Beitr. Ent. · Bd. 23 · 1973 · H. 5/8 · S. 325–340 · Berlin

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The density of the invertebrate summer fauna on the crowns of pine trees, *Pinus sylvestris*, in the central part of the Netherlands

With 7 text figures

Contents

1. Introduction

The study of the invertebrate fauna of pine tree crowns reported in this paper was originally started to assess the impact of predators on first instar larvae of the pine looper, *Bupalus piniarius* LINNAEUS (Geometridae), by way of the precipitine test. As shown earlier (KLOMP 1966) juvenile mortality is a predominant component in the causation of the density fluctuations of the moth, due to the great variability of the proportion of young larvae dying each year. Therefore, it proved desirable to analyse the agents causing this mortality, and invertebrate predators were the first to be considered.

However, when the study of the fauna had started, the pine looper population declined to extremely low density levels as a result of high pupal parasitism, which made the application of the precipitine test a rather useless enterprise. Therefore, in this paper the results of the sampling of the fauna will be given only to be compared with other faunal studies of pine trees performed elsewhere in Europe, and at a later stage, with the composition and the abundance of the fauna in the same pine forest when the pine looper will have returned to higher levels in later years.

In 1967 and 1968 the sampling was carried out in the area described by KLOMP (1966), the central part of 20 ha of pine forest, 25 km NW of Arnhem (plots 1 to 6; Fig. 1). The trees were about 15 m high, and their density amounted to 6 per 100 sq.m. From 1969 onwards samples were taken from the plots 9 and 10 (Fig. 1), the trees of which were about 10 m high with a density of 14 per 100 sq.m.

2. Methods

The sampling method used was that described by KLOMP (1966), to which the reader is referred for details. In one sample needled twigs cut from 2 randomly selected trees were collected, and mixed up in a big sack of cloth.

DOI: 10.21248/contrib.entomol.23.5-8.325-340

In 1967 three such samples were taken within a period of 3—7 days, and the three density measurements averaged, to give a mean density estimate for the sampling period. In 1968 and later years six such samples were taken within each sampling period of 2—3 (rarely up to 8) days. There were 4 sampling periods each year (usually one in each of the months June, July, August and September), except in 1968 when there were only 3 periods (Table 1). For mean dates of sampling periods see Figs . 4—7.

Table 1

Ranges of variation and mean numbers of shoots per sample (sack) in different years, and some other quantitative data on sampling

Years	Number of shoots per sample		No. of sampling periods	No. of samples per period	Total no. of samples
	Range	Mean			
1967	2030—4598	3137	4	3	12
1968	1886—3619	2561	3	6	18
1969	1628—3364	2363	4	6	24
1970	1508—3783	2549	4	6	24
1971	1697—3614	2679	4	6	24

The size of the samples was determined according to the method of KLOMP (1966), where the number of yearling shoots present in each sack was used as an index. The variation of this measure is indicated in Table 1.

The number of shoots per tree of average size amounted to 5500. The amount of twigs cut from one tree varied roughly from one tenth to three quarters of the crown for large and small trees respectively. All density estimates were expressed as numbers of animals present in a twig mass containing 1000 shoots of the current year, which roughly corresponds with $2^1/_4$ m^2 ground surface (KLOMP 1966). See Table 3 and Figs. 4—7.

After sampling the sacks were placed in a container filled with carbon dioxyde during a 24 hours period to kill the animals. Then the twigs were shaken separately over a large cloth spread on the ground of the field station, the animals collected and stored in ethyl alcohol.

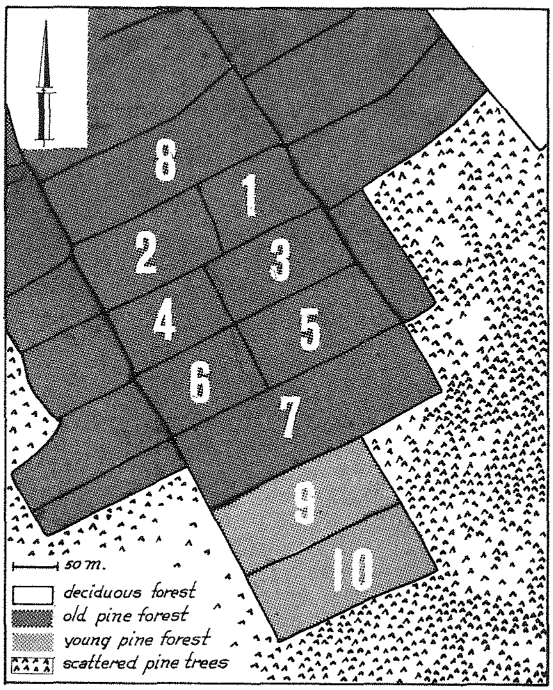

Fig. 1. The plots of pine forest where the density of the invertebrate fauna was assessed. Densely hatched areas (including the plots 1—8) are pine plantations 62 years old in 1967; thinly hatched areas (plots 9 and 10) are pine plantations 47 years old in 1967. These areas are surrounded by grounds covered with scattered pine trees of all ages, among which those of 40 to 60 years predominate, so that the dense parts resemble the plantations to a large extent

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3. Selection of the animals collected

The sampling method used was inappropriate for readily flying insects, and for leaf miners and species spinning silken tents, which can hardly be dislodged. Though such species are sometimes shaken off the twigs their numbers will be unreliable, and therefore are left out of consideration. Of the other animals the very small to small phytophagous species, like microlepidoptera, aphids, psocids, jassids, mites and the small neuropteron *Conwentzia psociformis* (CURTIS) were disregarded, because it appeared to be very time-consuming to pick them quantitatively from the cloth. All other animal groups were collected, both the phytophagous and the potentially predatory species.

The densities of the animals differ considerably. The rarest species go down to 0.04 per 1000 shoots, whereas the numbers of the commonest ones amount to 70 per 1000 shoots. When 6 samples are averaged, the coefficients of variation of the commonest species roughly equal 10–30%, and those of the rarest ones 100%. It is pointed out emphatically that for more reliable data at very low densities the size of the samples should be increased considerably, but in practice this proved to be impossible.

4. Results

The results of the sampling have been presented in four different ways:

a. The numbers of animals in different groups, mostly orders, have been summarized in histograms, to enable an easy comparison of the abundance within these groups, both within and between years (Figs. 4A–E).

b. A more detailed survey of the orders is presented in Table 3, where for species, present in at least 2 out of 5 years of study, the mean number over 1 sampling period is given for each year. The sampling period chosen is the one in which the species was most abundant over the year concerned.

c. The species present in only one year out of five years of study have been listed in Table 4 together with the year of their occurrence and the sampling period(s) in which they were found.

d. For the commonest species the complete data (numbers of juveniles plus adults in each sample) have been assembled in graphs (Fig. 5 A–C, Araneae; Fig. 6A–C, Coleoptera; Fig. 7A–C, Heteroptera), to show the annual levels of abundance and the changes in numbers in the course of the seasons.

The data presented in these tables and figures will be discussed in the sections 4.2 and 4.3, preceded by a brief consideration of the relation between the number of species and the number of individuals in the whole fauna of arthropods (section 4.1).

4.1. The number of species and the number of individuals

It has been stated by WILLIAMS (1964) that "if a random sample of individuals is taken from a mixed wild population of animals containing a large number of species, there appears to be a mathematical order in the relative abundance of the different species represented. In general, more species are represented by one individual than by two, more by two than by three, and so on. The frequency distribution of the number of species with different numbers of individuals is of the hollow curve type". It has been suggested by FISHER et al. (1943) that this distribution fits the logarithmic series, whereas PRESTON (1948) is of the opinion that it might be better represented by a log-normal distribution.

We have considered the species-abundance relations in the sampling collections of arthropods from the year 1970 as an example. The frequencies of the species represented by different numbers of individuals are given in the histograms of Fig. 2, which may be considered as approximating truncate normal distributions. This is corroborated by Fig. 3, where the frequencies of species obtained in August have been plotted as accumulated percentages on normal probability paper, and they appear to approximate a straight line. Similar distributions were found for the other months.

Further, it is shown in Table 2, where the total numbers of species and individuals for the 4 sampling periods of 1970 are given, that the numbers of species show notably little variation between periods. On the other hand, the numbers of individuals are much more variable: in August it is about twice the number of July. As shown in Fig. 4D, this is mainly due to the reproduction in the spider population.

DOI: 10.21248/contrib.entomol.23.5-8.325-340

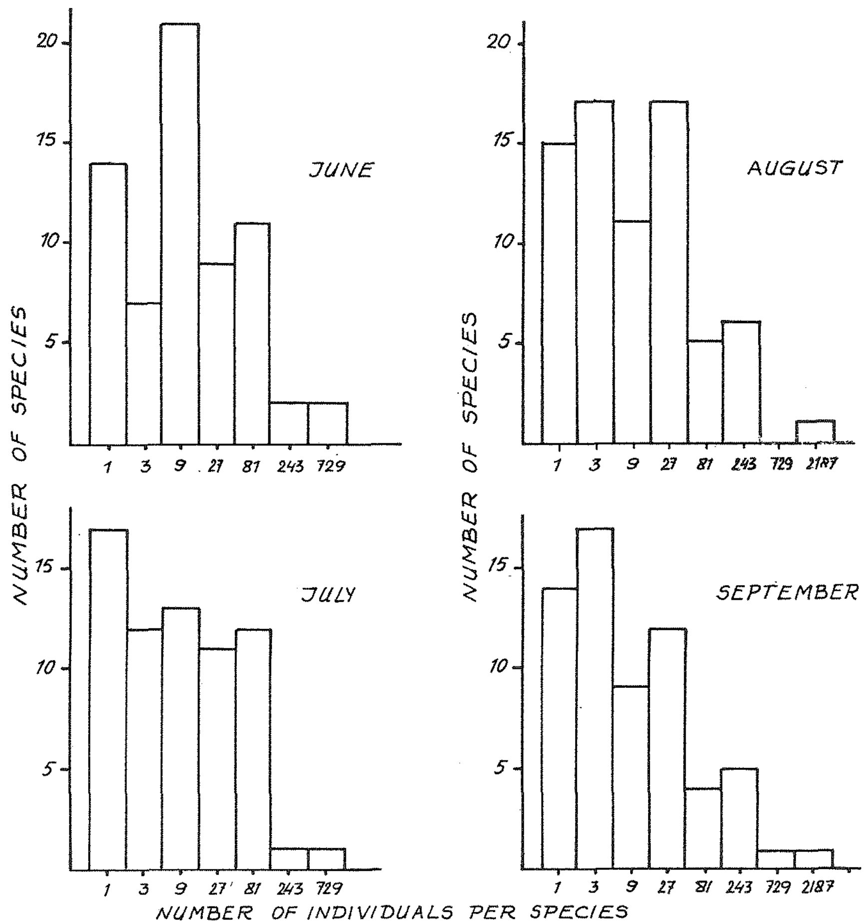

Fig. 2. Frequency distributions of the number of species over the number of individuals in the 4 sampling periods of 1970. The original data on abundance (abscissa) have been transformed to a log scale differing times 3: class 1 is composed of all species represented in the samples by 1 individual only; class 3 includes all species with 2, 3, and 4 individuals; class 9 all those represented by 5—13 individuals, and so forth

Table 2

The total number of species (S), the total number of individuals (N), and the index of diversity (α) for the 4 sampling periods of 1970

Sampling period	S	N	α
June	66	2838	12
July	68	1984	13
August	73	3751	13
September	64	3311	11

Using the numbers of Table 2, we determined the diversity indices for the sampling periods under consideration with the aid of the monogram presented by WILLIAMS (1964). The small variation of these indices, given in Table 2, indicates a fairly

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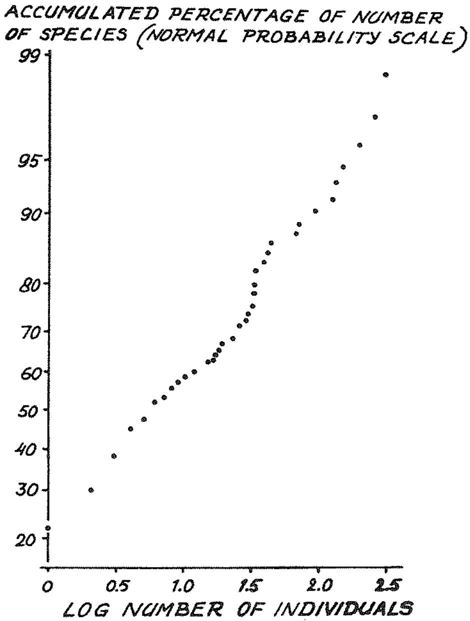

Fig. 3. Distribution of the accumulated percentage of the number of species over the number of individuals for the sampling period August 1970

constant diversity of the community over the year, notwithstanding a clear variability of the numbers of individuals.

4.2. The abundance and diversity in different orders of animals

All animals collected are arthropods and belong to 2 orders of arachnids (Araneae and Opilionida), and 8 orders of insects (Coleoptera, Dermaptera, Dictyoptera, Diptera, Heteroptera, Hymenoptera, Lepidoptera, and Neuroptera).

The numbers of individuals per 1000 pine shoots established within these orders have been assembled in Fig. 4 A—E. It is shown that the spiders constitute by far the most numerous group. This is due to the fact that nearly all species reproduce on the trees, mostly during mid- and late summer, giving an enormous increase of juveniles in the samples. All species are predacious and prey chiefly upon small animals not included in the census, such as aphids, psocids, jassids, and mites; web-building species additionally prey on small flies and wasps.

In contrast with the spiders, most species of beetles do not deposit their eggs on the needled twigs, and are mainly found as adults, except in early summer when some coccinellids are in the larval stage (Table 3). The adults are sluggish, and not prepared to fly, except on hot summer days, which are unsuitable for sampling for this reason. Most adults are phytophagous with some clear exceptions, such as the coccinellids, which are predacious both in the larval and adult stages. More knowledge on the food habits of the beetles is needed.

Third in rank of numerousness are the bugs, most species of which hatch from eggs in the early part of the summer. Their larvae generally grow up during the summer, causing a proportionate increase of adults towards the autumn, while their absolute numbers decrease. The adults die after egg deposition or hibernate outside the tree-crowns. The adult bugs cannot be sampled quantitatively during hot summer days, because then they fly readily when disturbed.

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Table 3

Maximum density of animals in different years for adults (A) and juveniles (J) separately

	A/J	1967 P[a]	1967 No.[b]	1968 P	1968 No.	1969 P	1969 No.	1970 P	1970 No.	1971 P	1971 No.
Araneae											
Argiopidae											
Araneus cucurbitinus CLERCK + *A. displicatus* (THORELL)	A	2	0.42	2	0.21	1	0.44	1	1.74	1	0.58
	J	4	13.22	4	4.26	4	6.15	3	12.76	3	13.81
Araneus diadematus CLERCK	A	1	0.11	4	0.07	3	0.07	—	—	—	—
	J	2/4	0.24	2	0.32	3	0.07	1/3	0.05	1	0.12
Araneus gibbosus (WALCKENAER)	A	1	0.11	2	0.19	3	0.14	1	0.21	1	0.70
	J	4	2.23	4	2.43	4	2.79	4	3.93	4	6.73
Araneus sturmi (HAHN.)	A	1	0.36	2	0.20	1	0.68	1	0.48	1	0.29
	J	4	6.98	4	4.57	4	7.96	3	19.61	3	9.64
Cyclosa conica (PALLAS)	A	—	—	—	—	—	—	—	—	—	—
	J	—	—	—	—	4	0.06	3/4	0.09	3	0.12
Meta segmentata mengei (BLACKWALL)	A	4	0.12	—	—	—	—	—	—	4	0.07
	J	—	—	—	—	—	—	—	—	—	—
spec. (2 species)	A	—	—	—	—	—	—	—	—	—	—
	J	4	0.14	3	0.65	2	0.19	3	0.34	—	—
Clubionidae											
Anyphaena accentuata (WALCKENAER)	A	—	—	—	—	—	—	—	—	—	—
	J	2	0.8	3	0.08	4	0.13	1	0.17	4	0.20
Clubiona subsultans THORELL	A	2	0.16	4	0.70	4	0.10	3	0.25	4	0.27
	J	4	1.27	4	2.57	4	0.74	3	2.70	4	2.14
Dictynidae											
Lathys humilis (BLACKWALL)	A	1	1.88	2	2.24	2	0.54	2	0.44	2	0.44
	J	4	2.89	3	18.45	3	0.57	3	2.27	4	1.50
Dysderidae											
Segrestia senoculata (LINNAEUS)	A	—	—	—	—	—	—	—	—	2	0.08
	J	—	—	2	0.05	4	0.06	3	0.11	—	—
Linyphiidae											
Drapetisca socialis (SUNDEVALL)	A	—	—	3	0.13	—	—	4	0.16	3	0.14
	J	3	0.25	3	0.15	2	0.16	2	0.08	2	0.23
Hypomma cornutum (BLACKWALL)	A	—	—	—	—	1	0.12	1	0.07	—	—
	J	—	—	—	—	4	0.10	—	—	—	—
Linyphia triangularis (CLERCK)	A	4	1.96	4	0.78	4	0.60	3	0.32	3	0.60
	J	2	2.07	2	5.78	2	0.80	2	0.36	1	0.41
spec.	A	—	—	2	0.08	3	0.07	—	—	—	—
	J	2	0.16	2	0.08	—	—	2	0.06	—	—
Micryphantidae											
Entelecara congenera (CAMBRIDGE)	A	1	0.11	2	0.17	2	0.06	—	—	—	—
	J	—	—	4	0.07	—	—	—	—	4	0.11
Erigone atra (BLACKWALL)	A	2	0.07	—	—	4	0.06	—	—	1	0.05
	J	—	—	—	—	—	—	—	—	—	—
Erigone dentipalpis (WID.)	A	1	0.07	4	0.08	—	—	1	0.04	—	—
	J	—	—	—	—	—	—	—	—	—	—
Salticidae											
Dendryphantes rudis (SUNDEVALL)	A	—	—	—	—	3	0.07	3	0.13	2	0.06
	J	—	—	—	—	—	—	4	0.07	—	—
Salticus cingulatus (PANZER)	A	—	—	—	—	—	—	4	0.09	—	—
	J	—	—	—	—	—	—	4	0.70	3	0.05
spec.	A	—	—	—	—	—	—	—	—	—	—
	J	—	—	—	—	—	—	—	—	3	0.07
Tetragnathidae											
Tetragnatha obtusa (C. L. KOCH)	A	1	1.16	3	0.40	1	0.67	1	1.51	1	0.98
	J	4	27.45	4	9.29	4	6.35	4	22.44	3	14.84
Theridiidae											
Theridion pallens BLACKWALL	A	2	0.33	3	0.08	2	0.07	1	0.52	2	0.06
	J	—	—	—	—	—	—	1	0.17	—	—
Theridion pinastri L. KOCH	A	—	—	2	0.70	1	0.17	3	0.88	3	0.33
	J	4	0.45	3	1.15	4	1.32	3	0.87	3	0.60
Theridion tinctum (WALCKENAER)	A	1/3	0.29	3	0.82	3	0.17	1	0.64	2	0.49
	J	4	2.56	4	0.44	4	0.95	4	2.61	4	2.48
Theridion vittatum C. L. KOCH	A	1	0.58	2	0.51	—	—	1	0.46	3	0.18
	J	4	5.80	4	1.28	4	1.17	4	2.31	3	1.92
spec.	A	—	—	—	—	—	—	—	—	—	—
	J	4	0.33	2	0.08	4	0.39	3	0.05	—	—
Thomisidae											
Philodromus aureolus (CLERCK)	A	1	0.73	2	1.14	1	2.34	1	1.31	1	1.60
Philodromus collinus C. L. KOCH	A	1	1.60	2	2.66	1	3.74	1	2.29	1	4.26
Philodromus aureolus + *collinus*	J	4	36.23	3	29.56	4	55.92	3	110.93	4	37.99c
Philodromus margaritatus (CLERCK)	A	3	0.15	2/3	0.07	1	0.07	2	0.15	—	—
	J	4	1.67	3	2.34	3	2.90	3	2.04	3	1.27

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Table 3. (continued)

	A	1967		1968		1969		1970		1971	
	J	P	No.	P	No.	P	No.	P	No.	P	No.
Xysticus audax (SCHRANK)	A	2	0.07	2	0.07	4	0.10	3	0.21	1	0.27
	J	4	1.24	4	2.63	3	5.79	3	5.69	3	12.47
spec.	A	—	—	3	0.08	1	0.07	—	—	—	—
	J	—	—	2	1.62	2	3.40	—	—	—	—
Family and/or species unknown	A	2	0.10	3	0.08	—	—	—	—	1	0.27
(3 species)	J	2	0.14	3	0.95	4	1.12	3	3.00	4	0.60
Coleoptera											
Anobiidae											
Ernobius nigrinus STURM	A	—	—	—	—	1	0.09	1	0.09	1	0.15
Carabidae											
Dromius quadrinotatus PANZER	A	4	0.29	4	0.20	2	0.21	4	0.34	3	0.21
Cerambycidae											
Pogonocherus fasciculatus DEGEER	A	—	—	—	—	3	0.06	4	0.09	3	0.07
Chrysomelidae											
Aphthona euphorbiae SCHRANK	A	—	—	—	—	4	0.10	4	0.16	4	0.06
Cryptocephalus pini LINNAEUS	A	4	0.24	—	—	3	0.42	—	—	2	0.37
Coccinellidae											
Adalia bipunctata LINNAEUS	A	4	0.16	4	0.10	—	—	—	—	—	—
Adalia decempunctata LINNAEUS	A	4	0.45	—	—	—	—	4	0.05	3	0.14
Anatis ocellata LINNAEUS	A	3	0.72	4	1.23	3	0.62	4	1.24	3	2.33
	J	1	2.82	2	3.72	—	—	1	2.86	1	2.98
Aphidecta obliterata LINNAEUS	A	4	0.16	4	0.08	—	—	—	—	—	—
Coccinella septempunctata LINNAEUS	A	2	0.10	—	—	4	0.19	1	0.05	3/4	0.07
Myrrha octodecimguttata LINNAEUS	A	4	3.67	4	4.44	4	1.88	4	10.15	3	7.75
	J	1	7.84	2	2.20	3	2.06	1	13.20	1	3.69
Neomysia oblongoguttata LINNAEUS	A	4	0.45	4	0.30	3	0.17	3	0.41	3/4	0.27
	J	—	—	—	—	4	0.29	3	0.07	1	0.05
Propylaea quatuordecimpunctata LINNAEUS	A	—	—	—	—	4	0.16	1	0.10	3	0.07
Scymnus suturalis THUNBERG	A	4	6.81	2	6.96	3	9.57	3	9.56	3	11.22
Curculionidae											
Anthonomus varians PAYKULL	A	2	0.61	2	1.45	2	6.13	2	4.35	1	7.06
Brachonyx pineti PAYKULL	A	—	d	4	3.04	3	15.13	4	9.95	3	6.65
Magdalis memnonia GYLLENHAL	A	2	0.25	2	0.07	1	0.40	1	0.40	1	0.14
Pissodes notatus FABRICIUS	A	4	0.33	3	0.15	4	0.19	4	0.23	2	0.12
Pissodes piniphilus HERBST	A	—	—	4	0.08	3	0.24	2	0.13	4	0.16
Strophosomus rufipes STEPHENS	A	4	8.97	2	6.21	4	12.29	4	39.07	4	29.43
Dermestidae											
Anthrenus fuscus OLIVIER	A	—	—	2	0.17	2	0.06	1	0.06	—	—
Elateridae											
Agriotes aterrimus LINNAEUS	A	1	0.11	2	0.09	1	0.05	—	—	—	—
Athous subfuscus MÜLLER	A	1	0.25	2	0.13	1	0.18	1	0.57	1	0.55
Dolopius marginatus LINNAEUS	A	1	0.14	2	0.07	1	0.15	1	0.67	1	0.08
Helodidae											
Cyphon variabilis THUNBERG	A	—	—	—	—	3	0.13	—	—	4	0.06
Lathridiidae											
Corticarina ? gibbosa HERBST	A	—	—	—	—	4	0.14	4	0.16	—	—
Lathridius nodifer WESTWOOD	A	—	—	3	0.57	3	0.07	4	0.05	—	—
Pythidae											
Salpingus castaneus PANZER	A	—	—	4	0.48	4	0.64	3	0.74	3	0.40
Scolytidae											
Blasthophagus piniperda LINNAEUS	A	—	—	—	—	3	0.17	3	0.44	1/4	0.05
Hylastes ater PAYKULL	A	—	—	—	—	4	0.06	—	—	4	0.07
Pityogenes bidentatus HERBST	A	1	0.61	4	0.67	2	0.26	1	0.33	—	—
Pityophthorus glabratus EICHHOFF	A	—	—	—	—	4	0.40	1	1.39	3	0.38
Tenebrionidae											
Cylindronotus laevioctostriatus GOEZE	A	2	0.41	2	0.70	1	0.95	1	1.72	1	0.76
Family and/or species unknown	A	1	0.11	—	—	3	0.21	1	0.11	—	—
	J	—	—	2/3	0.08	1	0.28	1	0.15	1	0.79
Heteroptera											
Anthocoridae											
Acompocoris spec.	J	2	0.10	—	—	2	0.06	—	—	—	—
Aradidae											
Aradus cinnamomeus PANZER	A	—	—	4	0.07	3	0.21	1	0.49	2	0.90
	J	2	0.15	—	—	1	0.54	4	5.10	2	1.10
Lygaeidae											
Gastrodes grossipes DEGEER	A	4	0.43	2	0.29	3	0.21	4	0.07	3	0.34
	J	3	0.81	2	0.07	—	—	2	0.08	—	—
Kleidocerys resedae PANZER	A	—	—	—	—	4	0.10	4	0.19	4	0.28
	J	4	0.12	4	0.23	3	0.07	—	—	—	—
Miridae											
Alloeotomus gothicus FALLÉN	A	3	6.12	3	11.46	3	2.15	2	2.28	2	7.18
	J	2	3.81	2	34.39	1	7.61	1	4.27	2	6.04
Atractotomus magnicornis FALLÉN	A	3	0.44	3	2.66	3	2.09	3	2.25	2	9.09
	J	—	—	2	1.13	2	0.66	2	1.06	2	0.06

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Table 3. (continued)

	A	1967		1968		1969		1970		1971	
	J	P	No.	P	No.	P	No.	P	No.	P	No.
Camptozygum pinastri FALLÉN	A	3	4.22	2	6.72	2	6.13	2	3.73	2	1.07
	J	2	3.52	2	0.39	1	19.98	1	19.47	1	3.63
Dichrooscytus rufipennis FIEBER	A	2	0.27	2	0.24	1	0.40	1	0.86	1	0.24
	J	1	0.11	—	—	1	0.09	1	0.05	—	—
Orthotylus fuscescens KIRSCHBAUM	A	—	—	—	—	1	0.26	—	—	1	0.25
	J	—	—	—	—	—	—	—	—	—	—
Phytocoris pini KIRSCHBAUM	A	3	1.95	3	1.33	3	0.41	3	0.46	2	1.05
	J	3	1.92	2	4.57	1	0.65	1	0.87	2	1.60
Pilophorus cinnamopterus KIRSCHBAUM	A	—	—	—	—	4	0.38	—	—	3	0.12
	J	—	—	2	0.07	1	0.05	—	—	—	—
Plesiodema pinetellum ZETTERSTEDT	A	1	1.67	—	—	—	—	1	0.67	1	0.08
	J	1	0.32	—	—	—	—	—	—	—	—
Psallus obscurellus FALLÉN	A	2	3.53	2	2.93	2	2.35	2	0.95	1	1.61
	J	—	—	—	—	—	—	—	—	—	—
Stenodema calcaratum FALLÉN	A	—	—	—	—	3	0.07	—	—	3	0.07
	J	—	—	—	—	—	—	—	—	—	—
spec.	A	—	—	—	—	3	0.07	—	—	—	—
	J	—	—	—	—	1	8.18	1	4.41	1	0.05
Nabidae											
Himacerus apterus FABRICIUS	A	—	—	—	—	3/4	0.10	3	0.51	2	1.40
	J	—	—	2	0.07	1	0.07	2	1.57	1	0.82
Nabis ferus LINNAEUS	A	4	0.16	—	—	3	0.15	3	0.32	3	0.27
	J	—	—	—	—	—	—	—	—	—	—
Pentatomidae											
Troilus luridus FABRICIUS	A	—	—	—	—	—	—	3	0.07	4	0.12
	J	4	0.24	2	0.60	—	—	2	0.05	2	0.67
Family unknown	A	—	—	—	—	—	—	1	0.05	1	0.09
	J	1	0.29	—	—	—	—	2	0.34	2	0.37
Opilionida											
Phalangidae											
Mitopus morio FABRICIUS	A	2	3.99	2	1.01	—	—	4	0.14	2	0.12
	J	1	1.73	—	—	—	—	1	0.04	—	—
Oligolophus hansenii (KRAEPLIN)	A	4	5.37	4	6.54	4	0.29	4	2.15	4	7.40
Paroligolophus agrestis (MEADE)	A	4	0.47	4	0.15	4	0.10	4	0.25	4	6.50
O. hansenii + *P. agrestis*	J	2	2.14	3	8.44	3	0.55	3	2.23	2	3.78
Phalangium opilio LINNAEUS	A	3	0.11	—	—	3	0.07	2	0.13	—	—
	J	—	—	—	—	—	—	—	—	—	—
Lepidoptera											
Geometridae											
Bupalus piniarius LINNAEUS	J	4	0.99	2	0.09	3	0.36	2	2.49	2	5.19
Ellopia fasciaria LINNAEUS	J	4	2.98	3	0.78	4	1.37	3	2.01	3	0.26
Eupithecia indigata HÜBNER	J	3	0.48	2	0.33	2	0.27	2	0.91	2	1.21
Semiothisa liturata CLERCK	J	4	0.29	4	0.14	3	2.03	3	4.56	2	1.14
Thera firmata HÜBNER	J	1	0.51	2	0.31	2	0.26	2	0.69	2	0.43
Thera obeliscata HÜBNER	J	4	1.35	2	0.16	4	1.58	1	4.23	1	0.65
Lasiocampidae											
Dendrolimus pini LINNAEUS	J	—	—	3	0.05	4	0.10	2	0.30	—	—
Lymantriidae											
Lymantria monacha LINNAEUS	J	1	0.11	3	0.06	1	0.16	1	1.65	1	0.20
Noctuidae											
Panolis flammea SCHIFFERMÜLLER	J	1	2.42	2	2.57	1	13.18	1	22.53	1	1.43
Sphingidae											
Hyloicus pinastri LINNAEUS	J	3	0.15	3	0.08	3	0.28	3	0.22	3	0.13
Tortricidae											
Archips piceana LINNAEUS	J	4	0.58	2	0.25	1	0.53	1	3.04	1	1.54
Family unknown (1 species)	J	—	—	2/4	0.09	3	0.20	1	1.12	2	0.05
Hymenoptera											
Formicidae											
Myrmica rubra (LINNAEUS) + *M. ruginodis* NYLANDER	A	2	0.08	2	0.56	2	0.68	3	0.18	2	0.13
Formica fusca LINNAEUS	A	—	—	4	0.07	3	1.02	2	0.15	3	0.35
Pamphiliidae											
Acantholyda nemoralis C. G. THOMSON	J	4	0.33	4	0.48	4	0.54	2	0.68	4	0.70
Tenthredinidae											
Diprion simile HARTIG	J	—	—	4	0.27	3	5.26	4	0.26	1	0.12
Gilpinia frutetorum FABRICIUS	J	1	0.11	3	0.37	3	3.22	1	3.11	4	0.97
Gilpinia virens KLUG	J	4	0.16	—	—	3	3.38	1	2.13	4	0.42
Diprion + *Gilpinia* spec.	J	2	1.28	3	0.41	4	17.40	1	6.15	3	1.27
Dermaptera											
Forficulidae											
Forficula auricularia LINNAEUS	A	4	0.79	4	0.55	—	—	3	0.23	4	0.23
	J	2	0.56	2	0.80	—	—	—	—	4	0.12
Dictyoptera											
Blattidae											
Ectobius sylvestris PODA	A	3	0.11	—	—	2	0.08	—	—	1	0.08
	J	—	—	3	0.07	1	0.05	2	0.33	3	1.01

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Table 3 (continued)

	A/J	1967 P	1967 No.	1968 P	1968 No.	1969 P	1969 No.	1970 P	1970 No.	1971 P	1971 No.
Diptera											
Syrphidae (2 species)	J	2	3.64	2	1.42	4	3.38	2	1.18	2	1.90
Neuroptera											
Hemerobiidae (4 species)	A	4	1.22	2	0.47	3/4	0.06	2	0.74	3	0.60
	J	1	2.78	2	1.30	4	1.85	1	6.34	2	1.69
Chrysopidae (2 species)	A	—	—	2	0.08	3	0.08	1	0.25	—	—
	J	3	2.61	3	2.25	3	2.79	3	1.00	2	1.26
Raphidiidae (3 species)	A	2	0.44	2	0.19	1	0.24	1	0.30	1	0.48
	J	3	0.38	2	0.13	2	0.13	3	0.20	2/3	0.06
Family unknown (Lacewing) (1 species)	J	3	1.32	3	0.28	4	7.93	3	0.08	2	0.46

a. P = sampling period; there were 4 such periods per year, usually one in each of the months of June (1), July (2), August (3), and September (4), except in 1968 when the June period (1) was absent; when two periods are given, they proved to have the same density.

b. No. = number of animals per 1000 shoots.

c. Juveniles born in 1971 excluded.

d. not collected in 1967.

Like beetles, the bugs are chiefly plant-feeders. Some of the phytophagous species living on pine trees have been recorded as being predacious under certain conditions, and we could establish this for *Alloeotomus gothicus*. Three of the species found have been described as merely predacious, viz. the rare *Acompocoris* spec. (Table 3) and *Anthocoris nemorum* (Table 4), and the commoner *Himacerus apterus* (Table 3). *Troilus luridus* was found to be phytophagous in the first larval stage, but obligatory predacious in the later stages (Kochler 1948).

So much for the three largest orders of animals represented in the samples, to which we will return later for a more detailed consideration of the commonest species. As to the other groups: the harvestmen, the caterpillars, and those collectively indicated as "various orders" in Fig. 4, we will enter into some more details in this section, since we do not reconsider these orders later.

The harvestmen invade the crowns as juveniles during early and mid-summer, reach adult age on the trees, and leave the crowns for egg deposition in autumn (Todd 1949). Their numbers are always low as compared to their relatives, the spiders. As shown in Table 3, *O. hansenii* and P. *agrestis* are rather common. Because it is hard to discriminate between the juvenile stages of these two species, they have been added in the Table. In September of 1971 there were about 14 specimens per 1000 shoots of these two species together, i.e. 75 on a medium sized pine tree. On the contrary, *M. morio*, and especially *P. opilio* are rare. Little is known concerning their food; some observations of Bristowe (1960) indicate that they are highly polyphagous.

The total numbers of "caterpillars" fluctuate rather erratically, having their maximum in June (1970), in mid-summer (1971), or in late summer (1967, 1969). This is partly due to the group being composed of two quite different categories: the larvae of moths, having their peak numbers in the first half of the summer, and the larvae of the tenthredinoids, most of which are bivoltine, and reach their highest numbers usually in the second generation in September. It is shown in Table 3 that *Panolis flammea* is by far the most numerous species, increasing about tenfold from 1967 up to 1970, followed by a rather steep decline. At a somewhat lower level there are some geometrids. of which *Bupalus* is on its way to recover from a heavy crash in 1968. The other geometrids are rather stable, especially *Thera firmata*. The great differences in the patterns of fluctuation between the populations of pine moths are quite interesting, particularly when surveyed over many years. We have now data on the fluctuations in numbers of 12 species over 20 years, on which we will report in a later paper.

DOI: 10.21248/contrib.entomol.23.5-8.325-340

Among the tenthredinoids there is one representative of the pamphilids. This species, *Acantholyda nemoralis*, is living solitarily in a silken tent. Therefore, the densities given in Table 3 are minimum values. We do not know the proportion of larvae dislodged when shaking the twigs.

There are at least 4 species of tenthredinids, 2 of the genus *Gilpinia* and 2 of the genus *Diprion*; their populations fluctuate relatively heavily, and may show a twentyfold increase or decrease from one year to the next (Table 3).

The species assembled in the category indicated as "various orders" in Fig. 4 A–E belong to 5 different groups (see text to Fig. 4 and Table 3). Firstly, the earwig (*Forficula*) and the cockroach (*Ectobius*) invade the trees from the soil in the course of the summer in the larval or adult stages. The earwig is predatory and polyphagous, but we never observed *Ectobius* to attack living prey.

Secondly, there are 5 species of syrphids, which can be distinguished as separate species in the larval stage (we do not know their names, because we never took the trouble to rear them to the adult stage). Two species do occur in the samples nearly annually (Table 3), three others have been observed in one year only (Table 4). We know nothing about their food, but syrphid larvae in general are said to be aphid predators.

Table 4
Survey of species found in the twig-samples of only one out of five summers

Species and year	A/J	P
Araneae		
1967		
Lepthyphantes tenuis (BLACKWALL)	A	2
Lepthyphantes zimmermanni BERTKAU	A	3
1968		
Theridion varians HAHN	A	2
1969		
Theridion blackwalli CAMBRIDGE	J	4
Lepthyphantes leprosus (AHLERT)	A	4
Gongylidiellum latebricola O. P. CAMBRIDGE	A	1
1970		
Philodromus emarginatus (SCHRANK)	J	3
Xysticus sabulosus (HAHN)	J	4
Philodromus dispar WALCKENAER	J	4
Species unknown	J	2
1971		
Theridion sisyphium (CLERCK)	J	4
Mangora acalypha (WALCKENAER)	J	4
Dipoena spec.	J	3/4
Heteroptera		
1967		
Elasmostethus interstinctus LINNAEUS	A	4
Myrmus miriformis FALLÉN	A	3
Anthocoris nemorum LINNAEUS	A	4
1968		
Elasmucha fieberi JAK.	A	4
Pilophorus spec.	J	2
1969		
Psallus betuleti FALLÉN	A	1
Orius spec.	A	4
1970		
Stygnocoris pedestris FALLÉN	A	3
1971		
Elatophilus nigricornis ZETTERSTEDT	A	1/2/3
Acompocoris pygmaeus FALLÉN	A	4
Lepidoptera		
Species unknown (1969)	J	1/4

Species and year	A/J	P
Coleoptera		
1967		
Cantharis obscura LINNAEUS	A	1
Dromius spec.	A	2
Crepidodera ferruginea SCOPOLI	A	3
Dasytes aerosus KIESENWETTER (?)	A	1
Pogonocherus decoratus FAIRMAIRE	A	3
1968		
Coccinella quinquepunctata LINNAEUS	A	4
Leperesinus fraxini PANZER	A	4
Orchesia minor WALKER	A	3
1969		
Corticaria elongata GYLLENHAL (?)	A	2
Dromius agilis FABRICIUS	A	2
Coccinella undecimpunctata LINNAEUS	A	3
Coccinella hieroglyphica LINNAEUS	A	4
Longitarsus spec.	A	4
Species unknown	A	3
1970		
Brachyderes incanus LINNAEUS	A	2
Anobium punctatum DEGEER	A	2
Chilocorus renipustulatus SCRIBA	A	3
Chilocorus bipustulatus LINNAEUS	A	4
Species unknown	A	4
1971		
Harmonia quadripunctata PONTOPPIDAN	A	3/4
Thanasimus rufipes BRAHM	A	4
Thea vigintiduopunctata LINNAEUS	A	4
Mycetophagus piceus FABRICIUS	A	4
Rhizobius litura FABRICIUS	A	4
Subcoccinella vigintiquatuorpunctata LINNAEUS	A	3
Hymenoptera		
Tenthredinoidea		
Diprion nemoralis ENSLIN (1967)	J	2
Neodiprion sertifer GEOFFROY (1970)	J	1
Formicidae		
Species unknown	A	2
Diptera		
Syrphidae		
Species unknown (1968)	J	2
Species unknown (1969)	J	4
Species unknown (1969)	J	4

A = adult; J = juvenile; P = sampling period(s) in which the species have been found.

DOI: 10.21248/contrib.entomol.23.5-8.325-340

Thirdly, there are 4 different types of larvae of Neuroptera, all voracious predators, belonging to at least 10 different species, and 3 or 4 families (Table 3).

Finally, 3 different species of ants have been recorded (Tables 3 and 4).

The total numbers of species in the various groups of arthropods and the numbers of species found in 1, 2, 3, 4, or 5 summers over the five successive years of study have been assembled in Table 5. There is a relatively high number of species that has been found in one summer only (Tables 4 and 5). Most of the species of this category are represented by 1 or, less common, by 2 or 3 specimen(s) in only one sample. They may be considered as vagrants, probably invading the pine forest in some, but not all, years.

Table 5
Numbers of species in various groups of arthropods collected on the twigs of pine trees over 5 successive summers

Group	Total no. of species	Numbers of species collected in 1, 2, 3, 4, or 5 summers				
		1	2	3	4	5
Araneae	46	13	8	5	2	18
Coleoptera	58	25	7	9	5	12
Heteroptera	27	10	3	2	3	9
Lepidoptera	13	1	—	2	—	10
Tenthredinoidea	7	2	—	—	2	3
Opilionida	4	—	—	1	1	2
Forficulidae	1	—	—	—	1	—
Blattidae	1	—	—	—	—	1
Syrphidae	5	3	—	—	1	1
Neuroptera	10	—	3	3	1	3
Formicidae	3	1	—	—	1	1
Total	175	55	21	22	17	60

There is also a relatively high number of species represented in all five summers (Table 5). These are the typical pine-dwelling species that reach relatively high numbers in most years. Some of the typical inhabitants of pine forest fluctuate more violently, others have lower population levels, and such species may be absent in the samples by chance, when they happen to go through a population low in a certain year, or over a number of successive years.

Further it should be realized that our method is inappropriate for a number of species. Thus, the larvae of *Dendrolimus pini* move to the needled parts of the twigs at twilight to forage on them during the night, but at day-time when we do our sampling, they have returned to the thicker branches not included in the samples.

4.3. The density of the commonest species among spiders, beetles, and bugs

In the Figs. 5—7 the detailed sampling data of some of the most numerous species of spiders, beetles and bugs have been assembled to show the variation between samples within sampling periods, the changes of numbers during the season, and the differences between levels in different years.

4.3.1. The densities of six species of spiders

In the Figs. 5 A—C the densities of 6 species of spiders are given, which have been selected because their densities surpassed a level of 10 specimens per 1000 shoots in at least one of the 5 summers. There are 2 species of the genus *Philodromus*, viz. *aureolus* and *collinus*, which can hardly be distinguished in the early juvenile stages. Therefore, their numbers have been added. Both species have a biennial life-cycle like some of the *Philodromus* species in Canada (DONDALE 1961). They mate and lay eggs in spring and early summer, though small egg-masses may be produced well into August. The young which hatch from the eggs do not reproduce next spring, but wait until another year has elapsed. As a result of reproduction the numbers show an increase towards the autumn, except in 1971, when the juveniles born in that year were disregarded (Fig. 5 C and Table 3). *P. collinus* is roughly two times as numerous as *P. aureolus*. They are the most abundant spiders on pine trees, preying mainly on the small arthropods not included in the census (p. 327).

As to the other species of spiders given in Figs. 5 A—C, with some exceptions they show a tendency to decrease from June to July due to mortality, and to increase towards August, and in some years September, as a result of reproduction. The specimens assembled under the name *Araneus cucurbitinus* most probably form a group of sibling species, including at least *A. displicatus* in addition to *A. cucurbitinus*.

DOI: 10.21248/contrib.entomol.23.5-8.325-340

4.3.2. The densities of four species of beetles

Detailed sampling data of the 4 commonest species of beetles, having density levels surpassing 5 specimens per 1000 shoots in at least 1 of the 5 summers, have been assembled in the Figs. 6 A – C.

From the 3 species of coccinellids, all hibernating as adults in the litter or in crevices of the bark of pine trees, *M. octodecimguttata* and *A. ocellata* deposit their eggs on the needles in May; their larvae are common on the needled twigs up to the second sampling period included (Table 3.). *S. suturalis* larvae, on the other hand, are rare on the needled parts of the twigs; the adults probably deposit the bulk of their eggs somewhere on the bigger branches which are not sampled, but this should be verified.

The newly emerged adults of *Anatis ocellata* are said to have an aestivation period in July-August in the litter (KESTEN 1969), but the exodus from the tree crowns which should attend this behaviour finds hardly expression in our sampling data, except perhaps in 1970.

S. rufipes, a flightless curculionid, the larvae of which live in the litter, is the most numerous beetle in some years (Table 3). There is one other curculionid, which may reach high density levels in the adult stage, viz. *Brachonyx pineti* (Table 3). The larvae of this beetle do not occur in the samples either, but this is because they mine in the pine needles. This species is not graphed in Fig. 6, because it was not collected in 1967.

4.3.3. The densities of five species of bugs

The sampling results of 4 common species of the mirid family, and 1 aradid, all chiefly or wholly phytophagous, have been detailed in the Figs. 7 A – C. Their densities surpass in at least one summer the level of 5 specimens per 1000 shoots. The mirids hibernate in the egg stage, and the young larvae have their main emerging period in May. The eggs of *C. pinastri* in general hatch earlier than those of the other mirids, and their larvae may have reached high numbers when the orthers are still relatively rare, or even absent, as in June 1969 (Fig. 7 B).

As a rule the numbers in the samples culminate in July, decreasing towards the autumn as a result of adult mortality.

Finally, the flatbug *A. cinnamomeus* being rare in most years, reached relatively high numbers in 1970 (Fig. 7). This species hibernates near the base of the host tree, and moves up in spring to lay eggs under the bark (SOUTHWOOD & LESTON 1959).

5. Discussion

There are some other studies of the fauna of pine tree crowns, the results of which will be compared with those gained by us. The reader should, however, realize that the methods used are rather divergent (see Table 7), and that most studies are based on sampling data over one year, so that differences in faunal composition may be largely due to annual fluctuations of numbers (p. 335).

To begin with the spiders, the numbers of species found by different authors have been presented in Table 6. As shown this number is exceptionally high in the study of ENGELHARDT. This might partly result from his collections coming mainly from spruce, *Picea excelsa*, but additionally an inspection of the species listed in his paper revealed that a relatively high proportion is composed of spiders normally inhabiting the field-layer; probably these species have run onto the cloth on which the trees were felled.

Table 6

Numbers of species of Araneae (Ar), Coleoptera (Co), Coccinellidae (Cc), and Heteroptera (He) recorded in faunal studies of the crowns of conifers performed by ENGEL 1941, HÖREGOTT 1960 (HRG), ENGELHARDT 1958 (ENH), DZIABASZEWSKI 1969 (DZI), KLAUSNITZER 1967 (KL), and reported in this study (K & T)

	K & T				ENGEL				HÖREGOTT				ENH	DZI	KL
	Ar	Co	Cc	He	Ar	Co	Cc	He	Ar	Co	Cc	He	Ar	Ar	Cc
K & T	**46**	**58**	**18**	**27**											
ENGEL	25	15	7	5	**46**	**18**	**11**	**12**							
HRG	16	16	5	12	24	13	8	8	**34**	**46**	**11**	**29**			
ENH	16	—	—	—	23	—	—	—	16	—	—	—	**68**		
DZI	13	—	—	—	14	—	—	—	13	—	—	—	14	**35**	
KL	—	—	14	—	—	—	8	—	—	—	8	—	—	—	**27**

Note. Numbers in bold type refer to the total number of species established; the others refer to the number of species occurring jointly in the faunas indicated.
For information on sampling methods and localities see general notes to Table 7. KLAUSNITZER (KL) collected exclusively coccinellids from pine woods near Dresden, Germany.

As shown in Table 6 there is a rather close agreement between the species compositions of the spider faunas studied by ENGEL and by us: the numbers of species are the same, and the faunas have more than 50% of the species in common. The

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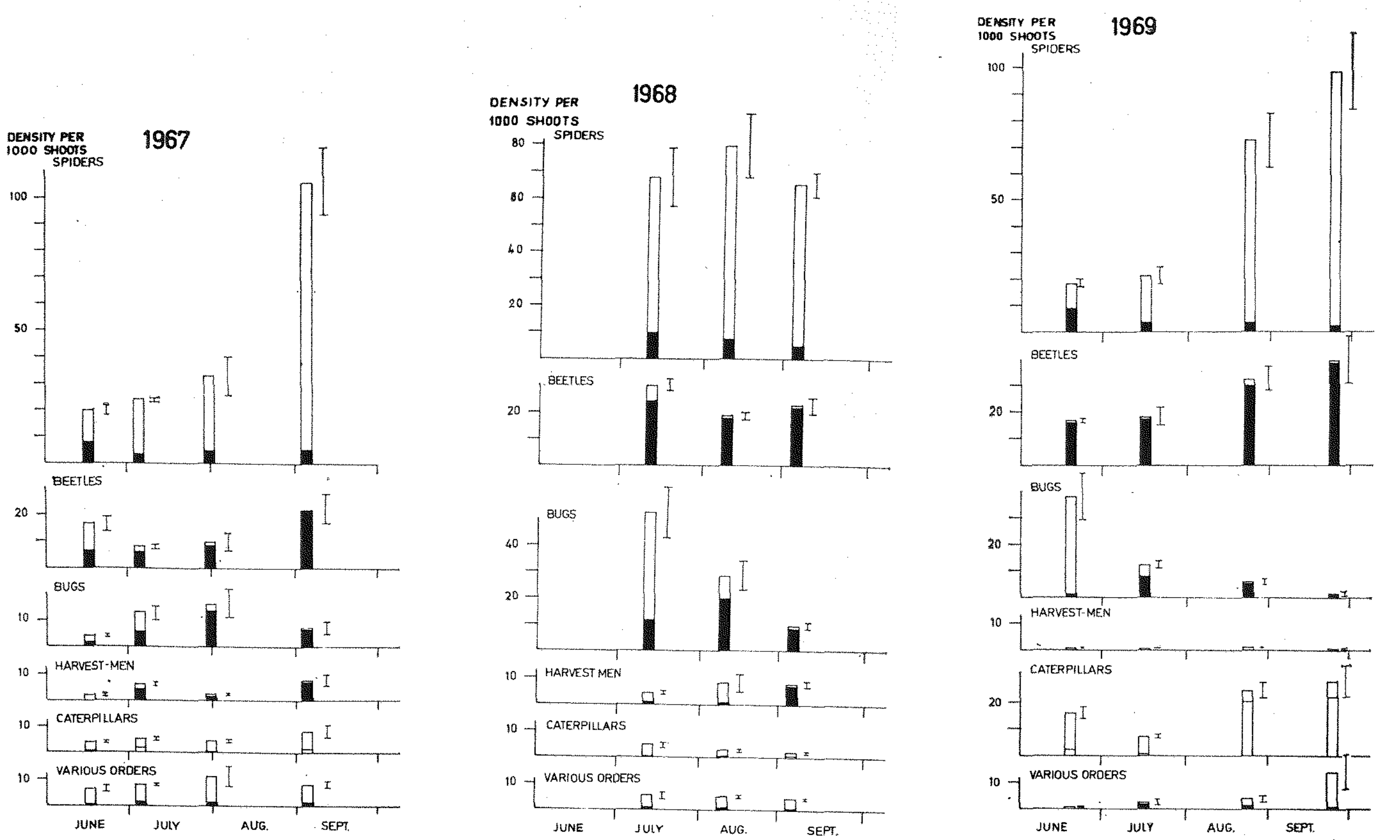

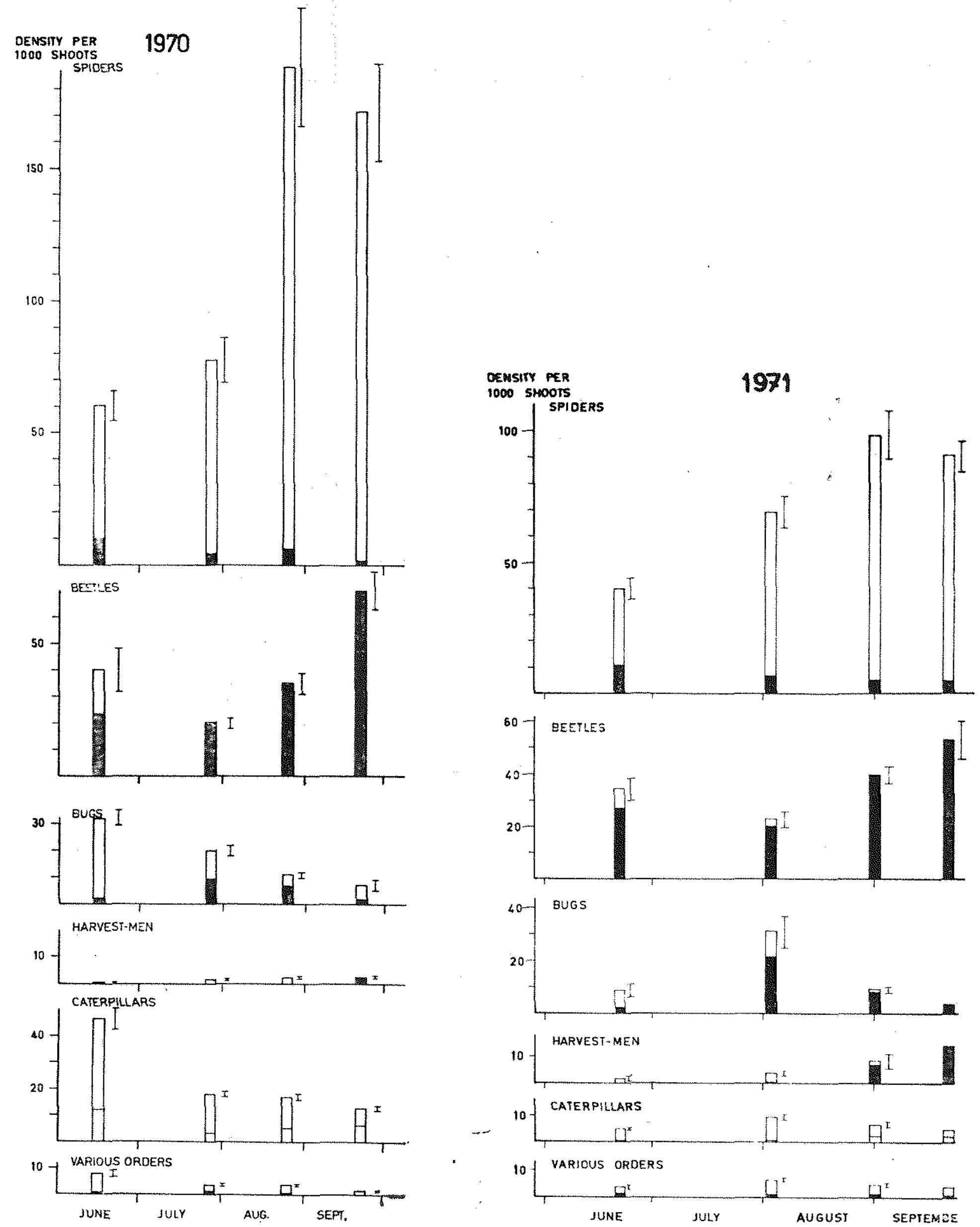

Fig. 4A—E. The mean numbers of animals on Scots pine in different invertebrate orders. Black parts of columns: adults; white parts: juveniles. Vertical lines near the columns indicate ranges of the mean ± the standard error. Each column represents the mean number of animals out of 3 samples (1967), or 6 samples (1968—1971), taken within one sampling period, the mean date of which is indicated by the middle of the base of the column. The columns for spiders, beetles, bugs, and harvestmen include all species of Araneae, Coleoptera, Heteroptera, and Opilionida, respectively. The horizontal lines in the columns for caterpillars separate the larvae of the Tenthredinoidea (Hymenoptera) (bottom), and the larvae of the Lepidoptera (top.).The columns for various orders include some representatives of the Hymenoptera (Formicidae), Dermaptera (Forficulidae), Dictyoptera (Blattidae), Diptera (Syrphidae), and Neuroptera (3 families). See Table 3

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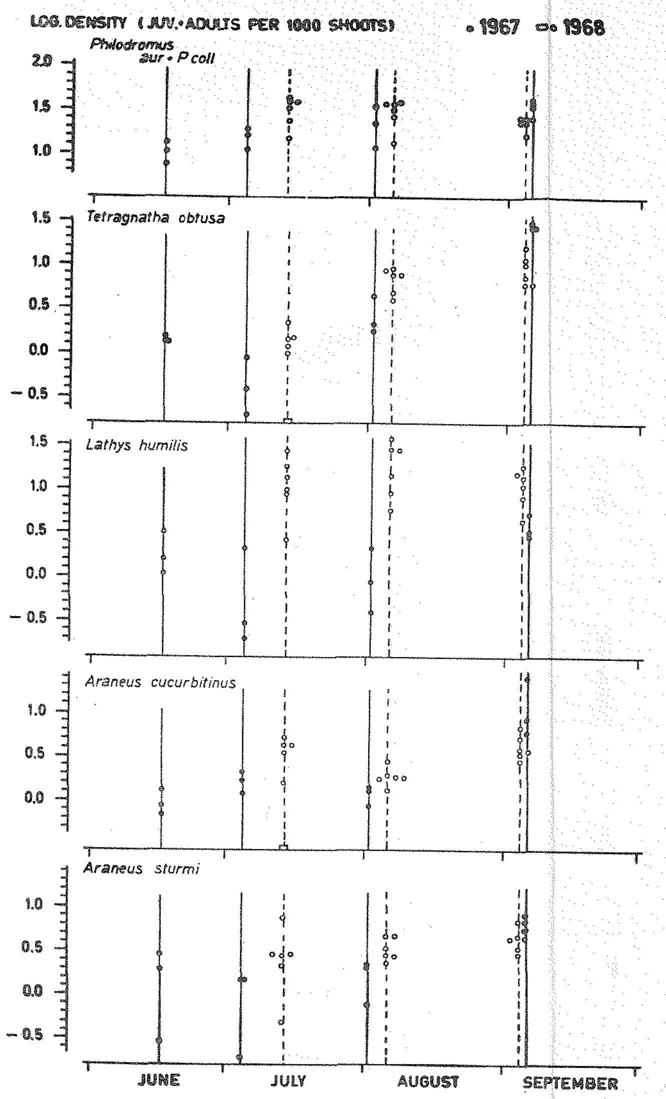

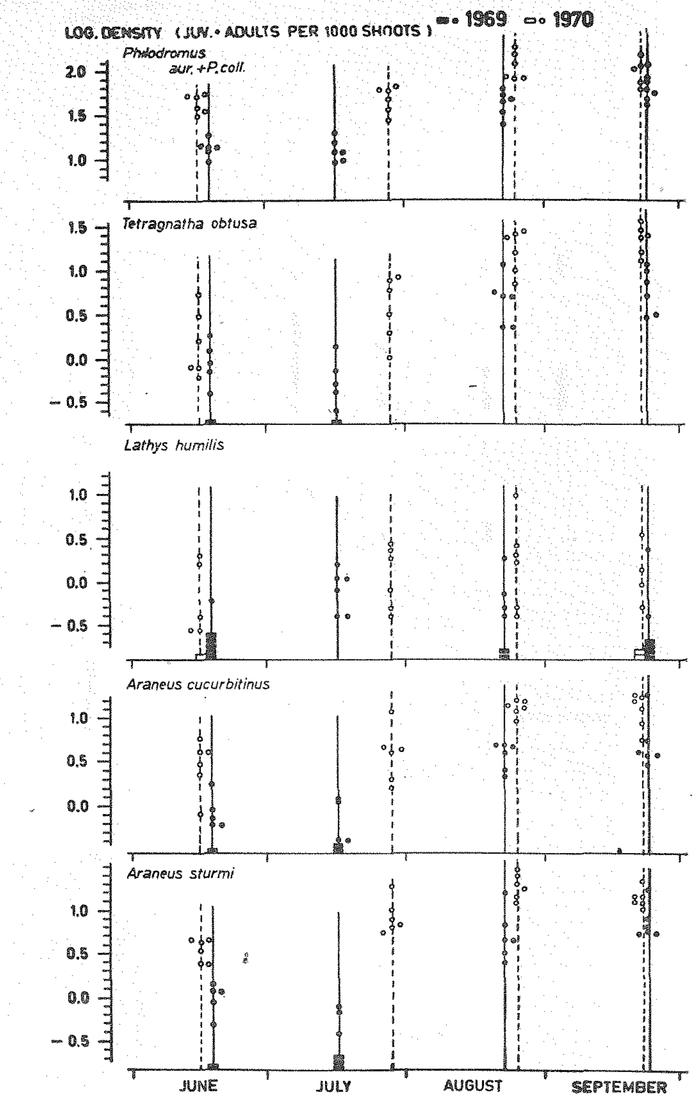

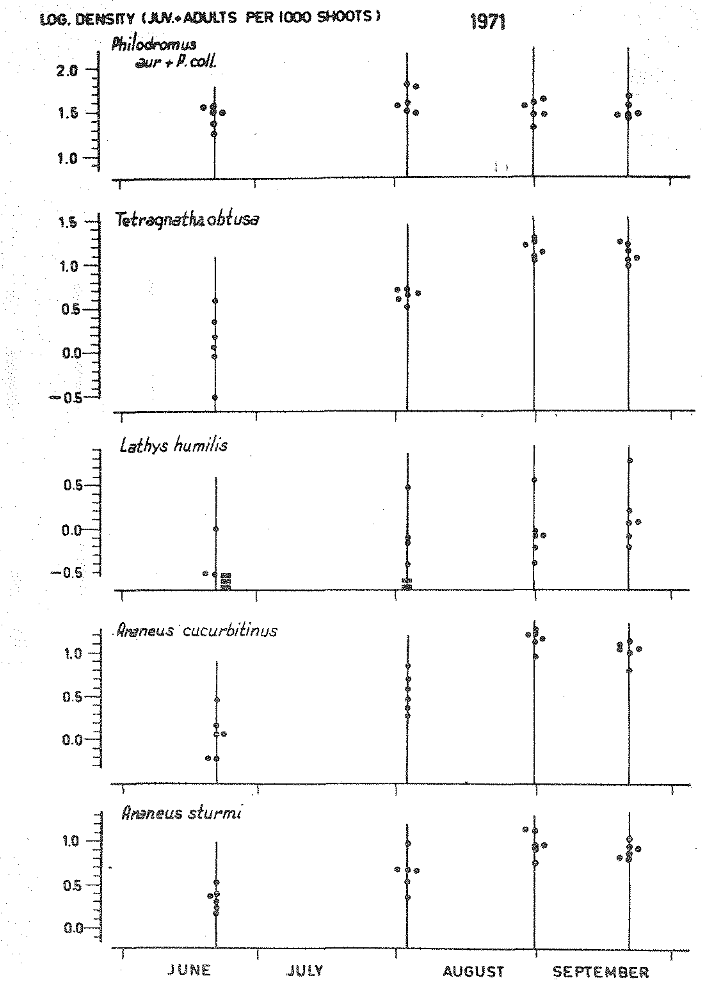

Fig. 5A—C. Densities of the 6 commonest species of Araneae in 5 successive years (figs. 5A, B, and C). Each symbol represents the density calculated from one sample. The samples belonging to one sampling period are given on, or near to (for the sake of clearness) a vertical line, the base of which indicates the mean date of the sampling period. Rectangles on the abscissa are used when a species does not occur in a sample

DOI: 10.21248/contrib.entomol.23.5-8.325-340

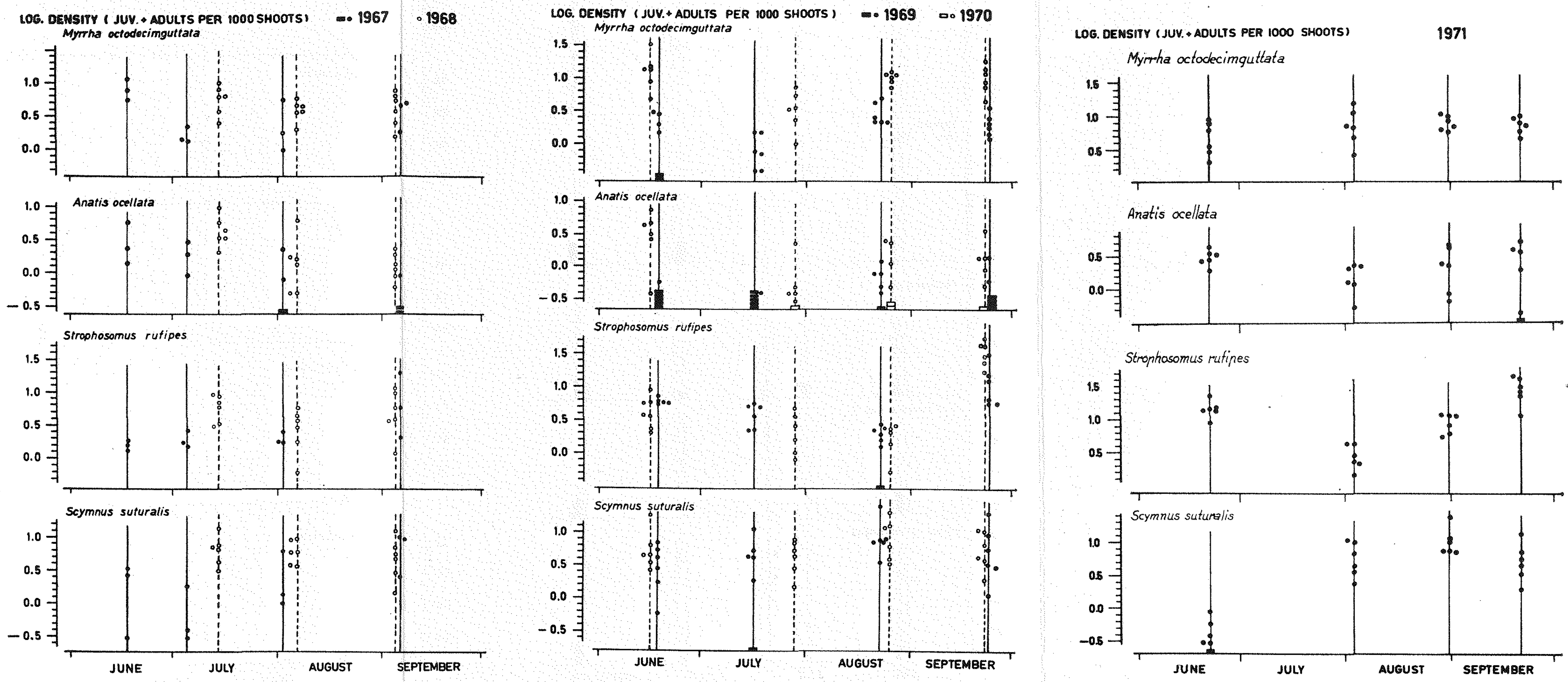

Fig. 6A—C. Densities of the 4 commonest species of Coleoptera in 5 successive years (figs. 6A, B, and C). See fig. 5A for further explanation

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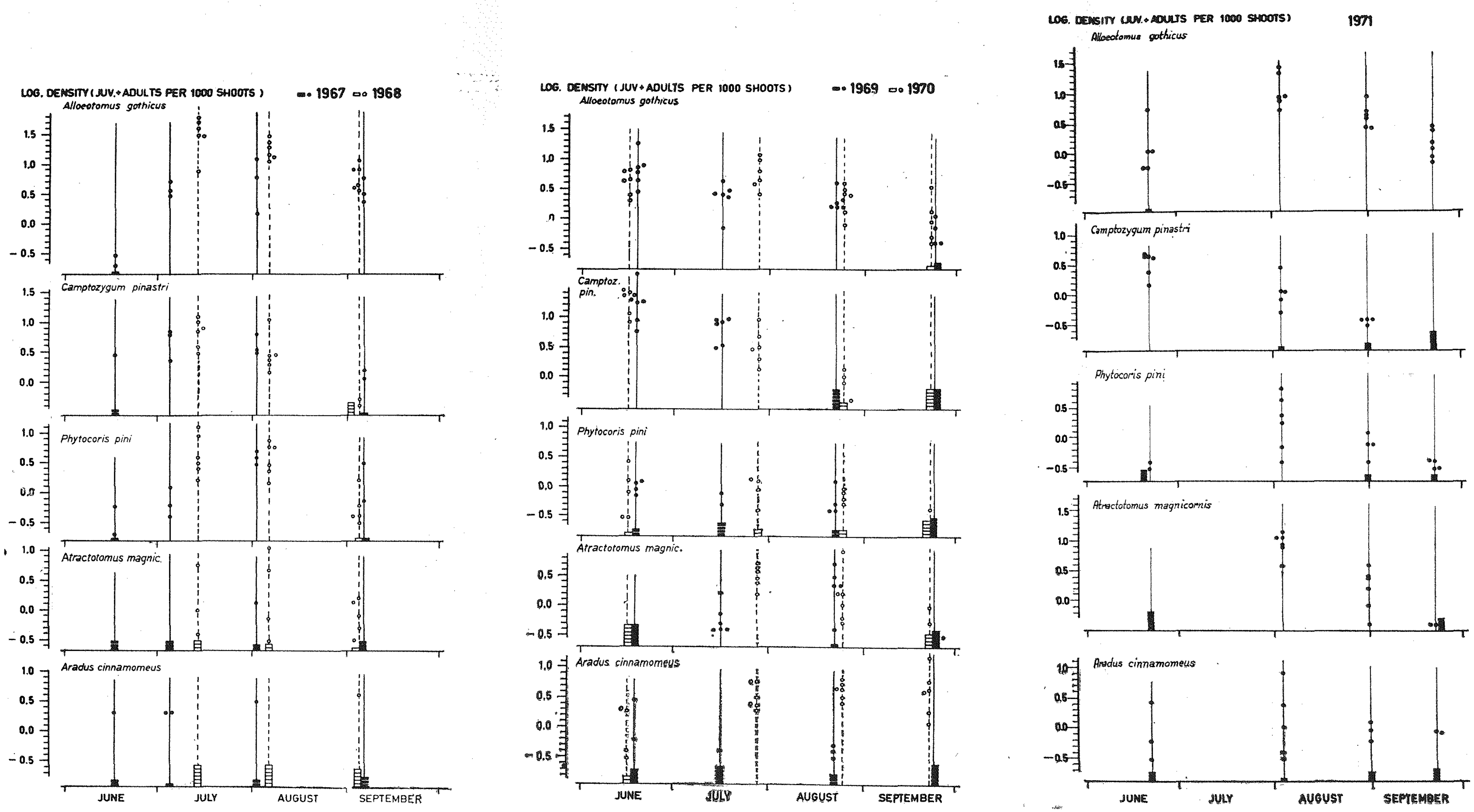

Fig. 7A—C. Densities of the 5 commonest species of Heteroptera in 5 successive years (figs. 7A, B, and C). See fig. 5A for further explanation

DOI: 10.21248/contrib.entomol.23.5-8.325-340

figures further suggest that there is a gap between the spider faunas of Poland, studied by DZIABASZEWSKI, and the faunas of more western localities, including that of eastern Saxony studied by HÖREGOTT.

Table 7

Comparison of the commonest species of spiders in studies of the fauna of conifers in Europe

Author, years of sampling	K. & T. 1967–71		ENGEL 1936–1937		ENGELH. 1954–1955		HÖREGOTT 1955–1956		DZIABASZEWSKI 1962	
	S	no. T	S	no. T	S	no. T	S	no. R	S	no. R
Philodromus aureolus + *collinus*	1	210	1	28 + 208[a]	1	41	1	58 + 473[c]	2	20
Tetragnatha obtusa	2	41	4	3.5	61	0.05	21	5	6	13
Araneus cucurbitinus + *displicatus*	3	31	9	1.5	37	0.2	30	1	8	9
Araneus sturmi	4	31	2	7	14	2	4	58	11	6
Lathys humilis	5	22	—	—	58	0.05	—	—	—	—
Xysticus audax	6	18	24	0.25	3	7.8	7	26	3	17
Xysticus species	—	—	3	5			6	33		
Linyphia triangularis	9	7	—	—	—	—	2	124	—	—
Clubiona subsultans	11	6	—	+[b]	20	1	14	10	—	—
Clubiona species	—	—	7	1.7	5	5.2	8	26	—	—
Theridion pinastri	12	4.5	6	1.7	65	0.05	—	—	4	13
Theridion species	—	—	—	—	18	1.1	3	76	—	—
Cyclosa conica	18	0.17	27	0.25	6	5.0	17	7	10	8
Dendryphantes rudis	19	0.10	5	2	4	6	11	16	—	—
Dendryphantes hastatus	—	—	—	—	—	—	—	—	5	13
Meta segmentata	22	0.06	—	—	50	0.1	5	56	15	4
Dismodicus elevatus	—	—	20	0.5	2	23	—	—	1	85

General notes. The species included in the table are the six most numerous ones in any one study; in the column K. & T. (presenting data of this study) they have been arranged in sequence of numerousness (S).
The studies of ENGEL (1941) and ENGELHARDT (1958) are based on numbers of spiders dislodged from the twigs of felled trees from a 60 years old pine plantation in central Germany in the former, and mostly spruce trees from plantations in southern Germany aging 35–80 years in the latter. As a result density is given in numbers per tree (no. T). HÖREGOTT (1960) shook pine twigs, sticked to differently aged trees of various plantations in eastern Saxony, above a cloth extended on the ground; DZIABASZEWSKI (1969) removed the herb and litter layers underneath pine trees in 30–50 years old plantations in Poland, and counted the spiders fallen on the sandy soil after insecticide application from aircraft. Densities are therefore in relative numbers (no. R.), and can be compared within columns only. All studies include samples taken during the months June to September, except that of DZIABASZEWSKI in which August and September are not represented.
Notes a. Juvenile spiders, collectively indicated by ENGEL as „Jungspinnen"; according to HESSE (1940), who identified the spiders collected by ENGEL, a large proportion of these belong to the species *P. aureolus* and *P. collinus*.
b. This species was present in very low numbers.
c. Unidentified juveniles, a substantial part of which may be *Philodromus* species.

In Table 7 the six commonest species in any one study have been listed for comparative purposes. The *aureolus-collinus* complex of the genus *Philodromus* is most abundant in at least 4, but possibly in all 5 localities. It is true, DZIABASZEWSKI has given *Dismodicus elevatus* the first rank, but he hardly collected juvenile spiders, and he did not sample in August and September, when the juvenile category of the *Philodromus*-complex is very abundant (Table 3).

It is remarkable that a similar situation has been described by DONDALE (1958) for the spider fauna living on apple trees in Nova Scotia, Canada, where two other biennial *Philodromus*-species are common.

Other species common in all localities are *Xysticus audax*, a webless species hunting by the sense of touch as *Philodromus*, and *Araneus sturmi*, a web-building spider. On the other hand, the web-building *Tetragnatha obtusa* is common in three localities, but seems to be rare in the study area of ENGELHARDT. Also, *Dismodicus elevatus* has a high score in two areas, but is very rare or absent in others; *Dendryphantes rudis* is common in most study plots, but is replaced by *D. hastatus* in Poland. Finally, *Lathys humulis* is abundant in Dutch pine woods, but is absent or very rare in central European regions.

DOI: 10.21248/contrib.entomol.23.5-8.325-340

Comparing the faunal studies in which the numbers could be expressed per pine tree of roughly the same size (Table 7), it will be evident that in general the levels of abundance are remarkably higher in our study. We are of the opinion that this difference has to be attributed to the higher accuracy of our census method rather than to real differences in abundance.

As to the beetles, it is shown in Table 6 that the number of species recorded in our study is particularly high. This is mainly due to the extensive sampling over five years as compared to one year in the other studies. We had 24 species in 1967, the first year of our sampling, to which 8 new ones could be added in 1968. As shown in Table 4, among the beetles there is a relatively large number of species occurring only one year, as a rule at low densities.

Most species recorded by ENGEL also occur in the faunas studied by HÖREGOTT and by us; on the other hand the fauna we studied had a small overlap with that of HÖREGOTT (Table 6). There is, however, much agreement with reference to the most numerous species. Out of the six commonest species of the Dutch fauna, three also occurred in the others, and only five species had to be added to the Dutch list to include the first six species of both the central and the eastern German faunas (Table 8). All in all there is more agreement among the beetle faunas than among those of the spiders (cf. Tables 7 and 8).

Table 8
Comparison of the commonest species of beetles in studies of the fauna of pine crowns in Europe. See Table 7 for explication

Author; years of sampling	K & T 1967–1971		ENGEL 1936–1937		HÖREGOTT 1955–1956	
Species	S	No. T	S	No. T	S	No. R
Strophosomus rufipes	1	44	2	1.6	1	70
Myrrha octodecimguttata	2	31	15[a]	0.1	22[a]	3
Scymnus suturalis	3	30	1	9	4	21
Scymnus nigrinus	—	—	—	—	2	33
Brachonyx pineti	4	27	6	0.7	23	3
Anatis ocellata	5	9.0	5	1	3	25
Anthonomus varians	6	6.7	7	0.7	8	11
Dolopius marginatus	15	0.33	—	—	7	16
Adalia decempunctata	20	0.23	4	1.0	—	—
Brachyderes incanus	38	0.02	8	0.7	6	17
Exochomus quadripustulatus	—	—	3	1.2	5	21

[a] We have assumed that the species indicated by ENGEL and HÖREGOTT as *Halyzia octodecimguttata* is identical with *Myrrha octodecimguttata*.

In ours and in the faunal studies referred to above, the coccinellids are represented by a high number of species (Table 6). KLAUSNITZER (1967), sampling by beating twigs of pine trees, recorded 27 species over the period May to September included, about half of which also occurred on our study area. Only 8 of the species recorded have been characterized by KLAUSNITZER as typical pine-dwelling species, because their larvae were also found to be present. Of these, *Scymnus nigrinus* and *Exochomus quadripustulatus* have not been found on our sampling plot, though they may be common elsewhere (Table 8).

Among the Heteroptera or bugs there is much less agreement as to the species-composition of the various faunas studied. Firstly, as shown in Table 6, there is a great difference between the total numbers of species recorded: ENGEL has less than half the number established in the other localities. However, in our study the number of species recorded in any one year varied from 14 in 1968 to 19 in 1971, and based on these figures the number of species recorded by HÖREGOTT is too high rather than that of ENGEL too low.

DOI: 10.21248/contrib.entomol.23.5-8.325-340

Secondly, there is only a small overlap in species-composition: out of 27 species recorded by us only 5 also occurred on the area sampled by ENGEL, and only 12 also in the fauna studied by HÖREGOTT (Table 6).

Finally, there is little agreement between the groups of most abundant species of bugs in the faunas under consideration (Table 9). Out of the 6 commonest species in the Dutch fauna only 2 belong to this category in the fauna of central Germany (ENGEL), and again 2 others to that of eastern Saxony (HÖREGOTT). Moreover, several species with a high rank in Germany are rare or absent in the Dutch fauna. For instance, *Chlorochroa pinicola* is the commonest species in ENGEL's study area, but it did not occur in Holland. However, this situation may change radically, since this species fluctuates heavily in numbers (JAHN 1942). In Holland an outbreak of this species occurred in 1950—1951, but after its numbers had declined sharply, it has not been found in the study plot since 1954. This clearly shows that a good and usable comparison of the invertebrate faunas of similar habitats of different geographical regions should be based on data of at least five years, gained with the same census method. On p. 338 we already referred to the great differences between the density levels of some species of spiders occurring in ENGEL's and our study plots. This also holds, even more pronounced, for beetles and bugs (Tables 8 and 9), supporting our view that the much higher densities per tree of most species in Holland have to be attributed to a difference in accuracy between the methods of sampling.

Table 9

Comparison of the commonest species of bugs in studies of the fauna of pine crowns in Europe. See Table 7 for explication

Author; years of sampling	K & T 1967—1971		ENGEL 1936—1937		HÖREGOTT 1955—1956	
Species	S	No. T	S	No. T	S	No. R
Alloeotomus gothicus	1	38	6	0.25	14	6
Camptozygum pinastri	2	22	—	—	3	42
Phytocoris pini	3	7.3	—	—	19	3
Atractotomus magnicornis	4	7.2	2	1.2	—	—
Aradus cinnamomeus	5	5.0	—	—	7	20
Psallus obscurellus	6	4.0	—	—	—	—
Himacerus (= Nabis) apterus	7	1.9	—	—	2	76
Troilus luridus	11	0.8	3	1.0	18	4
Nabis (= Reduviolus) ferus	13	0.4	5	0.4	6	22
Pilophorus cinnamopterus	14	0.2	—	—	1	87
Chlorochroa pinicola	—	—	1	3.7	26	1
Stenodema virens	—	—	4	0.8	4	36
Elasmucha grisea	—	—	11	0.1	5	24

Summary

The density of the invertebrate fauna on the crowns of pine trees (microlepidoptera, aphids, psocids, jassids, and mites excepted) has been assessed in June, July, August and September over the years 1967—1971. Trees have been sampled by cutting twigs and carefully putting them into a large sack. After having been killed by carbondioxyde the animals were dislodged from the twigs by shaking the latter thoroughly over a cloth. — Densities have been expressed in numbers present in a twig-mass containing 1000 shoots of the current year, which roughly corresponds with $2^1/_4$ m² ground surface (Table 3, Figs. 4—7). — The total numbers of species and individuals for the 4 sampling periods of 1970 are presented in Table 2, together with the indices of diversity derived from these numbers according to WILLIAMS' method. — Comparisons are made between the density measurements reported in this study and those of other studies of the fauna of conifers elsewhere in Europe (Tables 6—9). It is shown that the density levels of several species of spiders, beetles, and bugs are remarkably higher in Holland than elsewhere in Europe, which is attributed to a higher accuracy of our census method rather than to a real difference in abundance. As to species-composition, the beetle faunas of different parts of Europe agree to a large extent, the spider faunas show less agreement, and the faunas of bugs differ still more. — Annual fluctuations of species may influence the species-composition considerably. Therefore, comparisons of invertebrate faunas should be based on data of at least five years.

Zusammenfassung

Die Dichte der Sommerfauna der Invertebraten in den Kronen der Kiefern (außer Mikrolepidopteren, Aphiden Psociden, Jassiden und Milben) wurde in den Jahren 1967—1971 für die Monate Juni, Juli, August und September ermittelt. Die Proben wurden den Bäumen entnommen, indem man Zweige vorsichtig in einen großen Sack schnitt. Nachdem die Tiere mit Kohlendioxyd getötet worden waren, wurden sie durch kräftiges Schütteln der

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Zweige über einem Tuch aus diesen entfernt. — Die Dichte wird in Zahlen angegeben, die das Vorkommen in einer Zweigmasse von 1000 Trieben des laufenden Jahres ausdrücken, was ungefähr 2,25 m^2 Bodenfläche entspricht (Tabelle 3, Abb. 4—7). — Die Gesamtzahlen der Arten und Exemplare für die 4 Untersuchungsperioden von 1970 sind in Tabelle 2 enthalten, dazu die nach der WILLIAMS-Methode aus diesen Zahlen errechneten Vielfältigkeitsindices. — Die in dieser Arbeit berichteten Messungen der Dichte werden mit den Ergebnissen anderer Untersuchungen der Koniferenfauna in Europa verglichen (Tabellen 6—9). Dabei zeigt sich, daß die Dichte verschiedener Arten von Spinnen, Käfern (Coleopteren) und Wanzen (Hemipteren) in Holland beträchtlich höher war als anderswo in Europa, was eher auf die größere Genauigkeit unserer Zählmethode als auf einen wirklichen Häufigkeitsunterschied zurückzuführen ist. In der Artenzusammensetzung stimmen die Käferfaunen der verschiedenen Teile Europas weitgehend überein, die Spinnenfaunen weniger, und die Wanzenfaunen unterscheiden sich noch mehr. — Jährliche Fluktuationen der Arten können die Artenzusammensetzung erheblich beeinflussen. Deshalb sollten sich Vergleiche von Faunen der Invertebraten auf Daten von mindestens fünf Jahren stützen.

Резюме

Отметилась плотность летней фауны безпозвоночных в кронах сосен (кроме Mikrolepidoptera, Aphidae, Psocidae, Cicadidae и Acari) в 1969—1971 гг для месяцев июнь, июль, август и сентябрь. Пробы брали с деревьев путём отрезания ветвей в мешок. После того, как убивали животных углекислородом, их вытряхивали из ветвей. Плотность выражается числами, которые отражают существование в массе ветвй из 1000 побегов настоящего года, это примерно равно 2,25 $м^2$ поверхностной площади (таблица 3, рисунку 4—7). — Общие числа видов и экземпляров для четырёх периодов исследования 1970-ого года составляются в таблице 2, в том числе и из этих чисел вычисленные по методу WILLIAMS указатели многообразия. — Полученные в этой работе данные плотности сравниваются с результатами других исследований фауны хвойных в Европе (таблицы 6—9). При этом видно, что плотность различных видов пауков, жуков и полужестко крылых выше чем в других районах Есропы, это объясняется прежде всего наверно более большой точностью нашего метода вычисления чем реальной разницой частоты. В видовом составе фауны жуков разных частей Европы имелись более большие соответствия, у фауны пауков они менее большие у фауны полужёсткокрылых отличаются ещё больше. — Флуктуации видов могут сильно влият на видовой состав. Поэтому сравнения фаун безпозвоночных надо опирать на данные не менее чем пяти лет.

References

BRISTOWE, W. S. The distribution of harvestmen (Phalangida) in Great Britain and Ireland, with notes on their names, enemies and food. Journ. an. Ecol. **18**, 100—114; 1960.

DONDALE, C. D. Note on population densities of spiders (Araneae) in Nova Scotia apple orchards. Can. Ent. **90**, 111—113; 1958.

— Life histories of some common spiders from trees and shrubs in Nova Scotia. Can. Journ. Zool. **39**, 777—787; 1961.

DZIABASZEWSKI, A. Investigations of pine crown spiders in some forestries of Poland and Pomerania. Pozn. Towarz. Przyj. Nauk **22**, 27—37; 1969. [Polish with summary in English.]

ENGEL, H. Beiträge zur Faunistik der Kiefernkronen in verschiedenen Bestandstypen. Mitt. Forstw. Forstwiss. **12**, 334—361; 1941.

ENGELHARDT, W. Untersuchungen über Spinnen aus Fichtenwipfeln. Opusc. Zool. Nr. 17, 1—9; 1958.

FISHER, R. A.; CORBET, A. S. & WILLIAMS, C. B. The relation between the number of species and the number of individuals in a random sample of an animal population. Journ. an. Ecol. **12**, 42—58; 1943.

HESSE, E. Untersuchungen an einer Kollektion Wipfelspinnen. Sitzungsber. Ges. Naturf. Freunde Berlin, 350—363; 1940.

HÖREGOTT, H. Untersuchungen über die qualitative und quantitative Zusammensetzung der Arthropodenfauna in den Kiefernkronen. Beitr. Ent. **10**, 891—916; 1960.

JAHN, E. Beitrag zur Morphologie und Lebensweise sowie zur Kenntnis des Lebensvereines von *Chlorochroa pinicola* M. & R. (Heteroptera, Pentatomidae). Ztschr. angew. Ent. **29**, 164—175; 1942.

KESTEN, U. Zur Morphologie und Biologie von *Anatis ocellata* (L.). Ztschr. angew. Ent. **63**, 412—445; 1969.

KLAUSNITZER, B. Zur Kenntnis der Beziehungen der Coccinellidae zu Kiefernwäldern. Acta Ent. Bohemoslovaca **64**, 62—68; 1967.

KLOMP, H. The dynamics of a field population of the pine looper, *Bupalus piniarius* L. (Lep., Geom.). In: Adv. Ecol. Res. 3. J. B. Cragg Edt.; 1966.

KOCHLER, W. *Troilus luridus* F., ein Schädling des Kiefernspanners. Abstract Rev. appl. Ent. **38**, 175; 1948.

PRESTON, F. W. The commonness and rarity of species. Ecology **29**, 254—283; 1948.

TODD, V. The habits and ecology of the British harvestmen (Arachnida, Opiliones), with special reference to those of the Oxford district. Journ. an. Ecol. **18**, 209—229; 1949.

WILLIAMS, C. B. Patterns in the balance of nature. In: Theor. exp. Biol. 3; 1964. [Academic Press, London].

DOI: 10.21248/contrib.entomol.23.5-8.325-340