/m², u C. flaveola Thunbg. 0,1 okazu/m². W pozostałych stadiach rozwojowych prawidłowości powyższe układały się różnie, a u młodych imagines C. rubiginosa Müll. i C. vibex L. nawet zagęszczenie malało.

Stwierdzono, że bezpośrednimi przyczynami migracji młodych imagines na zimowanie są czynniki abiotyczne: temperatura, nasłonecznienie, długość dnia, wilgotność; pośrednimi natomiast biotyczne — jakość pokarmu, stan fizjologiczny chrząszczy. Aktywność chrząszczy zależy od długości dnia, przy której nastąpił wylęg. Im później nastąpił pojaw chrząszczy, tym krótszy był okres ich aktywności. Temperatury minimalne niższe od +13,0°C, częste mgły oraz wzrastający stopień zacienienia łąki w jesieni wpływają stymulująco na migracje chrząszczy w rejony leśne, gdzie zimują one w ściółce na głębokości 5—8 cm. Wiosną następuje zjawisko powrotu starych chrząszczy z lasu na teren łąki. Przebieg migracji imagines badanych gatunków przedstawiono na ryc. 5—10.

Wpływ czynników abiotycznych (temperatura, opady, wiatr) na stopień redukcji jaj przedstawia tabela XII. Stwierdzono, że stopień ten wahał się u badanych gatunków w poszczególnych latach od 23,68 do 72,54%. Przebieg warunków pogodowych rzutuje również w ogromnym stopniu na rozwój i śmiertelność larw. Niskie temperatury, długie okresy opadów i wiatry powoduja silne zahamowanie rezwoju oraz redukcje larw, szczególnie w I i II stadium. Stopień redukcji poszczególnych stadiów rozwojowych tarczyków w terenie w latach 1969—1971 przedstawiono w tabeli XIII. Larwy I i II stadium sa redukowane w 1/3 swej liczebności przez czynniki abiotyczne, w pozostałych stadiach natomiast zdecydowana role odgrywaja czynniki biotyczne. W latach 1968—1972 przeprowadzono 4-krotnie kontrolowanie zimowania młodych imagines badanych gatunków w lesie gradowym, na zboczu o ekspozycji południowej w Dolinie Saspowskiej, co umożliwiło ocene stopnia śmiertelności chrzaszczy w tym okresie (tab. XIV). Stwierdzono, że śmiertelność okazów wahała się od 20,83 do 58,33%. Ponadto ustalono, że z ogólnej liczby chrząszczy zdechłych podczas zimowania aż 50-70% okazów ginie na przełomie zimowo-wiosennym. Czteroletnie obserwacje nad długością życia tych samych okazów z czterech

gatunków tarczyków umożliwiły sporządzenie tabeli życiowej tych chrząszczy (tab. XV).

Insolacja odgrywa ważną rolę i decyduje o występowaniu oraz rozwoju populacji tarczyków na łące. Stwierdzono wyraźną korelację dodatnią między występowaniem populacji tarczyków w obrębie zasięgów ich roślin pokarmowych na łące a stopniem jej nasłonecznienia w ciągu sezonu wegetacyjnego (ryc. 11—17). Nasłonecznienie wpływa istotnie na przebieg powrotu chrząszczy z zimowisk na łąkę oraz ich dojrzewania w okresie wiosennym, działa stymulująco na rozwój larw oraz na migracje młodych imagines w rejony zimowania.

Czynnikami biotycznymi, działającymi redukująco na liczebność populacji tarczyków, są pasożyty (endopasożyty, oofagi), drapieżcy oraz mikroorganizmy. Ich skład gatunkowy ustalony przez różnych autorów przedstawia tabela XVI, a przez autora pracy tabela XVII. Stopień redukcji jaj w latach 1969—1971 (tab. XIII) waha się u badanych gatunków od 10,92 do 51,39 %. Decydującą rolę w redukcji jaj tarczyków odgrywają pasożytnicze błonkówki (tab. XVII). Stopień spasożytowania przez nie jaj wahał się w kolejnych latach od 4,80 do 49,34 % (tab. XVIII). Procentowy udział poszczególnych gatunków błonkówek w redukcji jaj tarczyków w latach 1968—1971 przedstawiono w tabeli XIX. Liczba błonkówek w jednym jaju wahała się od 1 do 4 sztuk. Rozwój pasożyta trwa zawsze dłużej niż okres embrionalnego rozwoju tarczyków (tab. XX). Śmiertelność jaj wywołana zaburzeniami w rozwoju wahała się od 0,36 do 14,00 % (tab. XVIII). Stopień śmiertelności jaj zniszczonych przez drapieżne roztocze i kosarze wahał się od 0,76 do 6,12 % (tab. XVIII).

Ocenę stopnia redukcji stadiów larwalnych i poczwarek tarczyków przeprowadzano w latach 1969—1971. Stwierdzono (tab. XIII), że najsilniejsza redukcja występowała w I stadium larwalnym (niekiedy w stadium jaja) i wynosiła 15,54-63,08%. W następnych stadiach larwalnych procent redukcji stale zmniejszał się (oprócz V stadium C. viridis L.). Całkowita redukcja stadiów rozwejowych tarczyków, w odniesieniu do wyjściowej liczby jaj, które dotrwały zdrowe na roślinach, jest bardzo wysoka i waha się od 98,00 do 99,50 %. Krzywa redukcji stadiów rozwojowych ma kształt litery L (ryc. 18). Hodowle laboratoryjne stadiów rozwojowych tarczyków, prowadzone w latach 1968-1971 (materiał zebrano w terenie), umożliwiły ocenę procentowego udziału poszczególnych grup reducentów w niszczeniu larw i poczwarek tych chrząszczy (tab. XXI). Największą rolę w redukcji tych stadiów odgrywają pasożytnicze błonkówki. Stopień redukcji wywołanej przez nie wahał się od 11,05 do 73,68 %. Procentowy udział poszczególnych gatunków błonkówek w redukcji tych stadiów przedstawia tabela XIX. Błonkówki składają do ciała larw tarczyków od 1 do 65 jaj. Na jedną larwę przypada średnio 7,0—18,6 sztuk błonkówek. Wyleg błonkówek z ciała gospodarza następuje po upływie 3 do 5 tygodni od momentu złożenia jaj w ciele tego ostatniego. Istotną rolę w redukcji stadiów rozwojowych tarczyków odgrywają pasożytnicze nicienie (tab. XVII). Stopień redukcji larw i poczwarek, wywołanej przez nie (tab. XXI), wahał się od 1,85 do 37,41%. Procentowy

udział poszczególnych rodzajów nicieni w redukcji tarczyków przedstawia tabela XXII. Liczba nicieni w jednej larwie tarczyka waha się od 1 do 9 sztuk i wynosi średnio 1,6 do 4,0 sztuk.

W poważnym stopniu na ograniczenie liczebności larw tarczyków wpływają drapieżcy (tab. XVII). Stopień redukcji larw wywołanej przez nich wahał się od 2,04 do 23,68% (tab. XXI). Spośród nich najsilniejszą redukcję larw tarczyków powodują pluskwiaki, a zwłaszcza Picromerus bidens L., który w 1967 roku wpłynął istotnie na liczebność larw (por. ryc. 6). Stwierdzono, że jedna nimfa tego pluskwiaka wysysa w laboratorium średnio w ciągu doby 2,5 larw, a w terenie 1,2 larw; imago natomiast wysysa w laboratorium średnio 3,0 larwy na dobę, a w terenie 1,3 larw. Stopień redukcji larw i poczwarek tarczyków, wywołanej przez drobnoustroje (tab. XXI), wahał się od 0,60 do 53,33%. Stwierdzono ścisłą zależność między wielkością procentowego udziału poszczególnych czynników biotycznych w redukcji larw i poczwarek (tab. XXI) a warunkami klimatycznymi w kolejnych latach badań (por. ryc. 7—10). Ustalono, że nicienie i błonkówki redukują najbardziej V stadium oraz przedpoczwarki, mikroorganizmy — przedpoczwarki i poczwarki, a drapieżcy — I i II stadium larwalne tarczyków.

Stopień redukcji imagines tarczyków, spowodowanej przez pasożytnicze muchówki, przedstawia tabela XXIII. Stwierdzono, że u *C. rubiginosa* MÜLL. jest on bardzo wysoki i waha się od 62,57 do 85,00%. W latach 1966—1971 pasożyt powodował silny i gwałtowny spadek liczebności starych chrząszczy tego gatunku zawsze w I połowie maja (por. ryc. 5—10). Stopień redukcji chrząszczy *C. flaveola* Thunbg., wywołanej przez inną pasożytniczą muchówkę, wyniósł w 1970 roku 20,00%. Procentowy udział poszczególnych rodzajów pasożytniczych nicieni w redukcji imagines *C. rubiginosa* MÜLL. przedstawia tabela XXII. Śmiertelność naturalną chrząszczy z powodu wycieńczenia przedstawiono w tabeli XXIII; wielkość jej wahała się od 4,00 do 23,56%. Liczebność imagines przeżywających w latach 1967—1970 wynosiła zaledwie 5,00 do 15,00% (tab. XXIII).

Wartość konsumpcji (C), wydalonych ekskrementów (FU) i asymilacji (A) larw oraz młodych imagines C. rubiginosa Müll. i C. vibex L. przedstawiono w tabeli XXIV. Larwa C. rubiginosa Müll. konsumuje podczas swego rozwoju 110,1 mg biomasy liści (58,9 cal), a C. vibex L. 103,2 mg biomasy (55,2 cal). Tempo zjadania pokarmu podwaja się w kolejnych stadiach rozwoju (tab. XXIV), a maksymalna konsumpcja występuje w V stadium larwalnym. Młode imago C. rubiginosa Müll. konsumuje w ciągu 45 dni życia 305,6 mg biomasy liści (157,9 cal), a C. vibex L. 292, 3 mg biomasy (151,0 cal). Larwa C. rubiginosa Müll. wydala w ciągu swego rozwoju 23,6 cal w postaci ekskrementów, a C. vibex L. 21,7 cal. Młode imago C. rubiginosa Müll. wydala w ciągu 45 dni życia 33,0 cal, a C. vibex L. 29,4 cal. Całkowita asymilacja niezbędna dla odbycia pełnego rozwoju larwy C. rubiginosa Müll. wynosi 35,6 cal, a C. vibex L. 33,5 cal (tab. XXIV). Wartości asymilacji energii wynoszą u młodych imagines C. rubiginosa Müll. 125,0 cal, u C. vibex L. 121,6 cal.

Zawartość wody oraz suchej masy w poszczególnych stadiach rozwojowych obu gatunków przedstawiono na ryc. 19. Wartość kaloryczną jednego osobnika tarczyków C. rubiginosa Müll. i C. vibex L. podczas ich rozwoju przedstawia ryc. 20. Wartości produkcji ciała (P) larw oraz młodych imagines obu gatunków przedstawiono w tabeli XXV. Larva C. rubiginosa Müll. wyprodukowała w okresie swego rozwoju 17,8 mg biomasy ciała (20,5 cal), a C. vibex L. 18,4 mg biomasy (19,6 cal). Przyrost biomasy ciała w poszczególnych stadiach zwiększa się wyraźnie z wiekiem larw. Produkcja biomasy ciała u 45-dniowych młodych imagines, obliczona z różnicy ciężaru końcowego i początkowego, wynosi u C. rubiginosa Müll. 5,7 mg, u C. vibex L. 4,2 mg; jej wartość natomiast, uzyskana z sumy wszystkich przyrostów biomasy w okresie 45 dni, wynosi u pierwszego 8,3 mg, u drugiego 7,5 mg. Wartość produkcji, oceniona w suchej masie, wynosi u C. rubiginosa Müll. 6,6 mg (52,0 cal), u C. vibex L. 6,1 mg (40,7 cal). Przebieg krzywej konsumpcji pokarmu na tle krzywej wzrostu ciężaru ciała w stadiach rozwojowych obu gatunków przedstawiono na ryc. 21.

Wartości budżetu energetycznego, wyrażone w cal/okaz, przedstawiono w tabeli XXVI, współczynniki wydajności energetycznej natomiast w tabeli XXVII. Wydajność produkcji (P/C) jest najwyższa u larw I stadium i wynosi u C. rubiginosa Müll. 50,80%, u C. vibex L. az 57,02%; następnie spada stopniowo w kolejnych stadiach i osiąga najniższą wartość w V stadium, u pierwszego 33,44%, u drugiego 34,68%. Wartość średnia tego współczynnika waha się u larw tarczyków od 39,97 do 40, 44%. Natomiast u młodych imagines wydajność produkcji jest znacznie niższa i wynosi u C. rubiginosa Müll. 32,94%, u C. vibex L. 26,96%. Współczynnik asymilacji (A/C) u larw obu gatunków jest bardzo wysoki i wynosi średnio u C. rubiginosa Müll. 62,17%, u C. vibex L. 63,47%. W przypadku młodych imagines uderzają jeszcze wyższe wartości tego współczynnika, które wynoszą u pierwszego 79,13%, u drugiego 80,52%. Współczynnik R/C określa procentową wielkość strat oddechowych, związanych ze wzrostem okazów. Jego wartość średnia wynosi u larw C. rubiginosa Müll. 22,20%, u C. vibex L. 23,03%. U młodych imagines wartości te są bardzo wysokie i wynoszą odpowiednio 46,19% i 53,56%, a więc przewyższają aż dwukrotnie straty oddechowe larw.

Konsumpcja tlenu na jednostkę biomasy ciała (tab. XXVIII) jest najwyższa w I stadium larwalnym i wynosi u *C. rubiginosa* Müll. 27,7 mm³O₂/mg/h, u *C. vibex* L. 25,1 mm³O₂/mg/h; następnie wartość jej spada stopniowo wraz ze wzrostem ciężaru ciała okazów i wykazuje minimum u pierwszego w stadium poczwarki (2,8 mm³O₂/mg/h), u drugiego w stadium przedpoczwarki (2,4 mm³O₂/mg/h). U świeżo wylęgłych imagines jej wartość wzrasta do 5,5 mm³O₂/mg/h u *C. rubiginosa* Müll. i 6,1 mm³O₂/mg/h u *C. vibex* L.; po upływie 45 dni życia chrząszczy wykazuje ona nieznaczny spadek. Graficzny przebieg tych zmian ilustruje ryc. 22. Ilość energii zużytej przez osobnika w ciągu 24 godzin w procesach metabolizmu (tab. XXVIII) zwiększa się wyraźnie (z paroma wyjątkami) ze wzrostem ciężaru ciała. Straty energii w ciągu 24 godzin u młodych imagines są prawie dwukrotnie wyższe od maksymalnych strat larw i wynoszą u *C. rubi-*

ginosa Müll. 10,0 cal/okaz/dobę, u C. vibex L. 11,4 cal/okaz/ dobę. Podczas swego rozwoju od wylęgu z jaj do pojawu imago (tab. XXVIII), osobnik C. rubiginosa Müll. zużytkowuje 30 990,96 mm³O₂/151,7 cal), a C. vibex L. 31 925,52 mm³O₂/156,3 cal). Straty energii u młodych imagines w ciągu 45 dni ich życia wynoszą u pierwszego 385,0 cal, u drugiego aż 415,4 cal. Duże różnice między wartością R doświadczalną (tab. XXVIII) a wyliczoną z budżetu (tab. XXVI) mogą wynikać z różnic warunków, w których przeprowadzano doświadczenia żywieniowe i respirometryczne.

W wyniku obserwacji terenowych i hodowli laboratoryjnych stwierdzono, że C. rubiginosa Müll. i C. vibex L. niszczą silnie ostrożeń polny Cirsium arvense (L.) Scop.; C. viridis L. uszkadza skutecznie miętę polną Mentha arvensis L., czyściec błotny Stachys palustris L. i poziewnik miękkowłosy Galeopsis pubescens Bess., a C. flaveola Thunbe. gwiazdnicę pospolitą Stellaria media VILL. Ustalono ponadto, że C. nebulosa L. i C. nobilis L. niszczą głównie komosę białą Chenopodium album L., a rzadko i nieznacznie buraka cukrowego Beta vulgaris L.; H. subferruginea Schrnk. natomiast niszczy zdecydowanie powój polny Convolvulus arvensis L. Stwierdzono, że tarczyki z 4 pierwszych gatunków mnożą się masowo w warunkach laboratoryjnych, ich całkowity rozwój trwa zaledwie około 30 dni, istnieje więc realna możliwość użycia chrząszczy i larw tych gatunków do biologicznego zwalczania uciążliwych chwastów polnych.

**РЕЗЮМЕ** 

Исследования проведено в 1966—1971 гг. на лугу Arrhenatheretum elatioris alchemilletosum в Сонсновской Долине Ойцовского Национального Парка. В последующих годах с апреля по октябрь, в 7—30-дневных интервалах изучено 6 видов щитоносок: Cassida rubiginosa Müll. и С. vibex L. на листьях Cirsium oleraceum (L.) Scop., С. viridis L. на листьях Mentha longifolia (L.) Huds., С. flaveola Thunbg. на листьях Stellaria graminea L., а также вне исследуемой площади С. hemisphaerica Hbst. на листьях Silene nutans L. и С. prasina Ill. на листьях Achillea millefolium L. Кроме того велись наблюдения за С. nebulosa L. и С. nobilis L. на листьях Chenopodium album L. на территории парка, а также Hypocassida subferruginea Schrnk. на листьях Convolvulus arvensis L. вне его пределов.

В результате проведенных исследований мы познакомились с фенологией появления стадий развития щитоносок (рис. 1).  $C.\ rubiginosa\ M$ ÜLL. появляется раньше всех на лугу, а  $C.\ vibex\ L.$ ,  $C.\ viridis\ L.$  и  $C.\ flaveola\ Thungg.$  прилетают поочерёдно в недельных интервалах. Появление жуков на лугу зависит от климатических условий (температура, инсоляция) и происходит при максимальной температуре превышающей  $+13.0^{\circ}$  С. Измерения ареала питательных растений щитоносок на исследуемом участке, проведенные в 1966, 1968 и 1970 гг., обнаружили отчётливые количественные изменения у этих растений (рис. 2—4), вызванные не кошением луга. Перечень кормовых растений щитоносок представлено на таблице I. У жуков отмечается весной дополнительное питание, которое обуславливает их дозревание.

Копуляция у щитоносок, а также откладка яиц происходит при температурах превышающих 18,0°С, а оптимум температур составляет 20,0—25,0°С. Откладка яиц начинается, когда продолжительность дня составляет больше 15 часов (таб. II) и продолжается от мая до половины августа (ср. рис. 1). Средняя продолжительность жизни жуков щитоносок (таб. III) составляет ок. 1 года, минимальная ок. 1 месяца, максимальная — почти 4 года у С. rubiginosa Müll., 3 года у С. vibex L. и С. viridis L., 2 года у С. flaveola Thunbg. Самцы живут короче самок и разницы у обоего пола колеблются от 2 месяцев у С. flaveola Thunbg. до почти 2 лет у С. rubiginosa Müll. Исследуемые виды щитоносок принадлежат к группе мезо- и гигрофильных, проявляют дневную ритмику активности, а также ссобенную склонность к солнечному свету и отчётливый положительный фотстаксис.

Яйца щитоносок можно найти, главным образом, на нижней стороне листьев кормовых растений, а их количество в кладке у С. rubiginosa Müll. составляет 2—17 штук, у С. vibex L. и С. flaveola Thunbg. 1—3 штук, у С. viridis L. 5—15 штук. Эмбриональное развитие в полевых условиях продолжается 11—33 дней (таб. IV), а в лаборатории 7—17,5 дней (таб. V). Первые экземпляры личинок встречаются в конце мая или в начале июня (ср. рис. 1). Свеже вылупившиеся личинки питаются на нижней стороне листьев кормовых растений, кроме того, у них встречается т. наз. общительное питание, которое продолжается до конца второй стадии. Личинки  $C.\ rubiginosa\ \mathbf{M}$ ÜLL.,  $C.\ vibex\ \mathbf{L}.\$ и  $C.\ viridis\ \mathbf{L}.\$ сбрасывают линьку на протяжении всей своей жизни 5 раз (пятая линька до куколки), а C. flaveola Thunbg. лишь 4 раза. Развитие личинок на местности продолжается в среднем 21,4—37,7 дней (таб. IV), в лаборатории — 14—31 дней (таб. V). Окукливание происходит, главным образом, на нижней стороне листьев. Период преджуколки в полевых условиях продолжается 2—4,5 дней (таб. IV), в лаборатории 2—3 дня (таб. V). Развитие куколок исследованных видов на местности колеблется от 7 до 11 дней (таб. IV), в лаборатории от 5 до 9 дней (таб. V). Период, в течение которого обитают в природе предкуколки и куколки составляет 1—2,5 месяца (ср. рис. 1). Решающее влияние на развитие генерации имеют температура, влажность и осадки. Весь цикл развития в природе в среднем продолжается 50,6— 73,6 дней (таб. IV), в лаборатории 28—60,8 дней (таб. V). У исследованных видов отмечено лишь одно поколение в году.

Первые экземпляры молодых имаго *C. rubiginosa* Müll. встречаются в I или II половине июля, *C. vibex* L. часто во II половине июля, а остальных видов в начале августа (ср. рис. 1). У свеже вылупившихся жуков в течение первого дня их жизни происходит изменение цвета кутикулы переднеспинки и надкрылий, а полное потемнение наблюдается лишь после зимовки, непосредственно перед периодом спаривания. Строение образа жирования очень характерное для каждого вида. У молодых имаго, которые не достигают полового созревания в году вылупления отмечается диапауза. Причиной диапаузы является изменение длины

дня, а также качества корма; но о периоде её выступления, связанном тесно с миграцией на зимовку, решают температура, влажность и длина дня.

Сезонные колебания численности стадий развития щитоносок в 1966—1971 гг., в зависимости от климатических факторов, представлено на рисунках 5—10. Колебания численности тесно связаны с величиной популяции жуков (таб. VI). Констатировано, что С. rubiginosa Müll. доминирующий вид и наиболее многочислен на лугу, С. vibex L. и С. viridis L. немногочисленны, а С. flaveola THUNBG. — редкая. Кривые плодовитости различновозрастных самок изображены на рисунках 8—10. Количество яиц, откладываемое в среднем одной самкой щитоносок в природе представлено на таб. VII, а в лаборатории на таб. VIII. Плодовитость самок уменьшается во втором и третьем году их жизни. Изменения степени плотности стадий развития щитоносок в 1966, 1968 и 1970 гг. изображено на таб. IX—XI. Средняя степень плотности популяции старых жуков растёт вопреки увеличению поверхности участков их кормовых растений, а в остальных стадиях развития эти закономерности бывают различные. Активность жуков зависит от длины дня, при которой произошло вылупление. Чем позже произошло появление жуков, тем короче был срок их активности. Минимальные температуры ниже +13.0°C, частые туманы и возрастающая степень затемнения луга осению стимулирующим образом влияют на миграции жуков в лесные районы, где они зимуют в подстилке на глубине 5—8 см. Весной они возвращаются из леса на луг.

Влияние абиотических факторов (температура, осадки, ветер) на степень редукции яиц изображает таб. XII. Степень редукции отдельных стадий развития щитоносок в природных условиях в 1969—1971 гг. представлено в таб. XIII. Личинки I и II стадии редуцируются на 1/3 абиотическими факторами, а в остальных стадиях имеют значение биотические факторы. Проведенные 4 раза (в 1968—1972 гг.) контроли зимовки молодых имаго в суходольном лесу, на склоне с южной экспозицией в Сонсповской Долине, дали возможность оценить степень смертности жуков за этот период (табл. XIV), а также составить для них таблицу жизни (таб. XV). Констатировано отчётливую положительную корреляцию между присутствием популяции щитоносок в пределе ареала их кормовых растений на лугу и степению инсоляции его в течение вегетационного сезона (рис. 11—17). Инсоляция существенно влияет на возвращение жуков из зимовок на луг и их созревание в весенний период, стимулирующе влияет на развитие личинок и миграции молодых имаго в районы зимовки.

Биотическими факторами редуцирующе действующими на численность популяции щитоносок, являются паразиты (эндопаразиты, оофаги), хищники и микроорганизмы. Их видовой состав, установленный различными авторами представлено на таб. XVI, а автором настоящей работы в таб. XVII. Решающую роль в редукции яиц щитоносок играют паразитические перепончатокрылые (ср. таб. XVII), на что указывает степень поражения яиц (ср. таб. XVIII). Процентную долю отдельных видов перепончатокрылых в редукции яиц щитоносок в 1968— 1971 гг. представлено в таб. XIX. Развитие паразита продолжалось всегда дольше, чем период эмбрионального развития щитоносок (таб. XX). Полная редукция стадий развития щитоносок, в отношении к исходному количеству яиц, которые остались здоровыми на растениях, очень высокая и колеблется от 98,00 до 99,50%. Кривая редукции стадий развития напоминает букву L. (рис. 18). Процентный удел групп редуцентов в уничтожении личинок и куколок щитоносок в 1968—1971 гг. образует таб. XXI. Наибольшую роль здесь играют паразитические перепончатокрылые. Процентный удел отдельных видов перепончатокрылых в истреблении личинок и куколок изображает таб. XIX. Паразиты откладывают в тело щитоносок от 1 до 65 яиц. Существенную роль в редукции стадий развития щитоносок играют нематоды. Процентную долю отдельных родов нематод в редукции щитоносок представляет таб. XXII. Количество нематод в одной личинке щитоноски колеблется от 1 до 9 штук.

В большой степени на ограничение численности личинок щитоносок влияют хищники (ср. таб. XVII и XXI). Среди них сильнейшую редукцию личинок вызывают клопы и особенно *Picromerus bidens* L. Одна нимфа этого клопа сосёт за сутки от 1 до 4 личинок, а имаго от 1 до 6. Констатировано тесную зависимость между величиной процентной доли отдельных биотических факторов в редукции личинок и куколок (ср. таб. XXI), и климатическими условиями в очередных годах исследований (ср. рис. 7—10). Степень редукции имаго щитоносок паразитическими двукрылыми изображает таблица XXIII. В 1966—1971 гг. паразит вызывал сильное и резкое падение количества старых жуков *C. rubiginosa* МÜLL. в весенний период (ср. рис. 5—10). Численность имаго переживающих в 1967—1970 гг. составляла лишь 5,00—15,00% (ср. таб. XXIII).

Величину потребления пищи (С), выделенных экскрементов (FU) и ассимиляции (А) личинок и молодых имаго *C. rubiginosa* Müll. и *C. vibex* L. представляет таб. XXIV. Темп поедания корма удваивается в очередных стадиях развития, а максимальная консумпция отмечена в V стадии развития. Полная ассимиляция необходимая для полного развития личинок двух видов почти 4 раза ниже чем у молодых имаго. Содержание воды и сухой массы в стадиях развития обоих видов иллюстрирует рисунок 19, а величину калорий 1 щитоноски *C. ru-biginosa* Müll. и *C. vibex* L. во время их развития — рисунок 20. Величину продукции тела (Р) личинок и молодых имаго обоих видов изображает таб. XXV. Прирост биомассы тела у отдельных стадий отчётливо увеличивается с возрастом личинок. Кривую потребления корма на фоне кривой роста веса тела в стадиях развития обоих видов иллюстрирует рисунок 21.

Величину энергетического бюджета, выраженную в кал/экземпляр, представляет таб. XXVI, а коэффициенты энергетической производительности таб. XXVII. Средняя величина коэффициента производительности продукции (P/C) у личинок обоих видов выше чем у молодых имаго. Коэффициент ассимиляции (A/C) у личинок очень высок и в среднем составляет у *C. rubiginosa* МÜLL. 62,17%, у *C. vibex* L. 63,47%; у молодых имаго этот коэффициент ещё выше и соответственно составляет 79,13% и 80,52%. Средняя величина коэффициента дыхания (В/С) у молодых имаго обоих видов вдвое выше чем у личинок.

Потребление кислорода на единицу биомассы тела (таб. XXVIII) наиболее высокое в первой стадии развития личинки у обоих видов; величина его постепенно падает вместе с ростом веса тела экземпляров и минимума достигает при

диапаузе, а затем растёт у свеже вылупившихся имаго, а после 45 дневной жизни незначительно падает. Графический ход этих изменений показывает рисунок 22. Затраты энергии в течение 24 часов (ср. таб. XXVIII) у молодых имаго обоих видов почти вдвое выше максимальных затрат личинок. Во время развития от вылупления с яйца до появления имаго (ср. таб. XXVIII) —  $C.\ rubiginosa\ M\"ull.$  употребляет 30 990,96 мм³  $O_2$  (151,7 кал), а  $C.\ vibex\ L.\ 31 925,52\ mm³ <math>O_2$  (156,3 кал). Затраты энергии у молодых имаго в течение 45 дневной жизни составляют у первой 385,0 кал, у второй — 514,4 кал.

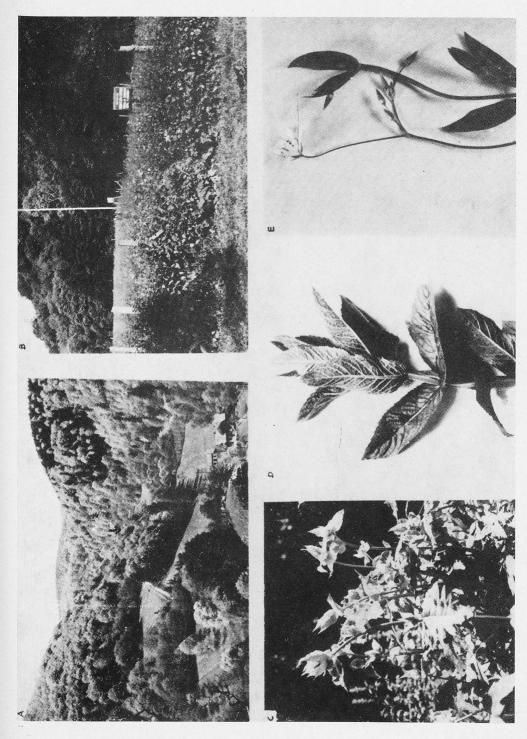
Констатировано, что *C. rubiginosa* MÜLL. и *C. vibex* L. повреждают сильно *Cirsium arvense* (L.) Scop.; *C. viridis* L. с успехом повреждает *Mentha arvensis* L., *Stachys palustris* L. и *Galeopsis pubescens* Bess., а *C. flaveola* Thunbg. — *Stellaria media* VILL. Кроме того констатировано, что *C. nebulosa* L. и *C. nobilis* L., главным образом, уничтожают *Chenopodium album* L., редко и незначительно *Beta vulgaris* L.; зато *H. subferruginea* Schrnk. решительно повреждает *Convolvulus arvensis* L. Щитоноски 4 первых видов в лабораторных условиях массово размножаются. Полное их развитие продолжается лишь около 30 дней. Существует реальная возможность использования жуков и личинок этих видов в биологической борьбе с сорняками.

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### Plate XXI

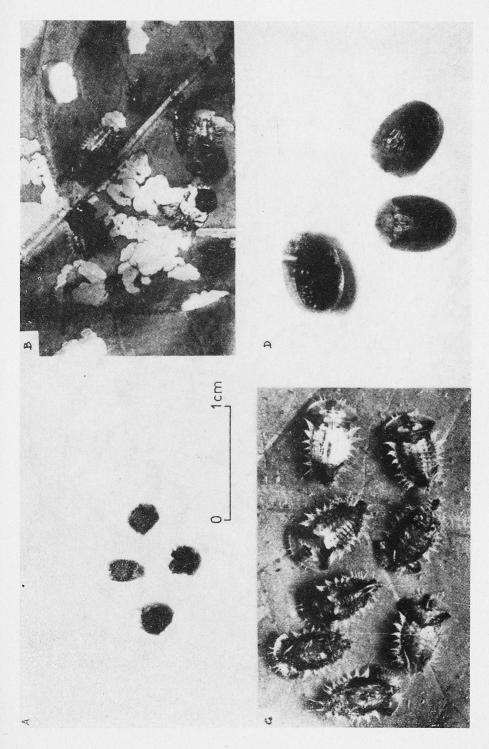
A — General view of the Sąspowska Valley in the Ojców National Park. The study area on the meadow Arrhenatheretum elatioris alchemilletosum is marked by an arrow, B — General view of the study area (July 4. 1970), C — Cirsium oleraceum (L.) Scop. — the host plant of Cassida rubiginosa Müll. and of C. vibex L., D — Mentha longifolia (L.) Huds. — the host plant of C. viridis L., E — Stellaria graminea L. — the host plant of C. flaveola Thunbg.



A. Kosior

# Plate XXII

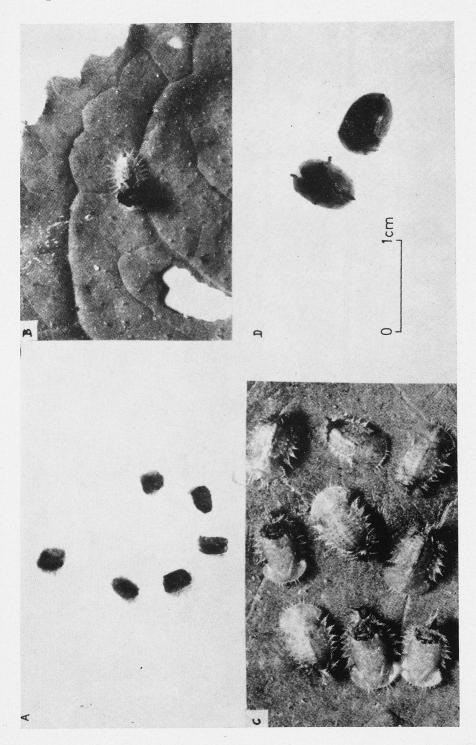
Development stages of Cassida rubiginosa Müll. A — egg batches, B — larvae, C — pupae, D — imagines



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## Plate XXIII

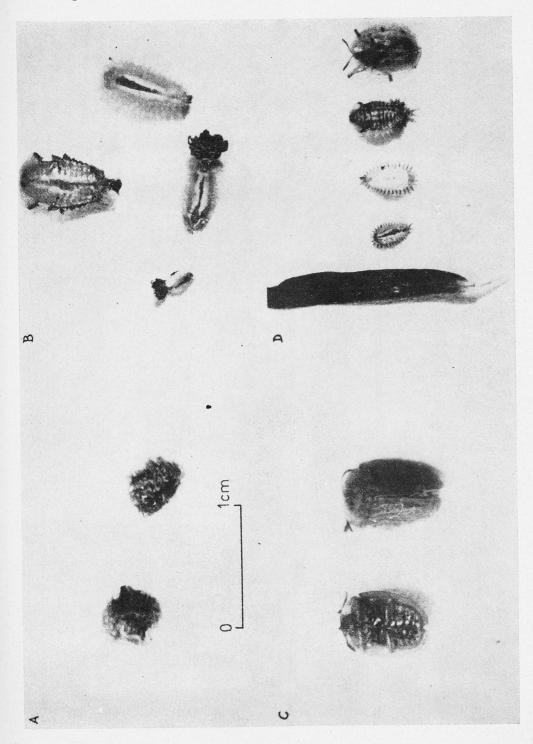
Development stages of Cassida vibex L. — A — egg batches, B — larva, C — pupae, D — imagines



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## Plate XXIV

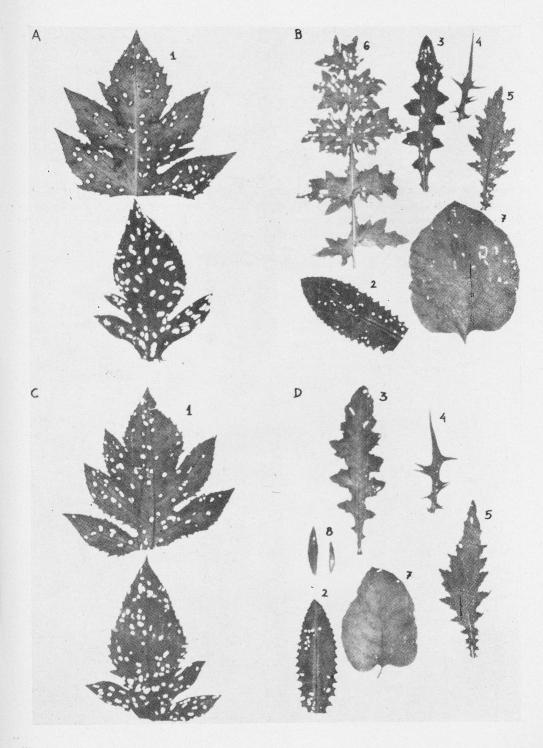
Development stages of Cassida viridis L. (A, B, C) and of C. flaveola Thunbg. (D). A — egg batches, B — larvae and pupa, C — imagines, D — egg, larvae, pupa, imago



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## Plate XXV

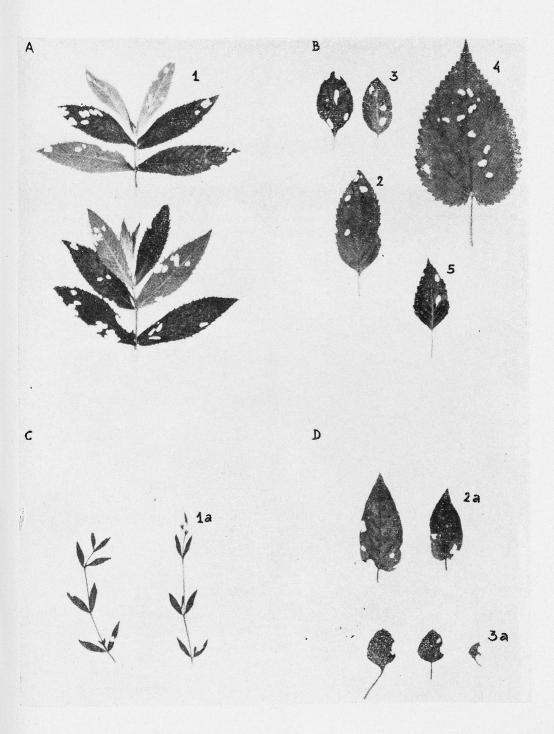
Leaves of host plants damaged by old imagines of Cassida rubiginosa Müll. (A, B) and of C. vibex L. (C. D): (1) Cirsium oleraceum (L.) Scop., (2) Cirsium rivulare (Jacq.) All., (3) Cirsium arvense (L.) Scop., (4) Cirsium lanceolatum (L.) Scop., (5) Cirsium palustre (L.) Scop., (6) Carduus acanthoides L., (7) Arctium lappa L., (8) Centaurea jacea L.



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## Plate XXVI

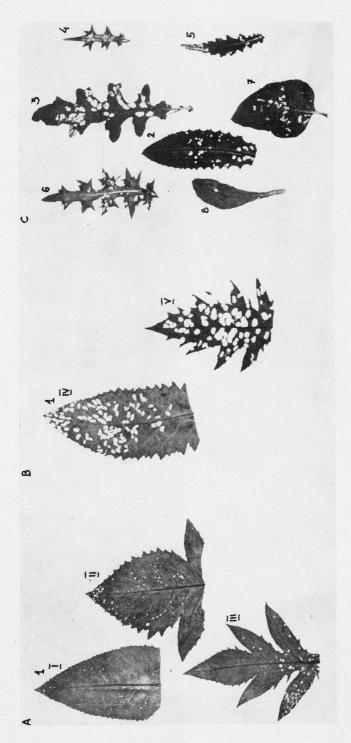
Leaves of host plants damaged by old imagines of Cassida viridis L. (A, B) and of C. flaveola Thunbg. (C. D): (1) Mentha longifolia (L.) Huds., (2) Mentha aquatica L., (3) Mentha arvensis L., (4) Stachys silvatica L., (5) Galeopsis pubescens Bess., (1a) Stellaria graminea L., (2a) Stellaria nemorum L., 3(a) Stellaria media Vill.



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### Plate XXVII

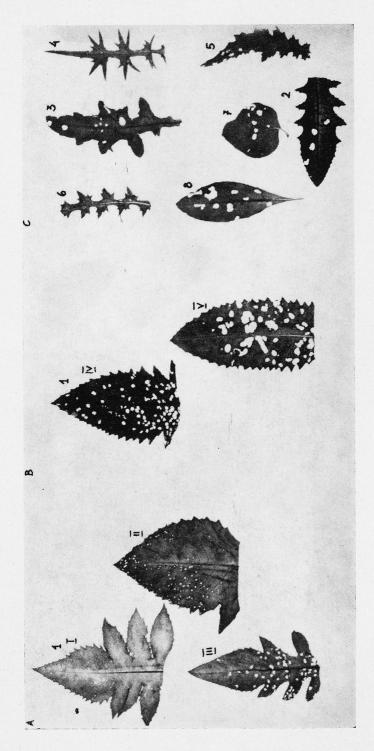
Leaves of host plants damaged by larvae of Cassida rubiginosa Müll. (A, B., C): (1) Cirsium oleraceum (L.) Scop. (I—V—successive larval instars), (2) Cirsium rivulare (Jacq.) All., (3) Cirsium arvense (L.) Scop., (4) Cirsium lanceolatum (L.) Scop., (5) Cirsium palustre (L.) Scop., (6) Carduus acanthoides L., (7) Arctium lappa L., (8) Sonchus arvensis L.



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## Plate XXVIII

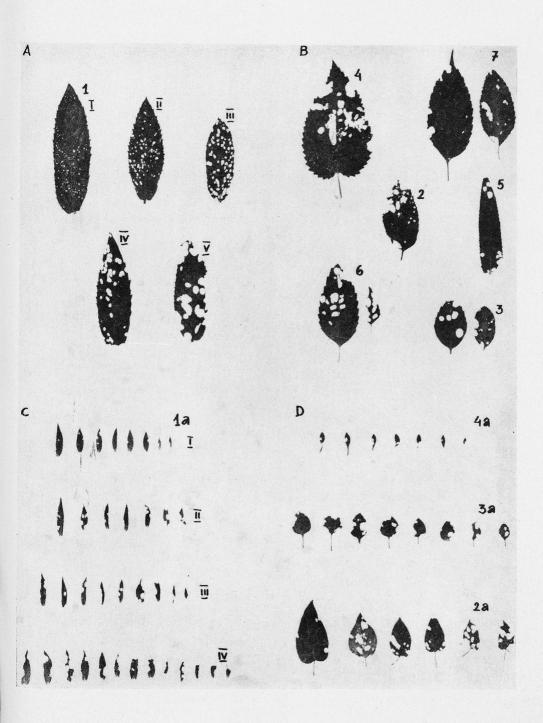
Leaves of host plants damaged by larvae of Cassida vibex L. (A, B, C): (1) Cirsium oleraceum (L.) Scop. (I—V—successive larval instars), (2) Cirsium rivulare (Jacq.) All., (3) Cirsium arvense (L.) Scop., (4) Cirsium lanceolatum (L.) Scop., (5) Cirsium palustre (L.) Scop., (6) Carduus acanthoides L., (7) Arctium lappa L., (8) Centaurea jacea L.



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### Plate XXIX

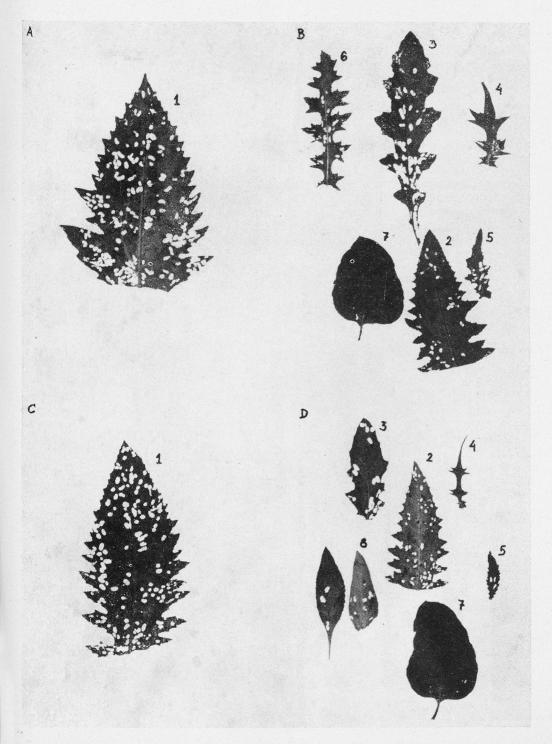
Leaves of host plants damaged by larvae of Cassida viridis L. (A, B) and of C. flaveola Thunbg. (C, D): (1) Mentha longifolia (L.) Huds. (I—V — successive larval instars), (2) Mentha aquatica L., (3) Mentha arvensis L., (4) Stachys silvatica L., (5) Stachys palustris L., (6) Galeopsis pubescens Bess., (7) Galeopsis tetrahit L., (1a) Stellaria graminea L. (I—IV — successive larval instars), (2a) Stellaria nemorum L., (3a) Stellaria media Vill., (4a) Cerastium vulgatum L.



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### Plate XXX

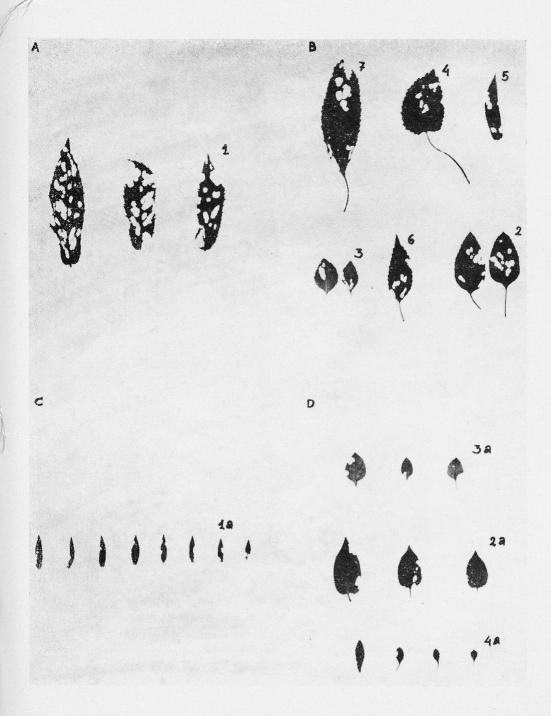
Leaves of host plants damaged by young imagines of Cassida rubiginosa Müll. (A, B) and of C. vibex L. (C, D): (1) Cirsium oleraceum (L.) Scop., (2) Cirsium rivulare (Jacq.) All., (3) Cirsium arvense (L.) Scop., (4) Cirsium lanceolatum (L.) Scop., (5) Cirsium palustre (L.) Scop., (6) Carduus acanthoides L., (7) Arctium lappa L., (8) Centaurea jacea L.



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### Plate XXXI

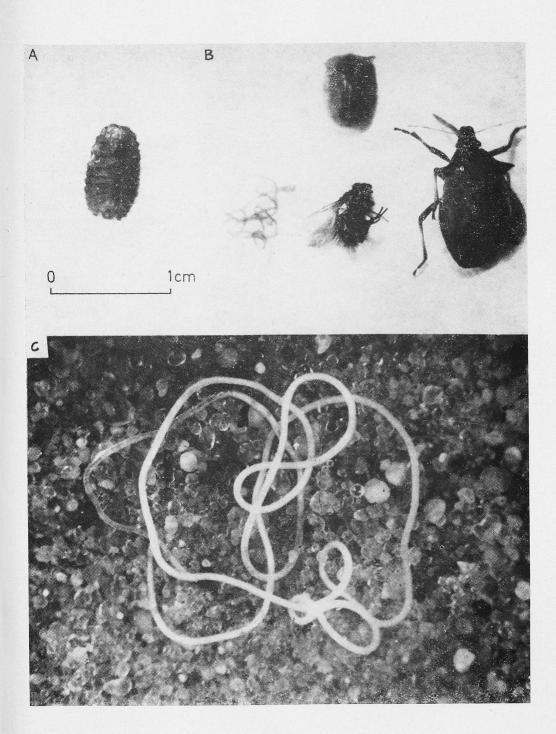
Leaves of host plants damaged by young imagines of Cassida viridis L. (A, B) and of C. flaveola Thunbg. (C, D): (1) Mentha longifolia (L.) Huds., (2) Mentha aquatica L., (3) Mentha arvensis L., (4) Stachys silvatica L., (5) Stachys palustris L., (6) Galeopsis pubescens Bess., (7) Galeopsis tetrahit L., (1a) Stellaria graminea L., (2a) Stellaria nemorum L., (3a) Stellaria media VILL., (4a) Cerastium vulgatum L.



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### Plate XXXII

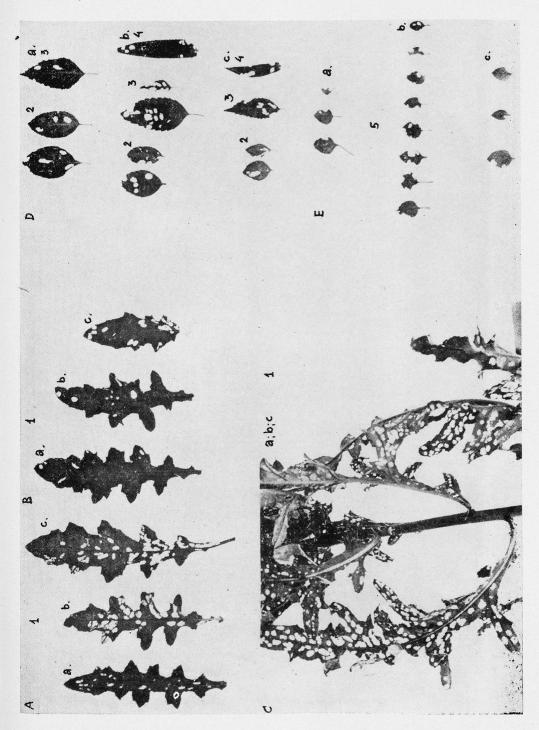
Parasites and predators preying upon the investigated cassid species. A—larva of Cassida viridis L. attacked by parasitic Hymenoptera (Chalcidoidea), B—(1) a dead imago of Cassida rubiginosa Müll. and (2) its parasite Dufouria chalybeata Meig. (Diptera), (3) a nematode Hexamermis sp. (Nematodes)—the parasite of larvae and of imagines, (4) a predatory bug Picromerus bidens L. (Hemiptera) attacks the larvae, C— a nematode Hexamermis sp. (Nematodes) (enlarged × 10)



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## Plate XXXIII

Leaves of host plants damaged by old imagines (a), by larvae (b), by young imagines (c) of Cassida rubiginosa Müll. (A, C), of C. vibex L. (B, C), of C. viridis L. (D) and of C. flaveola Thunbg. (E): (1) Cirsium arvense (L.) Scop., (2) Mentha arvensis L., (3) Galeopsis pubescens Bess., (4) Stachys palustris L., (5) Stellaria media VILL.



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Redaktor zeszytu: prof. dr W. Szymczakowski

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