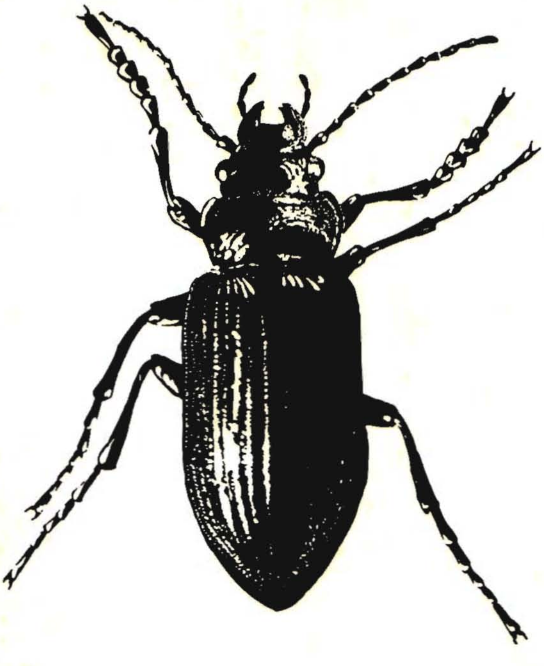
NORWEGIAN JOURNAL OF ENTOMOLOGY

Volume 25 · No. 2 · 1978



Universitetsforlaget

Norwegian Journal of Entomology

Norsk Entomologisk Tidsskrift

EDITOR

Dr. philos. Lauritz Sømme, Zoologisk institutt, Universitetet i Oslo, Blindern, Oslo 3, Norway.

EDITORIAL COMMITTEE

Førstelektor Eivind Østbye, Konsulent Per F. Waaler, Førstekonservator dr. philos. Albert Lillehammer.

PUBLISHER

Universitetsforlaget: P.O. Box 7508, Skillebekk, Oslo 2, Norway.
P.O. Box 142, Boston, Massachusetts 02113, U.S.A.

CONTRIBUTIONS

These should be sent to the Editor. Authors are requested to follow the instructions on page 3 of the cover.

Artikler som ønskes trykt i tidsskriftet sendes redaktøren. Bidragsytere må følge anvisningen på omslagets tredje side.

SUBSCRIPTIONS

Non-members of the Norwegian Entomological Society should send their orders to Universitetsforlaget. The subscription price per volume (two issues annually) is for 1978 U.S. $ 22.00 (N. kr. 110,-). U.S. $ price is subject to change without notice in case of devaluation/revaluation. Notice of change of adress should be accompanied by the old address. Back volumes should also be ordered from Universitetsforlaget.

NORSK ENTOMOLOGISK FORENING

ser sin hovedoppgave i å fremme det entomologiske studium i Norge, og danne et bindeledd mellom de interesserte. Medlemskontingenten er for tiden kr. 40,- pr. år. Medlemmar får tidsskriftet fritt tilsendt. Henvendelser om medlemskap sendes sekretæren: Cand. real. Trond Hofsvang, Zoologisk institutt, NLH, 1432 Ås-NLH.

© Universitetsforlaget 1978

BERLINGS, LUND

The influence of the substratum on the habitat selection of Bembidiini (Col., Carabidae)

JOHAN ANDERSEN

Andersen, J. 1978, The influence of the substratum on the habitat selection of Bembidiini (Col., Carabidae). *Norw. J. Ent.* Vol. 25, pp. 119–138. Oslo. ISSN 0029-1897.

In alternative choice chamber experiment the burrowing species *B. lapponicum* Zett. and *B. argenteolum* Ahr. select sand to silt irrespective of the moisture. *B. argenteolum* prefers moist, coarse-medium sand to moist, coarser and finer sand fractions, whereas dry, medium-fine sand is preferred to dry, coarser sand fractions. *B. petrosum* Gebl. selects compact silt to sand irrespective of the moisture. These results coincide with the habitat selection of the two latter species in nature. Other species were more dependent upon the moisture, but *B. semipunctatum* Don. and *B. tetracolum* Say. preferred dry, compact silt to dry sand. Some morphological peculiarities of the legs of *B. argenteolum* are regarded as psammophilous adaptations.

Johan Andersen, Institute of biology and geology, University of Tromsø, N-9000 Tromsø, Norway.

Field studies show that different species of the tribe Bembidiini select habitats with a particular substratum (Lindroth 1945, Andersen 1970). Generally it has often been doubted whether it is the properties of the substratum per se that are responsible for this specialized habitat selection among terrestrial arthropods. Thus water permeability, water absorption capacity, content of organic matter, vegetation cover and the microclimate vary with the substratum type and these factors may be more important for the animals than the texture of the substratum itself (vide also Schwerdtfeger 1963).

The aim of the present work is to study whether the species of the tribe Bembidiini are dependent upon the primary properties of the substratum. Such studies of terrestrial invertebrates are rather few, and some of the experiments made, for instance those on Carabidae (Lindroth 1949), are incomplete. This author has made his experiments with various substratum types of almost equal percentage moisture and hence of different moisture suction. Other experiments (Maelzer 1956) reveal that burrowing beetles select sharply between substratum of different moisture suction. During the present experimenting it was found necessary to work with different combinations of substratum and moisture, as done by Edwards & Epp (1965).

Previously some observations and experiments of digging and egg-laying behaviour have been carried out with a few *Bembidion* species (Andersen 1966). Some of these observations and experiments have later been supplied with additional material and hence are represented in the present work.

Material and methods

Except for a few field observations the studies were carried out in the laboratory. The material origins both from Central and Northern Norway. During observations of egg-laying and digging behaviour the adults were kept in 1-ltr. glass jars where adults of all the species mentioned in Andersen (1970) were kept on their natural substratum and with natural cover (grass, foliage, moss or stones). Larvae were always kept individually on their natural substratum in small glasses. Imagines were fed with bread and small dead or alive invertebrates, the larvae with various dead arthropods.

The different substratum fractions used in the experiments were gained by sieving the natural substratum through sieves of different mesh sizes. When nothing else is stated the substratum was collected at Rundhaug at the river Målselva in Troms county.

The following fractions were used:

		Particle diameter (mm)	
		Scale 1	*Scale 2*
A	Very coarse sand	2.0–1.0	2.0–0.8
B	Coarse sand	1.0–0.5	0.8–0.5
C	Medium sand	0.5–0.25	0.5–0.25
D	Fine and very fine sand	0.25–0.063	0.25–0.07
E	Silt	<0.063	<0.07
F	Clay	<0.025	<0.02

Scale 2 was used in some experiments with digging capacity, in the other experiments Scale 1 was used. The silt is mixed up with small amounts of clay (<1%) and humus (<5%) just as it is in nature. Fractions above 2 mm (gravel and stones) are not dealt with in this paper. Gravel and especially stones are objects that the beetles hide under (coverage) rather than something in which they dwell on or into. The beetles' reaction to the coverage thus needs a certain amount of study.

To study burrowing capacity, larvae and adults were kept without shelter in glasses with hard packed substratum of various grain sizes (in some experiments with *B. lapponicum* Zett. and *B argenteolum* Ahr., two stones were available as shelter). The beetles were exposed to a more or less wide range of light intensities (records made with an AEG luxmeter) and temperatures (records made 1-2 mm below the substratum surface with a Mavoterm termistor). The moisture at the beginning of the experiments was high and usually the same on equal substratum types used for different species, but the substratum was allowed to dry nearly completely up in the course of the experiments.

Two types of choice chambers were used in the preference experiments. Most of the experiments were carried out in petri-dishes of 11.6 cm diameter. In some experiments rectangular boxes of 13.5×6.5×2.7 cm size (for *B. argenteolum* and *B. lapponicum* 20 × 10.5 × 4 cm) were used. The boxes and petri-dishes were divided into two halves by a water-tight, about 5 mm high wall. Both zones were filled with substratum up to the upper part of the wall and the animals could easily pass from one zone to the other. The boxes and petri-dishes were covered with lids. Preference experiments were carried out with no more than 30 individuals which were observed several times (usually at intervals varying between 1/4 to 1 hour). The experiments with non-digging species and some with digging species (Table IV, VII and IX) were carried out at 20–24°C and, except during observation, in complete darkness. One experiment with *B. petrosum* Gebl. was carried out at 4°C.

In an alternative experiment (dry fine sand-dry silt) with *Bembidion semipunctatum* Don. the behaviour of individual specimens was observed continuously for a shorter period. A light bulb was placed 30 cm above the substratum surface to ensure even distribution of the light. The other preference experiments with the burrowing species were carried out in diffuse day-light at 8–14°C. In these experiments the beetles were taken away from the boxes or glasses after each observation, then the substratum was packed together and the beetles replaced. When the beetles were replaced they ran towards the light. The petri-dishes were always placed in such a way that this source of error was eliminated. The individuals did not seem to react to possible differences in colour or light reflection ability of different substratum types or moisture contents.

The substratum was washed and dried in exsiccators at more than 70°C for 24 hours before being used in further experiments. The silt had to be renewed after some experiments because the finest fractions were partly washed away by the cleaning of the substratum.

In experiments with dry silt the substratum was usually packed together in the petri-dishes or glasses in a moist condition and dried completely up. The silt retained its compact consistency after dessication as it does under natural circumstances (Andersen 1970). When nothing else is stated the silt had this compact consistency and an even surface in the experiments. In a few experiments dry compact silt with crevices or dry loose, dusty silt were used.

In the experiments with *B. argenteolum* and *B. lapponicum* the water content of the substratum just after the last observation was determined by weighing, drying and re-weighing. For these species the moisture content of each zone is given as an interval (the moisture content at the start and the end of the experiments). For the other species controls showed that this procedure was unnecessary because the moisture content did not change much (less than 10% of the original value) during the substratum experiments that usually lasted for 4½–5 hours.

The substratum moisture is given as weight per cent water of the dry weight of the substratum. Measurements of the relative moisture of the air (recorded with Feuchtmesstreifen, Union-Seidengaze, Frankfurt, placed 1–2 mm above the substratum surface) show that the moisture of the dry zone at the start of the alternative experiments with a moist and a dry zone was the same as in the laboratory, i.e. 35–45%. After two hours the moisture on the dry side increases to about 70%, within 4½ hours to 80% or more, but it is below 100% (no dew on the under side of the paper whereas this is the case on the moist side). Even after 24 hours the RH-value seems to be below 100%. This change in the moisture conditions is independent of the substratum types in the two zones. The beetles were always given sufficient water and food before the preference experiments started.

An experiment was set up to check whether the beetles react to differences in the odour of sand and silt (contrary to wet sand, wet silt has a smell perceptible to the human being). The apparatus used was principally the same as used by Perttunen (1953). One half of the bottom part was filled with silt of 25% moisture, the other half contained coarse sand of 5% moisture. Above this the animals could move freely between the two zones on a net arena of 13.6 cm diameter. The system was closed by a lid. The RH-value was 100% in the whole arena.

The ability of four species to survive on different types of dry substratum was tested. The specimens were kept without food and water in $\frac{1}{2}$-ltr. jars with dry, fine sand or dry compact silt. The experiments with the species *B.argenteolum*, *B. semipunctatum* and *B. schueppeli Dej.* were started at the same time. The temperature fluctuated between 20–22°C and the relative air moisture was 50%. In the experiments with *B. petrosum* the air temperature was 23°C and the relative air moisture 20–23%. Individuals still alive but without the ability to turn when put on their back are regarded as paralyzed. Usually such individuals do not recover even if they are taken away from the substratum and given water and food.

A morphological study of some of the species was made. The morphometric measurements and some of the figures (Figs. 9 and 12) are based on camera lucida drawings, whereas Fig. 10 and 11 are redrawn from scanning electron micrographs.

By the statistical treatment of the results of the substratum preference experiments and the alternative experiments with moisture preference of digging imagines of *Bembidion argenteolum* two-tail tests of first and last observations were used. The distribution of the animals at these two observations is regarded as independent of each other. The hypothesis $H_1:p_1=\frac{1}{2}$ is rejected if

$$\frac{x_1-n\cdot\frac{1}{2}}{\sqrt{n\cdot\frac{1}{2}\cdot\frac{1}{2}}}>C$$

and $H_l : p_l=\frac{1}{2}$ is rejected if

$$\frac{x_l-n\cdot\frac{1}{2}}{\sqrt{n\cdot\frac{1}{2}\cdot\frac{1}{2}}}>C.$$

n is the total number of individuals at each observation, X the number of individuals in one of the two zones, and the indices 1 and l concern the first and last observations respectively. C is given as follows:

$$1-[2\Phi(C)-1]^2=\alpha,$$

where α is the significance level and Φ the cumulative normal distribution.

A corresponding one-tail test based on the cumulative normal distribution was used for the statistical treatment of the results of the substratum moisture preference experiments. The morphometric study deals with the ratios between certain measures. It was found valid to give these data as confidence limits as they almost gave a straight line when plotted on probability papers.

Results

Digging behaviour and oviposition

Tabe I shows that imagines of *Bembidion argenteolum*, *B. lapponicum* and *B. velox* L. have a rather great digging capacity on sand, whereas the other species did not burrow. *B. argenteolum* is also able to dig on silt. Observations of the species in terrarium mostly confirm the results of these experiments. Especially at rather low temperatures and light intensities, most specimens of *B. argenteolum*, *B. lapponicum* and *B. velox* burrow and keep still in the sand. *B. argenteolum*, *B. velox* and *B. lapponicum* frequently burrow during, as well as outside the breeding phase.

Digging has (probably in connection with egg-laying) been observed a few times among adult *B. litorale* Ol. on fine sand-silt mixture, and on sand among *B. virens* Gyll. and *B. hasti* Sahlb. *B. schueppeli* Dej. and *B. petrosum* sometimes loosen sand particles, but they never make real burrows. Some specimens of *B. saxatile* Gyll. that were collected in their hibernation sites made real burrows in fine sand at 21°C in the laboratory. Among 24 specimens of *B. litorale* kept on medium sand covered with moss and leaves, several specimens had made shallow burrows. The specimens were collected as tene-

Table I. Digging capacity experiments with imagines of *Bembidion* spp. on substratum of varying grain size. Some of the results are from Andersen (1966). In each experiment the light intensity varied between 0-≥1000 lux and the temperature between 7-≥20°C

Species	Substratum type	N	O	Percentage buried
B. argenteolum	Medium-fine sand	26	156	73
	Silt	20	80	20
B. lapponicum	Coarse-fine sand	38	538	53
	Silt	28	332	0
B. petrosum	Coarse-fine sand	93	1695	0
	Silt	66	515	0
B. saxatile	Coarse sand	29	116	0
	Silt	20	100	0
B. schueppeli	Coarse-fine sand	85	1115	0[x]
	Silt	70	650	0
B. semipunctatum	Coarse sand	27	108	0
	Silt	20	100	0
B. velox	Coarse sand	13	40	38
	Silt	14	70	0

N: number of specimens. O: total number of position records. x: some specimens had put their head and thorax into the sand.

rals in August and had been kept at 4°C in darkness for two months. It is reasonable to conjecture that this treatment had initiated a hibernation situation for the animals.

The rest of the species were never observed digging as adults, either at low or at high temperatures and light intensities. Both tenerals and old, sexually mature specimens of most of the species have been kept in terrarium.

In the field, adults of *B. argenteolum* and *B. lapponicum* were often found in their burrows, which were usually situated at the transition between weakly moist and dry sand. Specimens of *B. argenteolum* which were dropped on dry sand during cold and cloudy days ran about until finding weakly moistened crevices where they began to burrow. An experiment showed that *B. argenteolum* and *B. lapponicum* dig even when they can shelter under stones (Table II). The experiment with the two species was set up at the same time and during the same external conditions. The temperature varied between 18–21°C, and the light intensity between 500–2000 lux. The experiment suggests that the digging capacity is greater for *B. argenteolum* than for *B. lapponicum*.

When *B. argenteolum, B. velox,* and *B. lapponicum* are burrowing, they loosen the sand particles with their jaws and push the sand backwards by means of the pro- meso- and meta legs. Observations in a binocular microscope show that especially the tarsi and the spurs, and to a less extent the outer part of the tibiae, are used to push away the sand. When a short burrow has been made, the tibiae are used to support the body during further digging.

Some preliminary experiments with larvae of *B. argenteolum* and *B. nitidulum* Mrsh. (Andersen 1966) indicate that the ability to dig on clean silt and clay is very small. For *B. argenteolum* this conclusion has been confirmed by further data (Table III).

Oviposition behaviour was observed in a few species in the laboratory. A detailed description of the egg-laying of *B. argenteolum* is given in Andersen (1966). Later observations have stated this description which could shortly be summarized as follows: At the end of a burrow (up to more than three cm deep) dug by the female, the eggs are deposited separately in small egg-chambers. The present work shows that the egg-chambers are made by the styli at the end of the abdomen. The chambers are separated from the burrow by sand, the distance between the chambers and the burrow being about 2–5 mm. Egg-laying was not observed among *B. lapponi-*

Table II. Hiding and digging tendency of imagines of two Bembidion spp. on natural sand (grain size 0.8-0.07 mm) with two stones of equal size on the surface. The figures give the number of specimens buried (b) in the sand or hiding (h) under the stones at each of the four observations. The rest of the specimens at each observation stayed on the surface of the sand.

Species	Number of specimens		Number of hours after beginning of experiment ½	5	8	24
B. argenteolum	34	b	12	17	9	11
		h	7	15	8	7
B. lapponicum	37	b	2	11	3	7
		h	19	25	16	16
chi square test		χ^2	10.37	2.69	4.03	2.71
		p	<0.01	n.s	<0.05	n.s

n.s: Not significant (p>0.05)

cum and *B. velox* but they possibly bury before ovipositing. No natural crevices were available for the imagines, but they made many burrows before larvae were seen at the bottom of the glasses.

Bembidion semipunctatum and *B. schueppeli* make no burrows and probably no egg-chambers; deposited eggs were observed in seemingly natural crevices in the earth.

Larvae of several other species have been reared (cf. Andersen 1970), but the imagines have usually not been observed digging and the eggs are probably deposited in natural crevices, either free or in small egg-chambers. In two boxes with very hard, compact and moist silt containing adult *B. petrosum* a number of small holes of equal size (barely 1 mm) were observed. The end of the abdomen of one female was dirty from silt. Two eggs were laid on the surface, but were soon afterwards eaten by the adults. The holes had obviously been made with the styli, but the oviposition was unsuccessful, perhaps because the silt was too hard.

Substratum moisture preference

The moisture reaction of some species on different substratum types is given in Table IV. At the first observation, all the species tested showed a significant preference for the dry zone at all the substratum types. The only exceptions were *B. petrosum* and *B. schueppeli* on fine sand and the latter species had a significant preference to the moist zone. At the end of the experiment *B. schueppeli* did not discriminate between the moist and dry zone of silt and coarse sand but it showed a significant preference for the moist zone of medium and fine sand. *B. argenteolum* and *B. litorale* preferred the dry zone of coarse and medium sand (for *B. argenteolum* also fine sand) during the whole experiment, but they did not discriminate significantly between dry and moist silt at the last observation. *B. petrosum* and *B. semipunctatum* preferred the dry zone of coarse sand and silt at the last observation. *B. petrosum* did not discriminate between dry and moist fine sand at the end of the experiment whereas *B. semipunctatum* showed a preference to the wet zone of that substratum type at the last observation.

As stated before, *Bembidion argenteolum* burrows only on moist substratum. Moistures of medium values seem to be preferable to those of high and low values (Table V). The lower limit of this optimal area is at a higher moisture content when the sand is fine grained than when it is coarse grained, being about 2.0% on fine sand, 1.3 – 1.4% on coarse and medium sand and about 0.5% on very coarse sand.

Table III. Digging capacity of larvae of Bembidion argenteolum on substratum of varying grain size.

Substratum type	Number of specimens	Total number of position records	Percentage buried
Coarse sand	11	66	89
Medium to fine sand	16	74	84
Silt	21	84	9
Clay	11	59	2

Table IV. Moisture reaction of imagines of five Bembidion species. Each experiment lasted for five hours. Water content of moist coarse sand: 1.5%, of moist medium sand: 2%, of moist fine sand: 5% and of moist silt: 20%. B. argenteolum sometimes buried in the moist zone.

Species	Substratum type	Total number of position records in D	Total number of position records in M	Number of individuals in each zone at first obs. D	first obs. M	last obs. D	last obs. M	N
B. argenteolum	Coarse sand	117	13	26^{x}	0	21^{x}	5	26
	Medium sand	187	45	48^{x}	10	48^{x}	10	58
	Fine sand	247	78	56^{x}	10	50^{x}	16	66
	Silt	183	107	37^{x}	21	30	28	58
B. petrosum	Coarse sand	190	80	35^{x}	19	41^{x}	13	54
	Fine sand	203	205	59	43	50	52	102
	Silt	197	23	37^{x}	7	38^{x}	6	44
B. semipunctatum	Coarse sand	413	97	95^{x}	19	75^{x}	39	114
	Medium sand	247	97	74^{x}	12	48	38	86
	Fine sand	305	335	86^{x}	42	40	90^{x}	130
	Silt	365	55	73^{x}	11	73^{x}	11	84
B. schueppeli	Coarse sand	320	136	65^{x}	11	38	38	76
	Medium sand	90	143	26^{x}	14	11	29^{x}	40
	Fine sand	41	199	7	33^{x}	6	34^{x}	40
	Silt	175	65	35^{x}	5	22	18	40
B. litorale	Coarse sand	258	62	52^{x}	12	53^{x}	11	64
	Medium sand	133	17	26^{x}	4	26^{x}	4	30
	Fine sand	56	34	21^{x}	9	19	11	30
	Silt	62	13	15^{x}	0	11	4	15

M: moist zone. D: dry zone. obs.: observation. x: preference to the actual zone significant ($p<0.05$). N: number of individuals.

Table V. Alternative experiments with moisture preference of digging imagines of Bembidion argenteolum on sand of different grain sizes. The upper and lower limits of the moisture alternatives of each zone are shown as figures within brackets. The upper and lower moisture limits are those at the first and last observation, respectively.

Exp. no	Substratum type	Moisture alternatives (% H_2O)	Total number of position records in each zone (buried specimens)	N	Significance level (two tail tests of first and last observation)
1.	Very coarse sand	(0.7;2.0)-(4.2;6.0)	43-0	12	0.05
2.		(2.1;2.5)-(3.8;4.5)	23-8	54	0.01
3.		(1.3;2.0)-(2.5;3.8)	61-39	66	n.s.
4.		(0.5;1.3)-(1.8;2.8)	57-43	66	n.s.
5.		(0.2)-(1.9)	2-11	18	0.05
6.	Coarse sand	(1.1;2.0)-(4.2;6.0)	50-8	25	0.01
7.		(2.1;2.5)-(3.8;4.5)	54-24	36	n.s.
8.		(1.3;2.0)-(2.5;3.8)	26-36	36	n.s.
9.		(0.5;1.3)-(1.6;2.5)	2-42	57	0.01
10.	Medium sand	(1.3;2.0)-(4.2;6.0)	78-37	50	n.s.
11.		(1.4;2.0)-(2.9;3.8)	35-25	25	n.s.
12.		(0.7;1.4)-(1.6;2.8)	2-41	25	0.001
13.		(0.4;1.2)-(2.7;4.1)	1-28	30	0.05
14.	Fine sand	(1.0;3.0)-(7.0;10.0)	127-40	42	0.05
15.		(2.1;3.0)-(4.7;6.0)	36-1	30	0.001
16.		(1.7;2.1)-(4.0;4.7)	13-31	30	0.01
17.		(2.1;2.5)-(3.8;4.5)	47-27	66	n.s.
18.		(1.2;2.0)-(2.2;3.8)	31-74	66	0.05
19.		(0.8;1.2)-(1.1;2.2)	14-86	36	0.001

n.s.: Not significant ($p>0.05$). N: Total number of specimens in the experiment (all of them were not necessarily buried)

Table VI. Alternative experiments with the substratum preference of digging imagines of Bembidion argenteolum at different moisture combinations. The upper and lower limits of the moisture alternatives of each zone are shown as figures within brackets. The upper and lower moisture limits are those at the first and last observations, respectively.

Experiment no.	Substratum alternatives	Moisture content (% H_2O) of the substratum alternatives	Total number of position records in each zone (buried specimens)	N	Significance level (two tail tests of first and last observation)
1.	Very coarse sand-medium sand	(0.9;2.0)-(9.0;10.0)	92-83	40	n.s.
2.		(0.8;2.0)-(4.7;6.0)	33-61	28	n.s.
3.		(1.0;1.5)-(2.5;3.0)	31-214	81	0.001
4.		(4.5;6.0)-(1.3;2.0)	13-85	36	0.01
5.		(1.4;7.0)-(1.6;7.0)	68-236	53	0.01
6.	Very coarse sand-coarse sand	(1.3;3.0)-(1.5;3.0)	52-123	27	0.05
7.		(1.4;2.0)-(3.0;4.0)	17-42	36	0.05
8.		(4.2;6.0)-(0.9;2.0)	32-125	36	0.05
9.	Coarse sand-medium sand	(1.4;3.0)-(7.2;10.0)	112-31	27	n.s.
10.		(≤10.0)-(1.4;3.0)	47-54	28	n.s.
11.		(1.7;3.0)-(1.8;3.0)	66-38	28	n.s.
12.	Medium sand-fine sand	(1.0;3.0)-(8.0;10.0)	192-6	57	0.01
13.		(1.3;3.0)-(3.0;4.7)	88-25	28	n.s.
14.		(3.0;4.7)-(3.0;4.7)	144-31	34	0.05
15.		(6.6;10.0)-(1.0;3.0)	182-124	24	n.s.
16.	Medium sand-silt	(0.5;1.5)-(25.0;30.0)	216-1	50	0.001
17.		(1.5;3.0)-(25.5;27.5)	203-0	45	0.001
18.		(1.0;1.5)-(1.0; ≤10.0)	94-0	55	0.001
19.		(1.5;4.5)-(17.0;20.0)	248-0	42	0.001
20.		(7.5;11.0)-(≤30.0)	91-3	30	0.001
21.		(≤10.0)-(≤10.0)	107-2	33	0.001

n.s.: Not significant ($p>0.05$). N: Total number of specimens in the experiment (not all of them were necessarily buried)

Table VII. Dry substratum preference of imagines of Bembidion argenteolum. None of the specimens burrowed but kept on the surface of the substratum.

Experiment no.	Substratum alternatives	Total number of position records in each zone	N	Significance level (two tail tests of first and last observation)
1.	Very coarse sand-medium sand	128-340	56	0.01
2.	Coarse sand-medium sand	44-128	28	0.05
3.	Coarse sand-fine sand	121-380	60	0.001
4.	Medium sand-fine sand	108-149	26	n.s.
5.	Coarse sand-silt	238-228	65	n.s.
6.	Medium sand-silt	134-182	42	n.s.

n.s.: not significant ($p>0.05$)

Substratum preference

The results of the experiments in which different substratum types and moistures were combined are given in Tables VI–XIII and Figs. 1–6. When no difference in substratum type and moisture content existed between the two zones in the petri-dishes, the distribution of four species tested was quite even and the difference not significant ($p>0.05$) in the two zones. The following species were tested (0: total number of position records, N: number of individuals): *B. litorale* (0 = 640, N = 40), *B. semipunctatum* (0 = 420, N = 20), *B. schueppeli* (0 = 300, N = 30) and *B. petrosum* (0 = 585, N = 40).

When burrowing, *Bembidion argenteolum* clearly preferred medium sand to silt (Table VI) and the species is a very poor digger on the latter

Table VIII. Substratum preference of digging imagines of Bembidion lapponicum at different moisture combinations. The upper and lower limits of the moisture of each zone are shown as figures within brackets. The upper and lower moisture are those at the first and last observations, respectively.

Experiment no.	Substratum alternatives	Moisture alternatives (% H_2O)	Total number of position records in each zone	N	Significance level (two tail tests of first and last observation)
1.	Coarse sand-medium sand	(1.2;5.0)-(1.5;5.0)	48-104	56	n.s.
2.		(8.2;10.0)-(1.4;3.0)	21-4	24	n.s.
3.		(0.8;2.0)-(6.6;8.3)	1-40	49	0.05
4.		(2.0;3.0)-(8.3;10.0)	25-8	24	n.s.
5.	Medium sand-silt	(10) -(2)	49-0	45	0.01
6.		(6.4;10.0)-(25.0;30.0)	37-1	20	0.01
7.		(7.3;10.0)-(6.5;10.0)	110-0	40	0.001
8.		(2.1;5.0)-(14.8;20.0)	74-0	40	0.01

n.s.: not significant ($p>0.05$)

Table IX. Dry substratum preference of imagines of Bembidion lapponicum. None of the specimens burrowed but kept on the surface of the substratum.

Experiment no.	Substratum alternatives	Total number of position records in each zone	N	Significance level (two tail tests of first and last observation)
1.	Very coarse sand-medium sand	106-74	18	n.s.
2.	Coarse sand-medium sand	91-69	16	n.s.
3.	Coarse sand-fine sand	188-134	32	n.s.
4.	Coarse sand - silt	50-110	16	n.s.

n.s.: not significant ($p>0.05$)

substratum. Several specimens were observed trying to scrape the silt, but usually were unable to make burrows. *B. argenteolum* also preferred medium and coarse sand to very coarse sand over a wide range of moisture combinations. However, when the moisture on the medium sand was high it did not discriminate sharply between this fraction and the very coarse sand. *B. argenteolum* did not select clearly between coarse and medium sand. More specimens burrowed on medium than on fine sand at the available moisture combinations but the preference for medium sand was not always statistically significant.

None of the specimens of *B. argenteolum* burrowed during the experiments with dry substratum. The species did not select clearly between dry sand and dry silt, but it preferred medium and fine sand to the coarser sand fractions (Table VII). The alternative experiment with dry coarse sand – dry fine sand lasted for nine hours and the preference for the fine sand was evident the whole time.

Burrowing specimens of *B. lapponicum* clearly preferred medium sand to silt independent of the moisture content of the two substratum types (Table VIII). But the reaction of the species to the alternative coarse sand – medium sand seemed to be dependent upon the moisture content of the substratum. In contrast to *B. argenteolum, B. lapponicum* did not select sharply between different fractions of dry sand (Table IX).

Experiments with the rest of the *Bembidion* species were mostly made with specimens in the breeding phase. Specimens of *B. tetracolum* Say, *B. semipunctatum, B. schueppeli* and *B. petrosum,* however, were partly non-breeding. By treatment of the material, the data of breeding and non-breeding specimens were pooled as there was no evident difference in the reaction of the two groups.

Table X. Substratum preference of imagines of three Bembidion species. Alternative experiments with natural sand (from Selbusjöen, South Norway) of grain-size 0.5-0.063 mm and silt.

Experiment no.	Species	% moisture of		Total number of position records on:		N	Significance level (two tail tests of first and last observation)
		sand	silt	sand	silt		
1.	B. petrosum	0	0	38	337	64	0.001
2.		0	20	238	456	120	n.s.
3.		5	0	159	443	120	0.05
4.	B. schueppeli	0	0	114	361	60	0.05
5.	B. semipunctatum	0	0	131	297	50	0.01

n.s.: Not significant ($p>0.05$)

Bembidion petrosum had a clear preference for silt irrespective of the moisture conditions (Fig. 1, Table X). Some of the experiments with this species lasted as long as eight hours, but no significant change in the frequency distribution could be observed during this period. Only in one case (experiment no. 2, Table X) did a two-tail test show no significant difference in the distribution on sand and silt. However, in this case separate tests showed that there was a significant preference towards silt by all the observations except for the first one. 38 specimens of *B. petrosum* were given the alternative between dry silt and dry fine sand at +4°C. A preference for the silt was significant ($p<0.01$), the number of position records being 355 on the silt and 137 on the sand. Whether the silt is even, as in the other experiments, or has crevices does not seem to affect the distribution of the species (Table XI).

Whereas *B. semipunctatum* markedly prefers dry silt to dry sand irrespective of the grain size of the latter, *B. schueppeli* and *B. litorale* do not sharply discriminate between dry silt and dry coarse sand (Figs. 2, 3 and 4). When one or both of the two zones of the alternative chamber are moist, these species either show no special preference or they prefer sand or silt largely dependent upon the moisture conditions. Thus

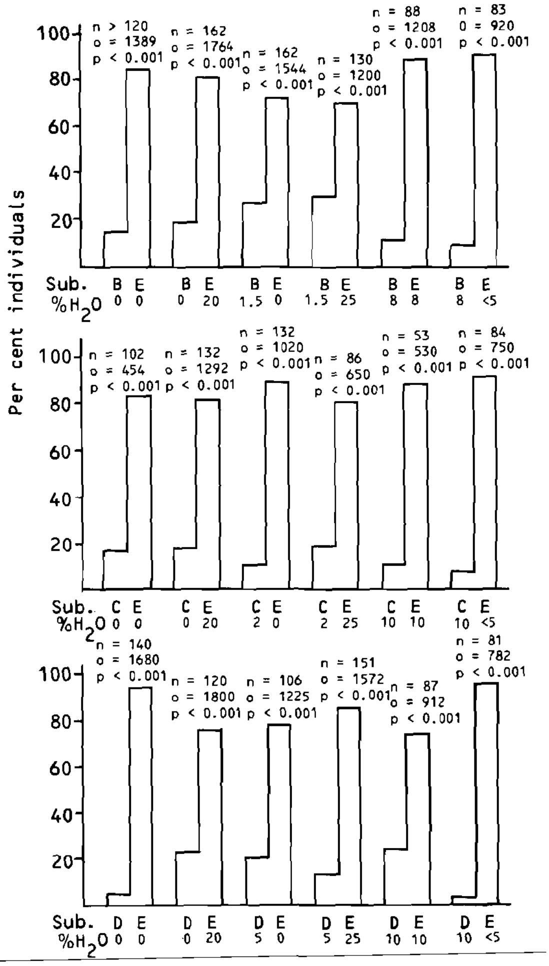


Fig. 1. Substratum preference of imagines of *B. petrosum* at different moisture combinations (% H_2O), Sub: substratum alternatives. B: coarse sand, C: medium sand, D: fine sand, E: silt, n: number of specimens, O: total number of position records p: probability (two tail tests of first and last observation).

Table XI. Substratum preference of imagines of Bembidion petrosum. Alternative experiments with dry, coarse sand and dry silt of different consistencies.

Experiment no.	Consistency of the silt	Total number of position records on:		N	Significance level (two tail tests of first and last observation)
		coarse sand	silt		
1.	Uneven, with crevices	44	166	30	0.05
2.	Even, without crevices	215	1389	>120	0.001

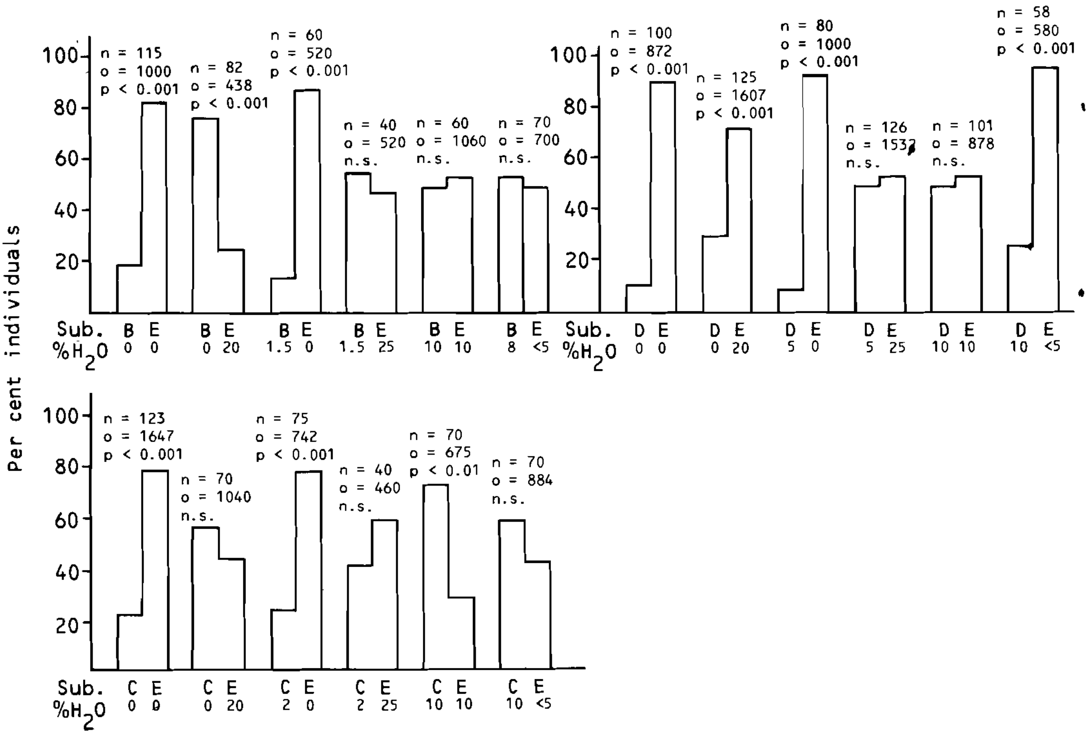


Fig. 2. Substratum preference of imagines of *B. semipunctatum* at different moisture combinations. n.s. difference not significant ($p > 0.05$). For further explanation of symbols see Fig. 1.

in the alternative experiments with coarse sand – silt and with medium sand – silt, *B. semipunctatum* largely preferred the dry substratum to the moist. However, in experiments with fine sand – silt, and with one of the zones dry and the other moist, this species as well as *B. schueppeli* preferred the silt. It is of great importance that the silt is compact and not loose and dusty (Table XII). The bodies of those individuals which had stayed on the loose dusty silt were full of silty particles.

On loose, dusty silt as well as on fine sand it has been observed that *B. schueppeli* and *B. semipunctatum* move less perfectly than they do

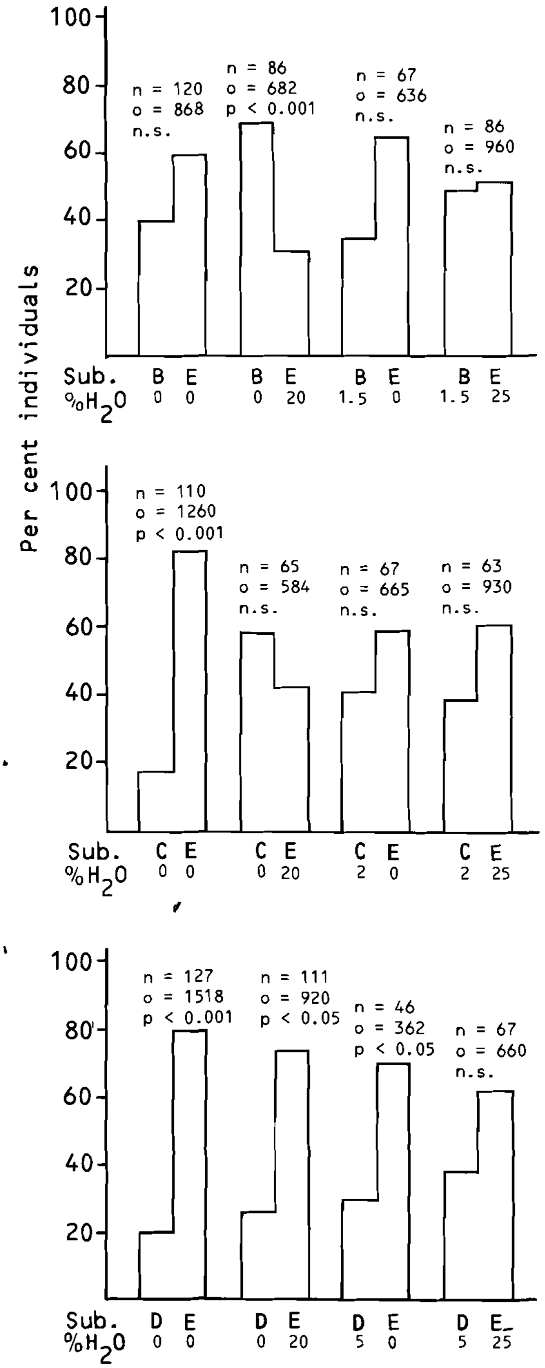


Fig. 3. Substratum preference of imagines of *B. schueppeli* at different moisture combinations. For explanation of symbols see Fig. 1 and 2.

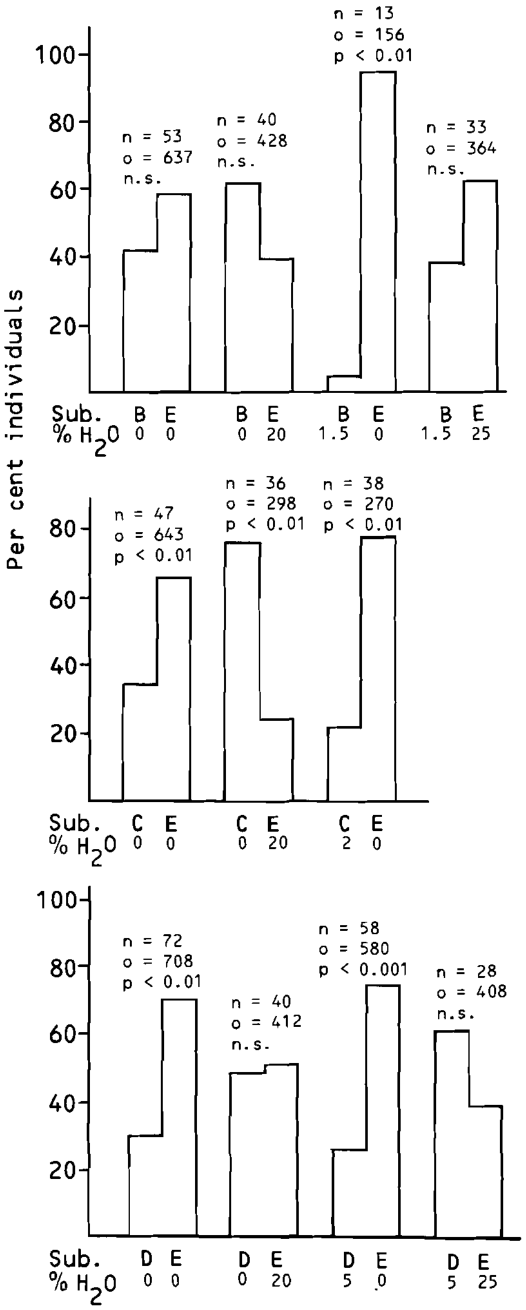


Fig. 4. Substratum preference of imagines of *B. litorale* at different moisture combinations. For explanation of symbols see Fig. 1 and 2.

Table XII. The reaction of imagines of two Bembidion spp. to an alternative of dry loose, dusty silt (L) and dry hard packed silt (H).

Species	Total number of position records on: L	H	N	Significance level (two tail tests of first and last observation)
B.schueppeli	33	232	58	0.001
B.petrosum	27	153	30	0.01

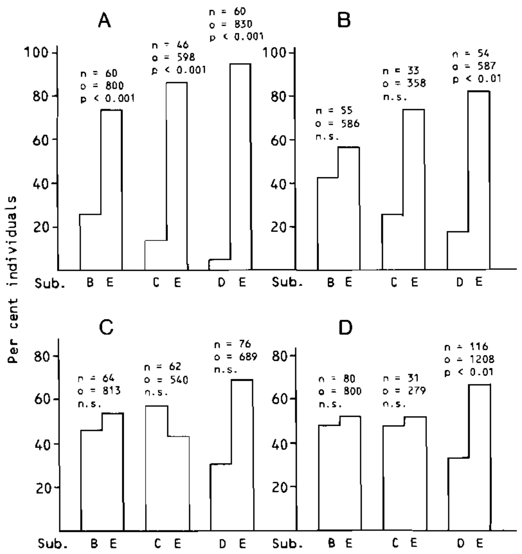


Fig. 5. Dry substratum preference of imagines of four *Bembidion* species A: *B. tetracolum*, B: *B. bruxellense*, C: *B. virens*, D: *B. quadrimaculatum*. For further explanation of symbols see Fig. 1 and 2.

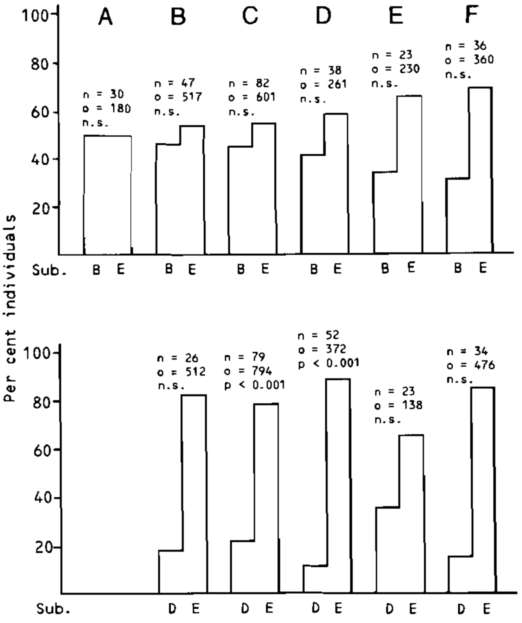


Fig. 6. Dry substratum preference of imagines of six Bembidiini species. A: *Bembidion mckinleyi* Fall., B: *B. bipunctatum* L., C: *B. hasti*, D: *B. prasinum* Dft., E: *Asaphidion pallipes* Dft., F: *Bembidion saxatile*. For further explanation of symbols see Fig. 1 and 2.

Table XIII. Substratum preference of imagines of five Bembidion spp. Alternative experiments with dry coarse sand and dry fine sand.

Species	Total number of position records on: coarse sand	fine sand	N	Significance level (two tail tests of first and last observation)
B. litorale	140	94	24	n.s.
B. petrosum	228	50	34	0.001
B. semipunctatum	291	29	32	0.01
B. schueppeli	427	115	60	0.01
B. virens	257	43	30	0.001

n.s.: Not significant (p>0.05)

on hard-packed silt. They have difficulties in passing up and down steep slopes of sand and often fall on their back. Other species seem to have less difficulties in moving on such substratum. This was stated in an experiment where *B. schueppeli* and *B. petrosum* were allowed to walk in a box with fine sand. Two specimens of each species were observed when running at the same time. Whereas 14 specimens of *B. schueppeli* fell 85 times on their back, the same happened only seven times with 14 specimens of *B. petrosum*. A similar experiment was made with *B. argenteolum* and *B. petrosum*. Four specimens of *B. petrosum* fell 17 times on their back, whereas the same happened two times with four specimens of *B. argenteolum*. Thus *B. argenteolum* seems to be the best adapted to move on fine sand among the three species.

Contrary to *B. argenteolum* and *B. litorale*, the species *B. semipunctatum*, *B. schueppeli*, *B. petrosum* and *B. virens* preferred the dry coarse sand to the dry fine sand (Table XIII).

For the rest of the species, experiments were made with dry substratum only (Figs. 5 and 6).

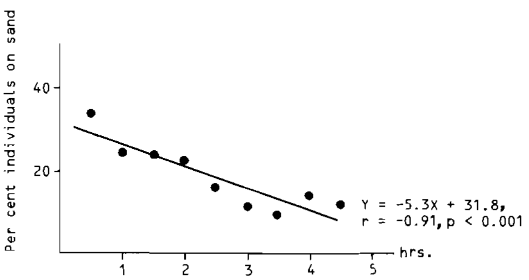


Fig. 7. Change of the substratum reaction of *B. schueppeli* with time. Alternative experiment with dry fine sand and silt of 20 % moisture.

B. tetracolum had a very marked preference for silt to sand irrespective of whether the sand was coarse or more fine-grained. Most of the other species also clearly preferred silt to fine sand, but they did not select significantly between coarse sand (for some species also medium sand) and silt. The two species that seemed to be least dependent upon the substratum were *B. virens* and *B. quadrimaculatum* L.

In only two cases did the distribution in the two alternative zones change significantly with time. This was the case with *B. schueppeli* in the experiments with dry, fine sand – dry silt and with dry, fine sand – moist silt (Fig. 7). In the first case the percentage of animals in the sand zone declined from 33 at the first observation to 6 at the last one $(Y = -5.3 \times +31.8;\ r = -0.94,\ p<0.001)$.

As stated before, the moist sand seems to be odourless whereas the wet silt has a perceptible odour perhaps due to its content of organic matter. It has not been confirmed that the beetles react to these differences in the properties of the two substratum types. Thus, in an 'odour' experiment with 46 specimens of *B. petrosum* the total number of position records above the sand was 145 and above the silt 140.

Observations of tracks in the arena

Twenty specimens of *Bembidion semipunctatum* were observed individually in petri-dishes with one zone of dry fine sand and the other of dry silt. Their tracks were drawn for a period varying between five and ten minutes. The position of the individuals was noted every 20 seconds.

Two individuals ran restless around in the apparatus during the whole period of observation. Two other individuals spent most of the time on the sand and at least during the last two minutes they kept still at the same place in that zone. The other 16 specimens stayed most of the time on the silt and here the majority stayed still till the end of the observation period after having moved around for some time. Two typical tracks are shown in Fig. 8. There was no apparent difference in the frequency of turnings in the two zones whereas the activity mostly was much lower on silt than on sand. The reaction of the beetles thus largely seemed to be ortho-kinetic (Fraenkel & Gunn 1961).

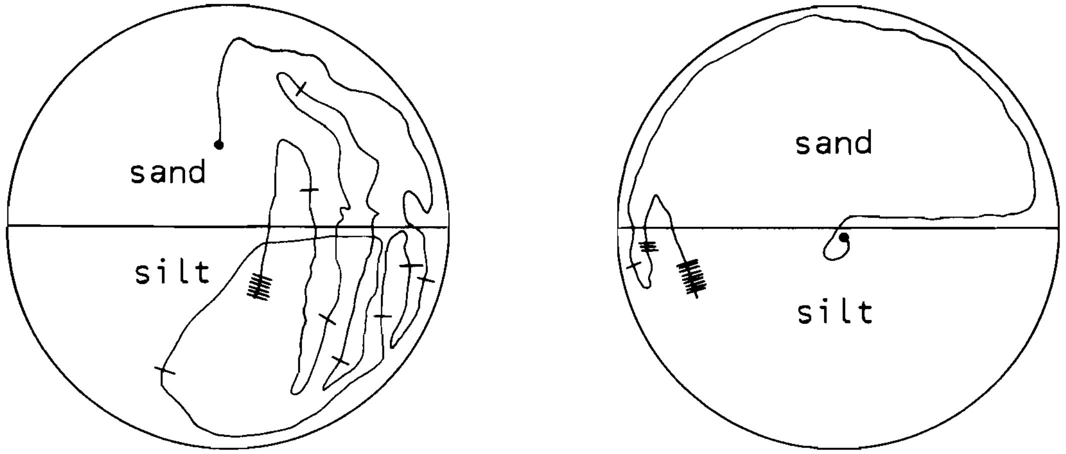


Fig. 8. Tracks of two specimens of *B. semipunctatum* in an alternative chamber with dry silt and dry fine sand. The position of the individuals every 20 seconds is denoted as small lines.

Table XIV. Comparison of the survival ability without food and water of imagines of four Bembidion species on dry, fine sand and dry, compact silt.

Species	Substratum type	R.H.	T°C	N	Mean time (hours) before paralysis	P (t-test)
B. schueppeli	Fine sand	50	20-22	20	>15; <17	n.s.
	Silt	50	20-22	21	>20; <22	
B. argenteolum	Fine sand	50	20-22	19	>25; <28	n.s.
	Silt	50	20-22	18	>30; <32	
B. semipunctatum	Fine sand	50	20-22	33	>30; <32	<0.001
	Silt	50	20-22	33	>39; <46	
B. petrosum	Fine sand	22-24	23-24.5	15	9	<0.001
	Silt	22-24	23-24.5	19	16	

n.s.: Difference not statistically significant (p>0.05)
R.H.: Relative air himidity
T°C : Air temperature

Survival ability on different types of dry substratum

The ability of four *Bembidion* species to survive on dry, fine sand and dry hard packed silt is shown in Table XIV. The time of paralysis is given as intervals because observations were not made regularly enough to determine accurately the paralysis point of all the specimens.

B. semipunctatum and *B. petrosum* lived essentially longer on dry silt than on dry, fine sand. The time required to paralyse 50 per cent of the individuals of the first species was estimated to be about 28 hours on fine sand and 40 hours on silt, for the latter species about 8 hours on fine sand and 16 hours on silt.

In contrast, the time required to paralyse the same percentage of individuals of *B. argenteolum* was almost the same on fine sand and silt (about 29 and 30 hours respectively) and the difference in the mean time before paralysis on the two substratum types was quite small and not statistically significant. Neither was the difference in the mean paralysis time of *B. schueppeli* on fine sand and silt statistically significant, but the time required to paralyse 50 per cent of all individuals seemed to be rather short on fine sand compared with on silt (about 15 and 20 hours, respectively).

Student tests showed that the mean paralysis time was significantly ($p<0.01$, at the least) higher for *B. semipunctatum* and *B. argenteolum* than for *B. schueppeli* on both the substratum types. There was no statistically significant difference in the mean paralysis time for *B. argenteolum* and *B. semipunctatum* on fine sand. The difference in the mean time that elapsed before paralysis of these two species on silt, however, was highly significant ($p<0.001$). The specimens that were kept on fine sand had considerable amounts of fine mineral particles.

Morphological adaptations

The significant differences that could be discovered between the burrowing and the non-burrowing species concern the building of their legs. The results of the morphometric studies are shown in Table XV. From the table it is evident that *B. schueppeli* has shorter legs (tarsus + tibia) than the other species studied. Relative to the total body the tarsi of *B. lunatum* Dft. and *B. petrosum* are at least equally as long as for the *Chrysobracteon* species. On the other hand, the tarsi of at least *B. argenteolum* and *B lapponicum* are generally clearly broader than those of *B lunatum*, *B. semipunctatum* and *B petrosum* (Fig. 12).

The claws of *B. argenteolum* and *B. petrosum* are somewhat longer than those of some of the other species studied (Table XV).

The spurs of the tibia of *B. argenteolum* are thicker and longer than in most other *Bembidion* species (Table XV, Fig. 9).

Table XV. Some morphological measures of the legs of imagines of different Bembidion species. The figures give the 95% confidence limits. The number of specimens investigated is given in brackets.

Species	Ratio of length of		Ratio of length of				Ratio of
	$\frac{\text{tarsus}^{x}}{\text{body}}$	$\frac{\text{tarsus+tibia}^{xx}}{\text{body}}$	$\frac{\text{longest spur}^{x}}{\text{tarsus}}$	$\frac{\text{longest spur}^{x}}{\text{1.tarsal joint}}$	$\frac{\text{claw}^{x}}{\text{tarsus}}$	$\frac{\text{claw}^{x}}{\text{5.tarsal joint}}$	$\frac{\text{tarsus}^{x}\text{ length}}{\text{body width}}$
B. argenteolum	0.19-0.20 (17)	0.51-0.52 (16)	0.23-0.24 (17)	0.61-0.62 (21)	0.19-0.21 (16)	0.73 (7)	0.43-0.45 (18)
B.lapponicum	0.18-0.19 (11)	0.47-0.51 (9)	0.17-0.24 (12)	0.51-0.57 (14)	0.16-0.18 (15)	0.70 (17)	0.42-0.44 (14)
B.litorale	0.18-0.20 (8)	0.50-0.54 (6)	0.16-0.20 (13)	0.34-0.52 (14)	0.16-0.17 (12)	0.61 (12)	0.42-0.46 (10)
B.lunatum			0.16-0.19 (8)	0.46-0.50 (12)	0.16-0.19 (12)	0.56 (15)	0.41-0.46 (8)
B.petrosum	0.18-0.20 (11)	0.49-0.51 (16)	0.17-0.18 (20)	0.45-0.49 (38)	0.19-0.20 (27)	0.68 (14)	0.47-0.49 (17)
B.schueppeli	0.16-0.17 (17)	0.44-0.45 (16)	0.19-0.20 (20)		0.18-0.21 (9)		0.39-0.41 (17)
B.mckinleyi		0.49 (3)		0.48 (5)			

^{x} of meso legs

xx of meta legs

One feature of the burrowing species *B. argenteolum*, *B. velox*, and *B. lapponicum* is an extension of the outside of the end of the pro-tibia (Fig. 9). This character is especially well developed in *B. argenteolum*. The extension seems to be absent among the non-digging species (hardly developed in *B. litorale*). The *Chrysobracteon* species (*B. argenteolum*, *B. lapponicum*, *B. velox* and *B. litorale*) have a greater number of thorns at the end of the pro-tibia than the other species. These thorns are most numerous in *B. argenteolum* and *B. velox*.

The meso- and meta-tibia of the *Chrysobracteon* species also have a much larger number of thorns, especially towards the end, than the other *Bembidion* species (Fig. 10). The number of visible thorns on the inside of the meso-tibia (in the position shown in Fig. 10) was more than 24 to up to 41 in the *Chrysobracteon* species, whereas it varies between 11 and 20 in the other species studied. Among the Scandinavian carabids (members of 37 genera of all the Scandinavian tribes were studied) a comparatively dense and long, thorny cover as that found in the *Chrysobracteon* species seems to be developed only among a few genera: *Omophron* sp., *Cicindela* sp., *Brachynus* sp., *Asaphidion* sp., *Trechus* sp. and to some extent *Elaphrus* sp. However, the thorns of *Asaphidion* sp. and *Trechus* sp. are finer and shorter than those of the *Chrysobracteon* species.

One remarkable feature of *B. argenteolum*, *B. velox* and *B. lapponicum* compared with other *Bembidion* species is the high number of setae on the tarsi. The number of setae in one row on the latero-ventral side of the three first-mentioned species is 4, 3 and 3 on each side of second, third and fourth joint, respectively (Fig. 11). In most other species the corresponding figures are 3, 2–3 and 2. In addition the three abovementioned species have extra setae on the dorsal

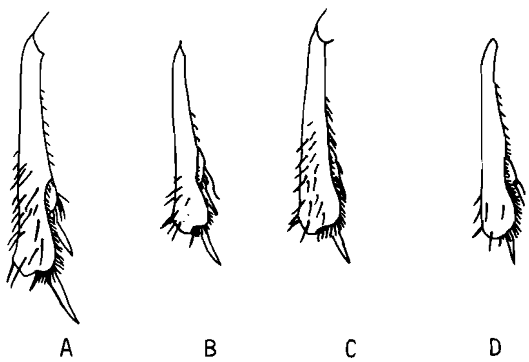


Fig. 9. The right pro-tibia of four *Bembidion* species A: *B. argenteolum*, B: *B. lapponicum*, C: *B. litorale*, D: *B. petrosum*.

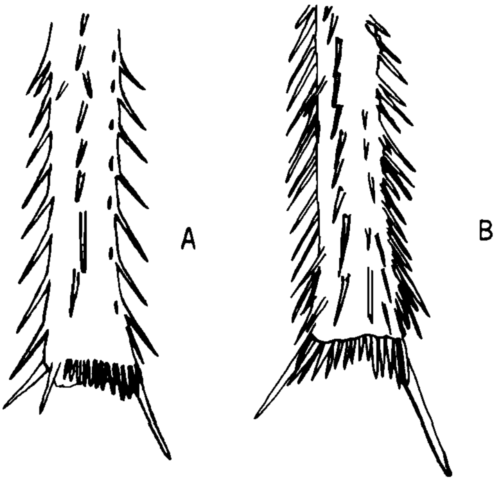


Fig. 10. The left meso-tibia of *Bembidion petrosum* (A) and *B. argenteolum* (B). Redrawn from scanning electron micrographs.

side of the same joints (Fig. 11A,a,b). The setae on the tarsi are especially strong and stiff in *B. argenteolum* whereas the setae often have a pointed and weak end in the non-digging species (Fig. 11 B).

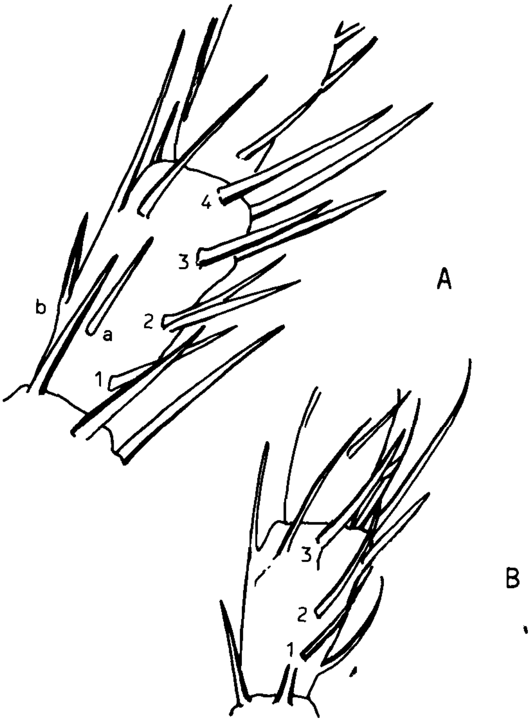


Fig. 11. Sideview of the second and parts of the third tarsal joint of the meso-leg of *Bembidion argenteolum* (A) and *B. petrosum* (B). The setae situated on one row on the lateroventral side are marked with figures. a, b: the additional setae on the dorsal side of the tarsi of *B. argenteolum*. Redrawn from scanning electron micrographs.

Discussion and conclusion

Many Carabidae show an initial preference to dry air (Perttunen 1951) just like the present species in most cases did to the dry substratum (Table IV).

The relative moisture of the dry zone in the substratum moisture apparatus changes with time. The fact that the air above the dry substratum initially has a low relative moisture indicates that the species studied here prefer dry air at least for a short time.

The relative air moisture in the dry and the moist zones as a function of time is independent of the substratum type. Despite this, the dry reaction to fine sand is little evident or not present in *B. semipunctatum, B. petrosum, B. schueppeli* and *B. litorale* (Table IV). Thus, these species also seem to react to differences in the texture of the dry substratum. This is also confirmed by the substratum preference experiments.

It is well documented that insects permanently living in soil are dependent upon the water suction of the substratum (Evans 1944, Hassan 1975, Maelzer 1956, Meats 1967). The preferred moisture content of the substratum for such species increases with decreasing grain size. For *B. argenteolum* the upper limit of the optimal area seemed to be rather independent of the grain size. It is supposed, therefore, that *B. argenteolum,* when digging, does not mainly react to the pF-value of the soil, but probably more to the mechanical properties of the substratum.

The present study reveals that, among the *Bembidion* species studied, *B. lapponicum, B. velox,* and above all *B. argenteolum* are the only regulary burrowing ones. Some of the other species may bury themselves down before hibernation or in connection with egg-laying.

The substratum choice experiments with *B. argenteolum* reveal that the species is almost unable to burrow on silt irrespective of the moisture conditions. In the experiments with two types of sand the moisture content was quite important for the substratum choice. However, a preference for medium and coarse sand to coarser or finer sand fractions is evident in those

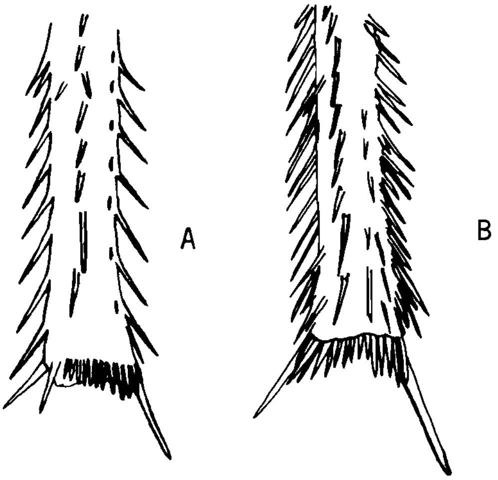


Fig. 10. The left meso-tibia of *Bembidion petrosum* (A) and *B. argenteolum* (B). Redrawn from scanning electron micrographs.

side of the same joints (Fig. 11A,a,b). The setae on the tarsi are especially strong and stiff in *B. argenteolum* whereas the setae often have a pointed and weak end in the non-digging species (Fig. 11 B).

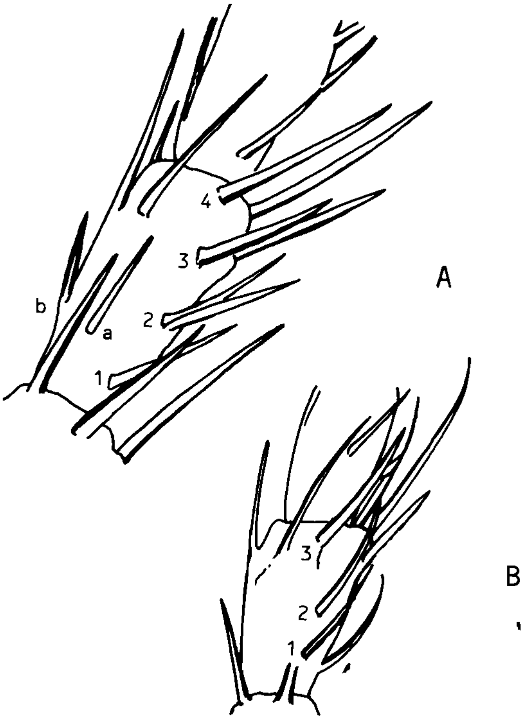


Fig. 11. Sideview of the second and parts of the third tarsal joint of the meso-leg of *Bembidion argenteolum* (A) and *B. petrosum* (B). The setae situated on one row on the lateroventral side are marked with figures. a, b: the additional setae on the dorsal side of the tarsi of *B. argenteolum.* Redrawn from scanning electron micrographs.

Discussion and conclusion

Many Carabidae show an initial preference to dry air (Perttunen 1951) just like the present species in most cases did to the dry substratum (Table IV).

The relative moisture of the dry zone in the substratum moisture apparatus changes with time. The fact that the air above the dry substratum initially has a low relative moisture indicates that the species studied here prefer dry air at least for a short time.

The relative air moisture in the dry and the moist zones as a function of time is independent of the substratum type. Despite this, the dry reaction to fine sand is little evident or not present in *B. semipunctatum, B. petrosum, B. schueppeli* and *B. litorale* (Table IV). Thus, these species also seem to react to differences in the texture of the dry substratum. This is also confirmed by the substratum preference experiments.

It is well documented that insects permanently living in soil are dependent upon the water suction of the substratum (Evans 1944, Hassan 1975, Maelzer 1956, Meats 1967). The preferred moisture content of the substratum for such species increases with decreasing grain size. For *B. argenteolum* the upper limit of the optimal area seemed to be rather independent of the grain size. It is supposed, therefore, that *B. argenteolum,* when digging, does not mainly react to the pF-value of the soil, but probably more to the mechanical properties of the substratum.

The present study reveals that, among the *Bembidion* species studied, *B. lapponicum, B. velox,* and above all *B. argenteolum* are the only regulary burrowing ones. Some of the other species may bury themselves down before hibernation or in connection with egg-laying.

The substratum choice experiments with *B. argenteolum* reveal that the species is almost unable to burrow on silt irrespective of the moisture conditions. In the experiments with two types of sand the moisture content was quite important for the substratum choice. However, a preference for medium and coarse sand to coarser or finer sand fractions is evident in those experiments where both sand types seem to have moistures not too far away from the optimal area. Thus, most likely, medium and coarse sand are the optimal substratum of the digging specimens of *B. argenteolum.*

From the experiments with digging specimens of *B. lapponicum* it is evident that the species has little or no ability to burrow on silt (Tables I, VIII), but it did not select sharply between medium and coarse sand.

According to Krogerus (1932), species less well adapted to digging (*B. argenteolum* is regarded as belonging to this group) prefer fine sand presumably because it should be easier to push away than coarse sand. This is probably correct when the substratum is dry but not when it is moistened. Usually *B. argenteolum* and *B. lapponicum* dig into more or less moistened sand. On moist sand these species loosen the sand particles with the mandibles and push them away with the legs. In this case a preference for medium or coarse sand is understandable. It is likely that very coarse particles are more difficult to grasp, lift and push away than the coarse or medium-sized particles. However, as the particle size decreases, the cohesion between wet particles increases. This makes it more difficult to loosen the wet particles of the fine sand and especially the silt, than those of the medium or coarse sand.

Some carabid beetles simply drop their eggs on the ground (Lumaret 1972–73), other species lay their eggs under stones, pieces of wood and so on (Bauer 1975), whereas others make holes where the eggs are deposited singly (Bauer 1974, Franz 1929, Willis 1967).

The most specialized species within the group with parental behaviour until egglaying are those making egg-chambers where the eggs are deposited singly in the bottom of a burrow (Brandmayr & Brandmayr 1977). Such behaviour is described in *Broscus cephalothes* L. (Kempf 1955) and the present study reveals a similar behaviour in *Bembidion argenteolum. B. lapponicum* and *B. velox* probably belong to the same group. This specialized breeding behaviour and the fact that burrows are made more or less frequently independent of oviposition may indicate that the substratum is important in the habitat selection of the three above-mentioned *Bembidion* species.

That *B. argenteolum,* and probably even *B. lapponicum,* prefer coarse and medium sand to coarser and finer fractions when digging seems partly to be contradicted by these species habitat selection. Thus *B. argenteolum* is confined to medium or rather fine sand in nature whereas *B. lapponicum* is present on a vide variety of substratum types (Andersen 1970, Lindroth 1945). However, a reasonable explanation can be given when the preference to dry substratum is also considered. Thus *B. argenteolum* mostly dwells on the surface of dry substratum (at least the uppermost layer shows incipient drying up) during day time provided that the temperature and light intensity are sufficiently high (Andersen 1966). The preference experiments reveal that in such circumstances medium or fine sand are preferred to coarser sand fractions.

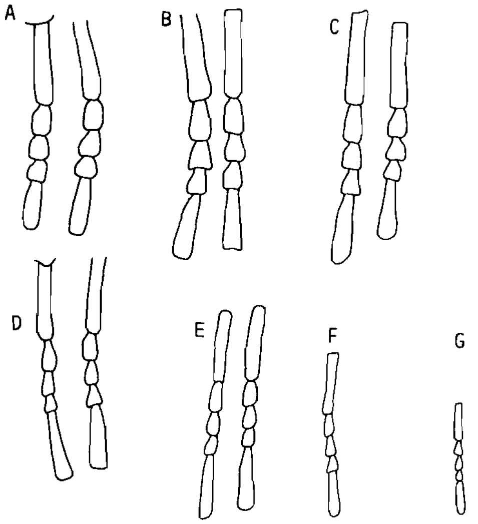


Fig. 12. Dorsal side of the meso-tarsus of seven *Bembidion* species. Claws and setae are not drawn. The five first species (A-E) are represented by specimens with extremely narrow (to the left) and extremely broad (to the right) joints. A: *B. lapponicum,* B: *B. argenteolum,* C: *B. litorale,* D: *B. lunatum,* E: *B. petrosum,* F: *B. semipunctatum,*G: *B. schueppeli.*

B. lapponicum, however, has no clear preferences for certain grain fractions when the substratum is dry. Furthermore the species has less need to dig than *B. argenteolum.*

The present study reveals that *B. velox* regularly burrows in nature as well as in the laboratory. It seems to be able to dig on sand, only (Table I). Reasonably even this species is more or less dependent on sand. This is also evident from its natural choice of habitat (Lindroth 1945). Some of the non-digging *Bembidion* species probably deposit their eggs in crevices in the earth or under available objects. Such species must be quite independent of a certain type of substratum in which to lay their eggs. Other species, such as *B. petrosum*, probably deposit the eggs singly in small holes made by the styli. The species known to belong to this group often seem to be more or less specialized in their choice of substratum and the experiments in the present study fully support this for *B. petrosum*. Thus this species selected silt to sand independent of the substratum moisture (Fig. 1). Therefore it is obvious that *B. petrosum* reacts markedly on differences of the properties in the substratum per se. This is also the experience from the distribution of the species in nature.

B. semipunctatum markedly prefers dry, hardpacked silt to dry sand. The same is the case with *B. schueppeli*, except that it does not select distinctly between dry coarse sand and dry, hardpacked silt. When the silt is moist, dry coarse sand is preferred by both species. However, as the grain size of the dry sand decreases, the tendency to prefer dry sand to moist silt declines. The substratum moisture experiments with *B. semipunctatum* and *B. schueppeli* (Table IV) may point in the same direction. *B. semipunctatum, B. schueppeli* and *B. petrosum* also clearly preferred dry coarse sand to dry fine sand (Table XIII).

Table XII demonstrates that not only the grain size but also the consistency of the substratum is important for the reaction of the beetles. This is also supported by the great difference of the results when both substratum zones were dry and when they were wet. Whereas *B. semipunctatum* and *B. schueppeli* discriminate sharply between dry medium to fine (for *B. semipunctatum* even coarse) sand and dry silt, they mostly show no special preference when both these substratum types are moist. Obviously there is a greater difference between the consistency of sand and hardpacked silt when both of them are dry than when both are moistened. The difference is especially great in the consistency of dry and moist fine sand. Observations show that *B. schueppeli* and *B. semipunctatum* have difficulties when moving on dry, fine sand, whereas they easily move on wet, fine sand and on hard, dry or moist silt.

B. semipunctatum and *B. schueppeli* did not clearly discriminate between moist sand and silt in the experiments and an occurrence on moist sand in nature could be expected. Contrary to this, field investigations show that they are limited to moist, silty habitats (Andersen 1970). However, the sandy habitats usually lack vegetation and they are very strongly exposed. The field investigations show that both the species avoid the exposed sites lacking vegetation irrespective of whether they have a sandy or a silty soil. In addition, the sandy sites very quickly dry out compared with the silty areas. Even if no differences in coverage, exposure, microclimate and so on exist, *B. semipunctatum* would prefer silt to sand if these substratum types were largely dried up. Observations of single specimens in alternative experiments (Fig. 8) reveal that the mechanism behind this reaction is orthokinetic. This leads the individuals which erroneously have come to the dry sandy sites away from them and over to the silty areas. Provided that the sand is not too coarse, the same as mentioned for *B. semipunctatum* applies to *B. schueppeli*.

B. litorale does not sharply discriminate between dry fine sand and moist silt, although the species prefers dry silt to dry medium and fine sand. In nature the species is largely found on silty spots, but occurrence on sand is not uncommon (Andersen 1970).

The majority of the other species which were tested on dry substratum showed a limited ability to discriminate between different substratum types. One exception was *B. tetracolum*, and this is in accordance with its distribution in nature where it prefers silty-clayish soils (Lindroth 1945, Andersen 1970). Under natural circumstances most of the other species occur on silt as well as on sand, some of them also on clay (Lindroth 1945).

As a rule, however, the *Bembidion* species avoid the dry, fine sand. An exception is the psammophilous species, above all *B. argenteolum*. *B. argenteolum* is the only investigated species of the genus preferring dry fine sand to dry coarse sand.

Survival ability experiments on dry fine sand and silt partially explain this difference between the sand species and the others. For *B. semipunctatum, B. petrosum* and perhaps *B. schueppeli* to stay on dry silt compared with dwelling on dry fine sand had a positive survival value whereas *B. argenteolum* survived about equally long on dry silt and dry fine sand. It is reasonable to suppose that the death of the beetles on the dry substratum is caused by drought.

That *B. semipunctatum, B. petrosum* and probably *B. schueppeli* died earlier on dry fine sand than on silt may be caused by scratching of the cuticula on the first substratum. Very fine particles fixed to the body when these species moved on the sand. It is well known that fine mineral particles scratch the wax-layer of the cuticula and hence increase the evaporation rate considerably (Wigglesworth 1945, 1947).

B. argenteolum is a burrowing species and as it had lived on its natural substratum before the experiment, the wax-layer may have been scratched. In accordance with this *B. argenteolum* lived about equally long on dry sand and dry silt.

B. argenteolum survives no better on dry, fine sand than does *B. semipunctatum*. When *B. argenteolum* nevertheless occurs on such a substratum whereas most of the other species avoid it, the explanation probably lies partly in differences in their behaviour. *B. argenteolum* is (together with *B. lapponicum* and *B. velox*), contrary to most other *Bembidion* species, an eminent flyer which very quickly may be able to change site according to its immediate requirements. *B. argenteolum* has an additional advantage in its burrowing capacity. When the conditions on the surface of the dry sand are unfavourable (i.e. too cold or too hot and dry), the species may quickly bury itself and hence avoid such circumstances.

Sharova (1960) regards the larvae of the *Bembidion* as non-digging species. Present as well as earlier investigations (Andersen 1966) show that this is not the case. The larvae of species inhabiting quite different habitats dig very well on sand or fine sand with silt mixture. The larvae bury themselves by pushing away the substratum with their mandibles. However, the experiments with the larvae of *B. nitidulum* (Andersen 1966) and *B. argenteolum* (Table III) show that the capacity of digging on clean silt and clay is diminutive. *B. nitidulum* is confined to clayish, *B. argenteolum* to sandy, habitats. A reasonable conclusion therefore is that the *Bembidion* larvae in general are able to burrow, but that the selection of substratum in nature is what determines whether the larvae appear as diggers or not. This conclusion indicates a less obvious relation between morphology and ecology than appears from the classification of Sharova (1960).

Reasonably the imagines of *B. argenteolum, B. velox* and *B. lapponicum* have morphological adaptations for their burrowing habits. A morphological study show no such remarkable specializations as Larsen (1936) has pointed out for *Dyschirius* sp. and *Bledius* sp. However, the members of these two genera burrow only with their mandibles, whereas *Bembidion argenteolum, B. velox,* and *B. lapponicum* also use their legs just as *Cicindela* sp. do (Willis 1967). The extension of the end of the foretibia in *B. velox, B. lapponicum* and especially in *B. argenteolum* is undoubtedly an adaptation to a burrowing habit. A character which the *Chrysobracteon*, the *Omophron,* and the *Cicindela* species have in common is the cover of strong and densely staying thorns towards the end of the tibiae. These thorns no doubt make it more easy for *Cicindela* sp. and *Chrysobracteon* to push away the sand when they dig. These thorns are also important as support during digging after a shallow burrow has been made. *Omophron* sp. makes burrows (Lindroth 1945, 1961–69) but nothing is stated about the digging method. The shape of the body, however, suggests that even this species partly uses the legs. Thus it is likely that the thorns of the tibiae of *Omophron* sp. serve the same function as for *Cicindela* sp. and *Chrysobracteon*.

The independent development of a thorny cover on the very elongate legs of *Cicindela* sp., *Omophron* sp., and *Chrysobracteon* suggests that this character is a morphological adaptation in species that partly burrow with their legs and besides are fast runners.

The substratum of a desert and a river bank have much in common. Therefore it is natural to compare the fauna of the two habitats regarding morphological adaptations. Gebien (1939) states that a prolongation of the legs is one of the possible adaptations among desert *Tenebrionidae*. This is rejected by Koch (1962). It is likely, however, that species with very short legs have a disadvantage compared to species with longer legs. *Bembidion schueppeli* is more helpless than several other *Bembidion* species when moving on dry fine sand. A probable explanation of this is that *B. schueppeli* has shorter legs relative to the rest of the body than many other *Bembidion* species. The small size of *B. schueppeli* may also play a role.

Some of the most common adaptations among the sand-dwelling *Tenebrionidae* are a strong development of the claws and the spurs of the tibia and an extension of the width of the tarsi (Gebien 1939, Koch 1962). These features enlarge the area of contact with the substratum. The psammophilous *B. argenteolum* has quite strong spurs compared with other species of the genus with about equally elongate legs. Furthermore, both *B. argenteolum* and *B. lapponicum* have wider tarsi than species living on silt, for instance *B. lunatun, B. petrosum* and *B. semipunctatum.* The large number of very strong setae on the tarsi of *B. argenteolum, B. lapponicum,* and *B velox* no doubt serve a double function: they enlarge the contact with the substratum, but at the same time they are important for pushing away the sand during burrowing.

Thus, a combination of rather long legs, strong spurs on the tibiae and broad tarsi with additional setae seems to make *B. argenteolum* especially well adapted to move rapidly on dry, fine sand. At the same time the species is a fairly good digger. Strong spurs, extension of the foretibia and additional thorns or setae on the tibia and the tarsi are probable adaptations for this mode of life.

It must be concluded that some *Bembidion* species largely react on the primary properties of the substratum. Other species are more dependent upon the moisture conditions but when the substratum alternatives are dry a certain category is preferred. Still other species are rather unaffected by the substratum but dry, fine sand and expecially dry, dusty silt are mostly avoided.

Acknowledgements. – I wish to thank cand.real Else Sandved and Dr. Tore Schweder for statistical help and advice, and Mrs. Maja Andersen for improving the language.

References

Andersen, J. 1966. *Økologiske undersøkelser av noen stenotope elvebreddbiller av slekten Bembidion* Latr. *(Carabidae).* 137 pp. Thesis, University of Oslo.

Andersen, J. 1970. Habitat choice and life history of Bembidiini (Col., Carabidae) on river banks in Central and Northern Norway. *Norsk ent. Tidsskr.* 17, 17–65.

Bauer, T. 1974. Ethologische, autökologische und ökophysiologische Untersuchungen an *Elaphrus cupreus* Dft. und *Elaphrus riparius* L. (Coleoptera, Carabidae). Zum Lebensformtyp des optisch jagenden Räubers unter den Laufkäfern. *Oecologia 14,* 139–196.

Bauer, T. 1975. Zur biologie und Autökologie von *Notiophilus biguttatus* F. und *Bembidion foraminosum* Strm. (Coleopt., Carabidae) als Bewohner ökologisch extremer Standorte. Zum lebensformtyp des visuell jagenden Räubers unter den Laufkäfern, (II) *Zool. Anz. 194,* 305-318.

Brandmayr, P. & Brandmayr, Z. T. 1977. Parental behaviour and aspects of the biology of *Carterus (Sabienus) calydonius* Rossi and considerations on parental behaviour already reported on Carabids (Coleoptera, Carabidae) *Redia. 55,* 143–174. (In Italian with English summary.)

Edwards, R. L. & Epp, H. T. 1965. The influence of soil moisture and soil type on the oviposition behaviour of the migratory grasshopper, *Melanoplus sanguinipes* (Fabricius). *Can.ent. 97,* 401–409.

Evans, A. C. 1944. Observations on the biology and physiology of wireworms of the genus *Agriotes* Esch. *Ann. appl. biol. 31,* 235–250.

Fraenkel, G. S. & Gunn, D. L. 1961. The orientation of animals. In *Kinesis, Taxes and Compass Reactions.* 376 pp. Dover publications, Inc., New York.

Franz, H. 1929. Morphologische und phylogenetische Studien an *Carabus* L. und den nächstverwanten Gattungen. *Z. wissensch. Zool. 135,* 163–213.

Gebien, H. 1939. Körperbau und Lebensweise der Wüstentenebrioniden. *Int. Kongr. Ent. 7,* (Berlin) 1938. Verhandl. 1, 118–132.

Hassan, S. T. 1975. Effects of high temperature and soil moisture on survival of first–instar larvae of the scarab *Anoplognathus porosus* (Dalman) (Coleoptera). *J. Appl. Ecol. 12,* 749–754.

Kempf. W. 1955. Zur Biologie von *Broscus cephalotes* L. *Zool. Anz. 155,* 30–33.

Koch, C. 1962. Zur Ökologie der Dünen–Tenebrioniden der Namibwüste Südwest–Afrikas und Angolas. *Acta. Univ. Lund N. F. 2, 58,* (5). 25 pp.

Krogerus, R. 1932. Über die Ökologie und Verbreitung der Arthropoden der Triebsangebiete an den Küsten Finnlands. *Acta Zool. fenn. 12,* 1–308.

Larsen, E. B. 1936. Biologische Studien über die tunnelgrabenden Käfer auf Skallingen. *Vidensk. Meddr. dansk naturh. Foren. 100,* 1–231.

Lindroth, C. H. 1945. Die fennoscandischen Carabidae. I. *Göteborgs K. Vetensk. - o. Vitterh. samh. Handl. Ser. B4,* 709 pp.

Lindroth, C. H. 1949. Die fennoscandischen Carabidae. III. *Göteborgs K. Vetensk. - o. Vitterh samh. Handl. Ser. B4,* 911 pp.

Lindroth, C. H. 1961–69. The ground–beetles (Carabidae, excl. Cicindelinae) of Canada and Alaska. 2–6. *Opusc. Ent.* Suppl. *20, 24, 29, 33, 34,* 1–1192.

Lumaret, J.-P. 1972–73. Biologie et écologie d'un Coléoptère Carabique *Aptinus displosor* L. Dufor (Famille des Brachinidae). *Vie Milieu 23,* 95–123.

Maelzer, D. A. 1956. Value of the pF scale for water in an ecological study of an insect living in soil. *Nature, Lond. 178,* 874.

Meats, A. 1967. The relation between soil water tension and growth rate of larvae of *Tipula oleracea* and *T. paludosa* (Diptera) in turf. *Ent. exp. & appl. 10,* 312–320.

Perttunen, V. 1951. The humidity preference of various Carabid species (Col., Carabidae) of wet and dry habitats. *Suom. hyönt. Aikak. 17,* 72–84.

Perttunen, V. 1953. Reactions of diplopods to the relative humidity of the air. Investigations on *Orthomorpha gracilis, Iulus terrestris* and *Schizophyllum sabulosum. Annls. zool. Soc. zool. bot. fenn. 16,* 1–69.

Schwerdtfeger, F 1963. *Ökologie der Tiere, Autökologie.* 461 pp. Paul Parey, Hamburg und Berlin.

Sharova, I. K. 1960. Morpho–ecological types of Carabid larvae (Carabidae). *Zool. Zh. 39,* 691–708. In Russian with English summary.

Wigglesworth, V. B. 1945. Transpiration through the cuticle of insects. *J. exp. Biol. 21,* 97–114.

Wigglesworth, V. B. 1947. The site of action of inert dusts on certain beetles infesting stored products. *Trans. R. ent. Soc. 22,* 65–69.

Willis, H. L. 1967. Bionomics and zoogeography of tiger beetles of saline habitats in the central United States (Coleoptera: Cincindelidae). *Kans. Univ. Sci. Bull. 47,* 145–313.

Received 2 March 1978

Relative abundance and flight periods of Ephemeroptera, Plecoptera, and Trichoptera in a regulated West Norwegian river

TROND ANDERSEN, ARNE FJELLHEIM, ROALD LARSEN & CHRISTIAN OTTO

Andersen, T., Fjellheim, A., Larsen, R. & Otto, C. 1978. Relative abundance and flight periods of Ephemeroptera, Plecoptera, and Trichoptera in a regulated West Norwegian river. *Norw. J. Ent.* Vol. 25, pp. 139–144. Oslo. ISSN 0029-1897.

In a West Norwegian river, where minimum discharge is considerably reduced due to hydroelectric exploitation, the lotic fauna did not show aberrant features. The number of species of Ephemeroptera was 8, of Plecoptera 15, and of Trichoptera 19. The most abundant species of the respective groups were *Baetis rhodani* (Pict.), *Capnia pygmaea* (Zett.), and *Potamophylax cingulatus* (Steph.). Emergence of stoneflies, mayflies, and caddisflies started in April, May, and June, respectively, and from November onwards no imagines were found.

Trond Andersen, Arne Fjellheim, Roald Larsen & Christian Otto, Zoological Museum, N-5014 Bergen-Univ., Norway.

The fauna of rivers subjected to hydroelectric exploitation has been shown to diverge enormously from similar rivers not affected by exploitation (Ulfstrand et al. 1971). One general feature of many regulated rivers is the heavy fluctuations of discharge. Thus, rivers which for periods may be almost dry suddenly transport large water volumes. The purpose of the present study was to investigate the species composition of some common amphibiotic insect orders (Ephemeroptera, Plecoptera, and Trichoptera) in the 'moderately' disturbed river Ekso. The term 'moderately' here means that maximum discharge equalled, while minimum was only about 1/10 of the discharge present before the regulation, which took place in 1971.

Study area

The river Ekso runs into the sea about 100 km NE of Bergen. The river runs in an east-west direction and is about 42 km long. The altitude at the river's easterly part is about 780 m a.s.l. The present study was performed about 4 km downstream at an impounding reservoir with an altitude of 580 m a.s.l. Here at Ekse (60°15'N, 6°15'E) the width of the river is about 40 m, and the discharge usually ranged between 0.5 and 15 m^3/s (Fig. 1). Apart from mosses, no aquatic macrophyte vegetation was present at the study area. The water temperature is given in Fig. 2, and it can be seen that ice covered the river from November to the middle of April. The study area was situated within the sub-alpine birch woodland belt.

Methods

Relative abundance of the different species of Ephemeroptera and Plecoptera is based on data obtained with bottom and drift samples and from emergence traps, collected from December 1975 through November 1976. The bottom samples were taken by a suction device driven by a vacuum pump. Each month 50 samples spaced out over a distance of about 0.5 km were taken. Each sample covered a surface of 283 cm^2. Drift samples (mesh size 250 μ) were taken at fortnightly intervals throughout the year. Presence of eggs was looked for by direct observation in the field. Nine emergence traps (1 ×0.6 m, height 0.6 m) were placed along the banks. They were usually inspected at fortnightly intervals. Flight periods were also checked by direct observations at regular visits to the study area.

Because of the meagre larval material, flight periods and relative abundance of Trichoptera are mainly based on light trap material. A Robinson trap fitted with a mercury vapour bulb (Philips HP 125 W) was placed about 20 m from

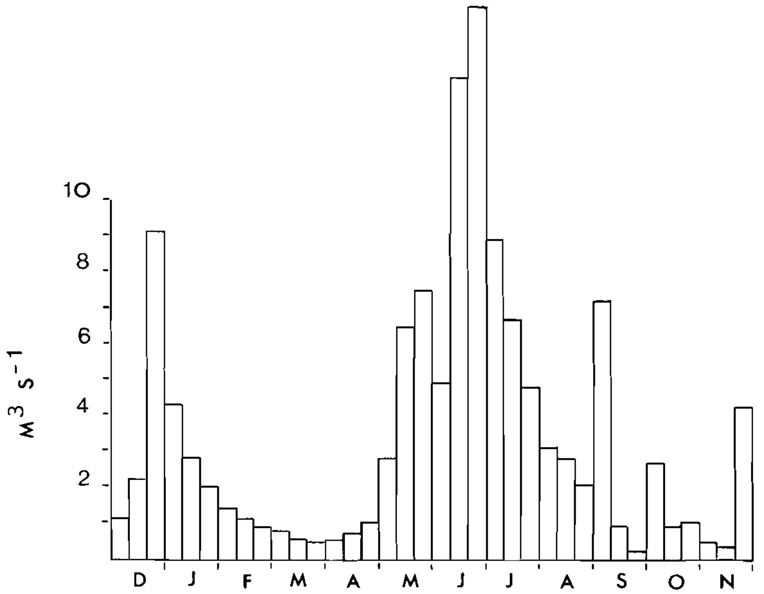


Fig. 1. Average water flow at Ekso in terms of m³/s per 10-day period from December 1975 through November 1976.

the bank. The trap was run from May to the middle of October and emptied every fifth to fifteenth day.

Ephemeroptera

Of the 44 Ephemeroptera species found in Norway (Brekke 1938, Dalby 1973), eight were collected in the present study, Table I. Only *Ameletus inopinatus* Eat., *Siphlonurus aestivalis* Eat., and *Baetis rhodani* (Pict.) have previously been reported from western Norway (Brittain 1974, Larsen 1968). *B. rhodani* was by far the most dominant species making up more than 90% of the total Ephemeroptera material; the density of nymphs usually ranged between 100–2000 individuals m^{-2}. Since *Baetis niger* (L.) is known to inhabit slow flowing rivers rich in macrophyte vegetation (Müller-Libenau 1969), the presence of this species was notable.

All species were found in numbers large enough to draw conclusions as to their flight periods (Table I), and egg and nymphal periods could also be distinguished for most species. The first mayfly to emerge during spring was *B. rhodani*, the last one found as imago was *Baetis lapponicus* (Bengts.).

In Ephemeroptera, winter quiescence has been reported as a common phenomenon (Brittain 1974, Macan 1971). In relation to the quiescence period the growth curves of many stream-living insects often show two different basic patterns. Thus Ulfstrand (1968) distin-

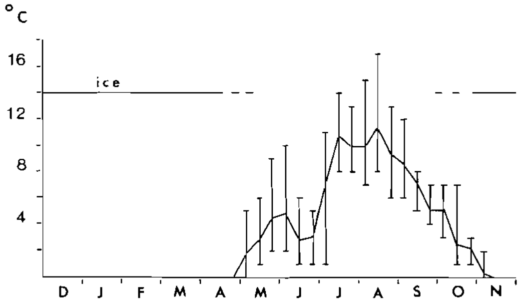
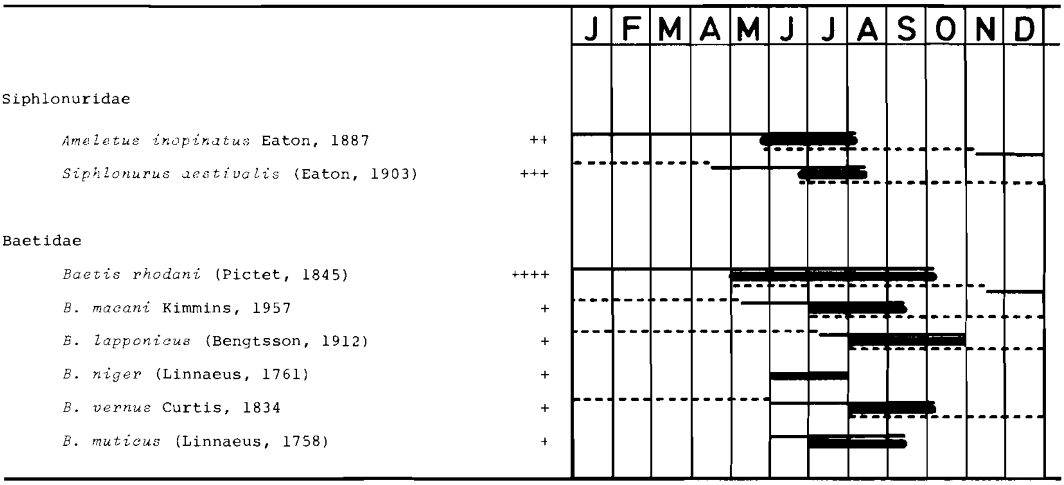


Fig. 2. Maximun, minimum and mean water temperature per 10-day period at Ekso from December 1975 through November 1976. Mean temperature is given as arithmetic mean of maximum and minimum values for each day.

Table I. Relative abundance (+, ++, +++, ++++), flight periods (▬), presence of nymphs (——) and eggs (- - - -) of ephemeropteran species at the study area in the Ekso river.



Siphlonuridae	
Ameletus inopinatus Eaton, 1887	++
Siphlonurus aestivalis (Eaton, 1903)	+++
Baetidae	
Baetis rhodani (Pictet, 1845)	++++
B. macani Kimmins, 1957	+
B. lapponicus (Bengtsson, 1912)	+
B. niger (Linnaeus, 1761)	+
B. vernus Curtis, 1834	+
B. muticus (Linnaeus, 1758)	+

guished between (I) considerable growth commencing shortly after oviposition leading to the presence of more or less large sized nymphs during a long period, and (II) intense growth concentrated to a period preceding emergence.

A winter quiescence was observed also among the mayflies in Ekso. Both *A. inopinatus* and *B. rhodani* were representatives of category no. I of Ulfstrand, while *S. aestivalis, Baetis macani* Kim., *B. lapponicus,* and *B. vernus* Curt. all belonged to category no. II. *Baetis muticus* (L.) seemed to fit category no. II, but low numbers made conclusions dubious.

Plecoptera

Of the 35 Plecoptera species found in Norway (Lillehammer 1974), 15 were collected in this study (Table II). In addition, Steinar Haaland (unpubl.) has collected *Siphonoperla burmeisteri* (Pictet, 1841) about 25 km further downstream. According to Lillehammer (1974), all the species except *Leuctra fusca* (L.) belong to the category 'present in all parts of Norway'. Only two other Plecoptera species, *Isoperla obscura* (Zetterstedt, 1840) and *Dinocras cephalotes* (Curtis, 1827), have been taken in south west Norway (Lillehammer 1974). *Capnia pygmaea* (Zett.) was the most common stonefly species, the nymphal density usually ranging between 100–2500 individuals m^{-2}.

Most species obtained in numbers large enough to draw conclusions as to their flight periods were found as imagines during June and July, Table II. Two species, viz. *Taeniopteryx nebulosa* (L.) and *C. pygmaea,* emerged in April, while *Amphinemura standfussi* (Ris) and *L. fusca* were the only species present as imagines from the middle of September onwards.

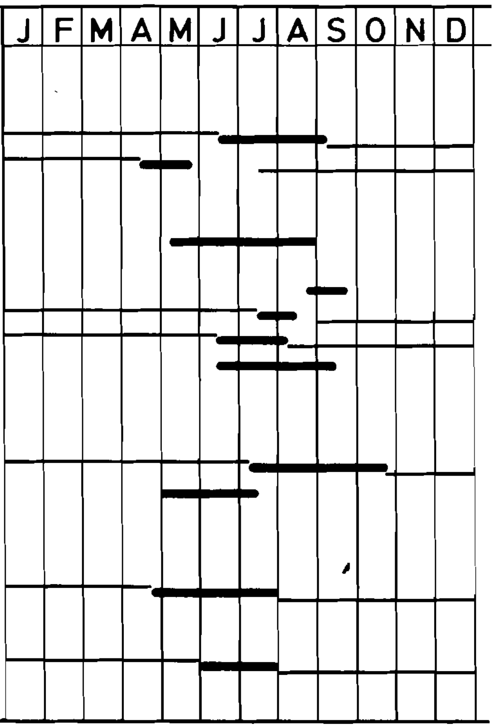
Among Plecoptera, winter quiescence, as also observed at Ekso (unpubl.), has been reported in many species (Brinck 1949, Svensson 1966, Ulfstrand 1968). In the present study growth pattern no. I (see Ephemeroptera) was represented by *T. nebulosa* and *Diura nanseni* Kemp., while *Amphinemura standfussi, A. sulcicollis* (Steph.), *Leuctra fusca* and *L. hippopus* (Kemp.) all belonged to category no. II. The growth pattern of the remaining species was either not easily classified or the nymphal material was insufficient for conclusions.

Trichoptera

The information concerning relative abundance and flight periods of Trichoptera, Table III, was primarily based on the light-trap material. A total of 1890 specimens belonging to 25 species were caught in this trap. The Limnephilidae was the dominating family, comprising 77.8 % of the material. Four other families with altogether five

Table II. Relative abundance, flight periods and presence of nymphs of plecopteran species at the study area in the Ekso river. Legends as in Table I.

Taeniopterygidae	
Brachyptera risi (Morton, 1896)	++
Taeniopteryx nebulosa (Linnaeus, 1758)	+
Nemouridae	
Protonemura meyeri (Pictet, 1841)	+
Amphinemura borealis (Morton, 1894)	+
A. standfussi (Ris, 1902)	+
A. sulcicollis (Stephens, 1836)	++
Nemoura cinerea (Retzius, 1783)	+++
Nemurella picteti Klapálek, 1900	++
Leuctridae	
Leuctra digitata Kempny, 1899	+
L. fusca (Linnaeus, 1758)	++
L. hippopus Kempny, 1899	+++
L. nigra (Oliver, 1811)	+
Capnidae	
Capnia pygmaea (Zetterstedt, 1840)	++++
Perlodidae	
Diura nanseni (Kempny, 1900)	+
Isoperla grammatica (Poda, 1761)	+



species were represented. The three dominant species were *Potamophylax cingulatus* (Steph.) (30.7 %), *Rhyacophila nubila* (Zett.) (11.4 %), and *Rhadicoleptus alpestris* (Kol.) (11.2 %). Additional material from the emergence traps yielded 105 specimens belonging to eight species. Limnephilidae comprised 85.7 % of this material, the three dominating species being *P. cingulatus* (42.9 %), *Halesus radiatus* (Curt.) (19.0 %), and *Limnephilus extricatus* McL. (11.4%). The larval density of *P. cingulatus* usually ranged between 0–5 individuals m^{-2}.

Many caddis flies, especially among the limnephilids, are good flyers. This can make it difficult to decide if a species collected as imago near a special biotope really originates there. In the light-trap material from Ekso, six species, *Limnephilus borealis* (Zetterstedt, 1840), *L. elegans* Curtis, 1834, *L. pantodapus* McLachlan, 1875, *L. rhombicus* (Linnaeus, 1758), *L. stigma* Curtis, 1834, and *Agrypnia obsoleta* (Hagen, 1864) all have larvae which are known to prefer lentic waters, and they are therefore excluded from the table. Of the 172 Trichoptera species so far recorded in Norway (Andersen 1975, Svensson & Tjeder 1975), only 19 species can thus be supposed to inhabit Ekso.

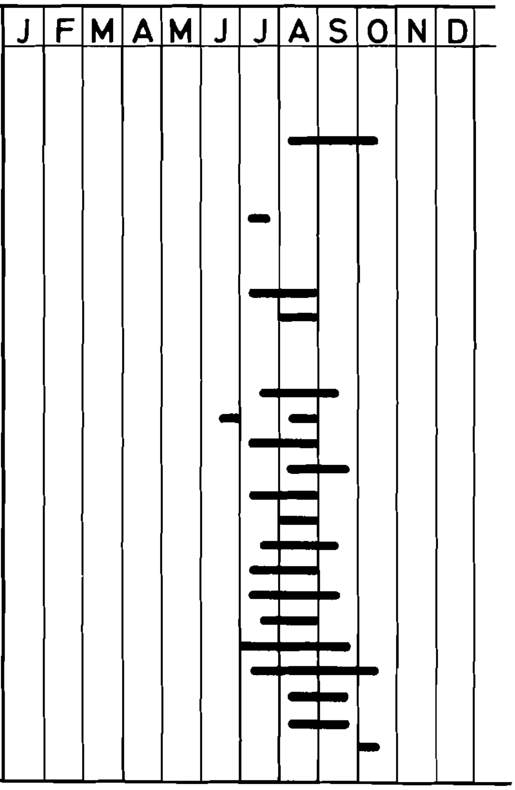
Except for *Limnephilus sericeus* (Say), *Potamophylax nigricornis* (Pict.), and *Haleus digitatus* (Schrk.), all the species listed are common and widespread in western Norway. In Hordaland *H. digitatus* can be found near small brooks especially in the inner part of the province. *L. sericeus* and *P. nigricornis* seem to be rather common in the lower mountain regions in the inner parts of Hordaland, the record of *L. sericeus* being so far the westernmost.

At Ekso, Trichoptera began to fly regularly in the second half of July; one female of *Apatania zonella* (Zett.) was already caught in the last part of June. The light-trap catches were greatest during August, and some species were still flying until the beginning of October. The late and relatively short flight period of *R. nubila* should be noted.

In the Bergen region, this species is one of the

Table III. Relative abundance and flight periods of trichopteran species at the study area in the Ekso river. Legends as in Table I. Species marked with asterix were taken in the emergence traps.

Rhyacophilidae	
★ *Rhyacophila nubila* (Zetterstedt, 1840)	+++
Philopotamidae	
Philopotamus montanus (Donovan, 1813)	+
Polycentropodidae	
★ *Plectrocnemia conspersa* (Curtis, 1834)	+++
★ *Polycentropus flavomaculatus* (Pictet,1834)	++
Limnephilidae	
Apatania stigmatella (Zetterstedt, 1840)	++
A. zonella (Zetterstedt, 1840)	+
★ *Limnephilus centralis* (Curtis, 1834)	++
L. coenosus (Curtis, 1834)	++
★ *L. extricatus* McLachlan, 1865	+++
L. sericeus (Say, 1824)	++
L. sparsus Curtis, 1834	+
Rhadicoleptus alpestris (Kolenati, 1848)	+++
★ *Potamophylax cingulatus* (Stephens, 1837)	++++
P. nigricornis (Pictet, 1834)	++
Micropterna lateralis (Stephens, 1837)	++
M. sequax McLachlan, 1875	+++
★ *Halesus digitatus* (Schrank, 1781)	++
★ *H. radiatus* (Curtis, 1834)	+++
Chaetopteryx villosa (Fabricius, 1798)	+



earliest encountered, starting to fly in the middle of May and continuing until November. The species were found in the emergence traps during the same period as they were caught in the light trap; only *L. extricatus* appeared a few days earlier in the emergence traps than in the light trap.

The sex ratio in the light-trap catches was rather uneven, the females constituting only 13.1% of the total material. Of *R. alpestris* 211 males but no females were caught. More surprising is that the sex ratio also in the emergence traps was rather uneven. The proportion of females here was 27.6%. *P. cingulatus* showed 24.4% females (n = 45), *H. radiatus* 25% (n = 20), and *L. extricatus* 33.3% females (n = 12). Uneven sex ratio of Limnephilidae species at emergence has previously been reported by Tobias (1967) and by Tobias & Tobias (1971).

Conclusion

Judging from experience and previous surveys, the number of Ephemeroptera species was higher than expected, in Plecoptera the number agreed, and in Trichoptera the number was below the number expected. Thus, our general conclusion is that the moderate disturbance of this river in terms of reduced minimum discharge does not adversely affect the number of species. It should be pointed out that not even in periods of minimum discharge did real lentic conditions evolve at the study area. A small discharge (0.1–0.2 m^3/s) apparently was enough to sustain a considerable number of specimens of the lotic fauna. However, only a couple of years have passed since the regulation took place, and long-term effects can possibly occur in the future.

Acknowledgement. – Financial support was received from the Norwegian Water Resources and Electricity Board.

References

Andersen, T. 1975. Caddis flies (Trichoptera) from Vestfold, south-eastern Norway. *Norw. J. Ent. 22,* 155–162.

Brekke, R. 1938. The Norwegian mayflies (Ephemeroptera). *Norsk ent. Tidsskr. 5,* 55–73.

Brinck, P. 1949. Studies on Swedish stoneflies (Plecoptera). *Opusc. Ent. Suppl. 11,* 250 pp.

Brittain, J. E. 1974. Studies on the lentic Ephemeroptera and Plecoptera of southern Norway. *Norsk ent. Tidsskr. 21,* 135–154.

Dahlby, R. 1973. A check-list and synonyms of Norwegian species of Ephemeroptera. *Norsk ent. Tidsskr. 20,* 249–252.

Larsen, R. 1968. The life cycle of Ephemeroptera in the lower part of Aurland river in Sogn and Fjordane, western Norway. *Norsk ent. Tidsskr. 15,* 49–59.

Lillehammer, A. 1974. Norwegian stoneflies. II. Distribution and relationship to the environment. *Norsk ent. Tidsskr. 21,* 195–250.

Macan, T. T. 1961. A key to the nymphs of British species of Ephemeroptera. *Freshwater Biol. Assoc. Scient. Publ. 20,* 68 pp.

Müller-Liebenau, I. 1969. Revision der europäischen Arten der Gattung *Baetis* Leach, 1815 (Insecta, Ephemeroptera). *Gewässer und Abwässer 48/49,* 214 pp.

Svensson, B. W. & Tjeder, B. 1975. Check-list of the Trichoptera of north-western Europe. *Ent. scand. 6,* 261–274.

Svensson, P. O. 1966. Growth of nymphs of stream living stoneflies in northern Sweden. *Oikos 17,* 197–206.

Tobias, W. 1967. Zur schlüpfrhytmik von Köcherfliegen (Trichoptera). *Oikos 18,* 55–75.

Tobias, W. & Tobias, D. 1971. Köcherfliegen und Steinfliegen einiger Gewässer in Sør Varanger (Nord-Norwegen) (Trichoptera, Plecoptera). *Senckenbergiana biol. 52,* 227–245.

Ulfstrand, S. 1968. Life cycles of benthic insects in Lapland streams (Ephemeroptera, Plecoptera, Trichoptera, Diptera Simuliidae). *Oikos 19,* 167–190.

Ulfstrand, S., Svensson, B., Enckell, P. H., Hagerman, L. & Otto, C. 1971. Benthic insect communities of streams in Stora Sjöfallet National Park, Swedish Lapland. *Ent. scand. 2,* 309–336.

Received 22 December 1977

Swarming and habitat segregation in the family Leptoceridae (Trichoptera)

JOHN O. SOLEM

Solem, J. O. 1978. Swarming and habitat segregation in the family Leptoceridae (Trichoptera). *Norw. J. Ent.* Vol. 25, pp. 145–148. Oslo. ISSN 0029-1897.

The study was carried out in Central Norway (Trøndelag area) at standing water localities. *Athripsodes aterrimus* (Stephens), *A. cinereus* (Curtis), *Ceraclea nigronervosa* (Retzius), and *C. fulva* (Rambur) performed a zig-zag pattern when swarming, with species-specific amplitudes. Swarming was restricted to the height of up to 10–15 cm above the water surface. *Mystacides azureus* (Linnaeus) formed clouds and each individual had up and down movements with amplitudes of 20–25 cm. The height of the clouds above the water surface varied according to the height of the vegetation boardering the lake. When systematically closely related species appeared together, they were not only separated by behaviour but also by different swarming sites. Swarming patterns of leptocerids are compared with their classification.

John O. Solem, University of Trondheim, Royal Norwegian Society of Sciences and Letters, the Museum, Erling Skakkesgt. 47B, N-7000 Trondheim, Norway.

Among aquatic insects the caddisflies have the unique feature of building cases which the larvae bring along when moving around. The case-building behaviour has fascinated naturalists and a lot of information on behaviour has been compiled (e.g. Wesenberg-Lund 1943, Malicky 1973). Knowledge of adult behaviour is, however, scanty, but Wesenberg-Lund (1943) reported that adult Trichoptera congregated and established swarms. He also mentioned that males of leptocerids had a dancing performance much like that of ephemerids. Reports on swarming places were made by Mori & Matutani (1953), Morgan (1956), Gruhl (1960), Schumacher (1969), Benz (1975), and Statzner (1978). Gruhl (1960) also gave information about the swarming pattern of *Hydropsyche saxonica* McLachlan, and Solem (1976) reported on emergence, swarming, and copulation behaviour of *Agrypnia obsoleta* (Hagen) and *Phryganea bipunctata* Retzius. Slight differences in the behaviour of *A. obsoleta* and *P. bipunctata* were revealed.

Cummins (1964), Grant & Mackay (1969), Mackay (1972), and Resh (1976) have shown that food, substrate, life histories, and seasonal occurrence may be involved in the ecological segregation of coexisting congeneric species of Trichoptera. Mori & Matutani (1953) and Statzner (1978) reported that species had different swarming sites, but what about behaviour of e.g. congeneric species? Many leptocerids like the species reported on here are dayfliers, and should therefore be an easy subject for observation and collection of data on behaviour. Systematically closely related species treated in this paper had a considerable overlap in the flight periods and they were frequently found together. The objectives of the study were to look at swarming sites and adult behaviour. In addition, adult behaviour of semiaquatic insects may influence larval distribution (Macan 1973), and a better knowledge of the adult behaviour among Trichoptera will undoubtedly also give better evidence and understanding of larval distribution patterns (c.f. Solem 1973, Statzner 1978).

Methods and area

The data were obtained by direct observations with and without use of binoculars. Swarming patterns were studied at several lakes in the district of Trøndelag, Norway. The swarming patterns of an individual were followed when few individuals were present at the swarming place. But all stages of a swarm, from the congregation of a few individuals and up to tremendous numbers in a swarm, were observed. The observations refer to calm weather, as windy conditions could alter swarming patterns. Depending on suitable conditions, swarming occurred at various hours during daytime.

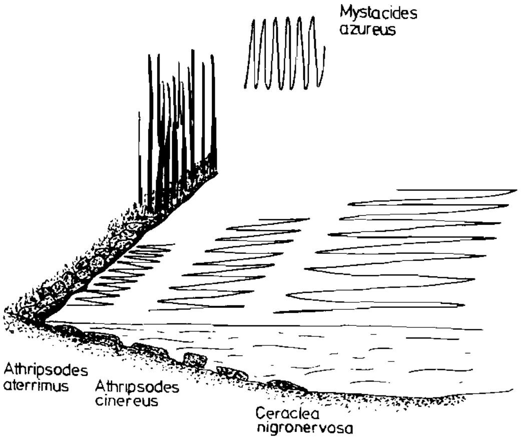


Fig. 1. The zig-zag swarming patterns and the swarming sites of various leptocerids.

Results

Athripsodes aterrimus (Stephens)

A. aterrimus swarmed above the water very close to the shore. Swarming was confined within a distance of 0.5–1.0 m from the water line (Fig. 1). When there was a high density of swarming individuals they made a band along the shore as described by Morgan (1956). Each individual flew about 2–4 cm above the water surface, and performed horizontally a zig-zag pattern. The amplitude in this pattern was about 0.3–0.5 m. Each individual zig-zagged a distance of 1–2 m, turned and zig-zagged back again. The size of the swarming area varied greatly according to the number of the individuals participating. When only a few individuals were seen, they covered only a length of 1–2 m, but when mass swarming occurred, they made a band along the shore. I have not been able to detect whether or not high densities altered the swarming patterns.

Athripsodes cinereus (Curtis)

The swarming pattern of *A. cinereus* was very much like that of *A. aterrimus;* however, each individual covered a larger area than *A. aterrimus*. The amplitude of the zig-zag pattern was about 1–1.5 m, and the length of the distance about 4–5 m. The height above the water surface was 5–10 cm, and swarming was exhibited further out from the shore than that of *A. aterrimus*.

Ceraclea fulva (Rambur) and *C. nigronervosa* (Retzius)

These species are treated together, as so far I have not been able to distinguish any specific pattern of swarming. This may be because I have not observed them swarming together.

Basically *C. fulva* and *C. nigronervosa* had the same pattern as *A. aterrimus*, the noticeable difference being that *Ceraclea* had a much more enlarged pattern. The amplitude of the zig-zag patterns I estimated to 3–5 m, and the length of the distance they covered to 10–15 m. The height above the water surface was about 10–15 cm. Swarming occurred further out from the shore than that of *A. cinereus*. In one pond where *C. fulva* and *C. nigronervosa* occurred, *C. fulva* was seen swarming along one shore and *C. nigronervosa* along the opposite one.

Mystacides azureus (Linnaeus)

When *M. azureus* swarmed, the specimens formed a cloud. Each individual performed a dancing pattern, resembling that of mayflies. During a forward movement the individuals flew up and down. The zig-zag patterns of *Athripsodes* and *Ceraclea* were in the horizontal level, while that of *M. azureus* was in the vertical level. The amplitude of the up- and down movements was about 20–25 cm. Gruhl (1960) indicated the up- and down movements to 10–15 cm. The distance of the forward movements was one to two metres. The height above the water surface of the swarms varied according to the height of the vegetation. At one locality where *Carex rostrata* boarded the shore, *M. azureus* congregated and swarmed at the top level of *C. rostrata*, about 0.5–0.6 m above the water surface. At another site where *Phragmites communis* boarded the shore and emerged 3–4 m above the water surface, *M. azureus* gathered at the top of *P. communis*. Statzner (1978) reported that *M. azureus* avoided flying closer than 40 cm to any object. The swarm of *M. azureus* consisted almost, if not entirely, of males. Wesenberg-Lund (1943) remarked the same about *M. nigra*. This is the only species I have managed to sample swarming individuals in a sufficient number to make a statement about the sex ratio in swarms.

Discussion

The species exhibited during swarming a definite flight pattern that was repeated over and over again, and thus followed the definition on swarming given by Dahl (1965), who defined swarming of Trichoceridae (Diptera) as a distinct flight pattern performed by the male individual and repeated over and over again until controlling microclimatic factors or physiological exhaustion forces the individual to a resting place. When new individuals approached and participated in the swarming of *M. azureus*, a very dense spot was seen within the swarm. This was particularly obvious when females appeared, and they immediately attracted many males. Shortly afterwards pairs were seen leaving the swarm and heading for the vegetation where mating was completed. In periods when swarming was very intense, single individuals were frequently seen approaching and leaving the swarm.

A comparison of the swarming behaviour of the congeneric species *A. aterrimus* and *A. cinereus* reveals specific species patterns. The flight period of these two species overlap considerably in time in the areas where the study was made, and they also occur frequently together at the same localities. However, the adults of *A.aterrimus* and *A. cinereus* are clearly separated both by swarming behaviour patterns and by swarming places.

Congeneric species had greater similarities in their swarming patterns than when swarming of species of different genera were compared. This was demonstrated for *Athripsodes* and *Ceraclea,* but may be true also for *Mystacides,* as swarming places and general appearance of swarms of *M. longicornis* and *M. nigra* (Gruhl 1960, Statzner 1978) seem to be very much the same as that of *M. azureus.*

The swarming places of *Athripsodes* and *Ceraclea* were found to be restricted to only a few centimetres above the water surface, while the height above the water level for the swarms of *M. azureus* varied according to the height of the vegetation boarding the lake.

Basically, *A. aterrimus, A. cinereus, C. nigronervosa,* and *C. fulva* have very much the same swarming behaviour. The most obvious differences were that the amplitudes of the zig-zag pattern of *A. cinereus* were larger than that of *A. aterrimus,* and that of *Ceraclea* much more enlarged than that of *A. cinereus.*

The swarming patterns of *Athripsodes* and *Ceraclea* differ significantly from the swarming patterns of *Mystacides* species. Although the exact swarming patterns of *Oecetis lacustris* (Pictet) and *O. testacea* (Curtis) are not known, they have up and down movements, and their swarming places are very similar to that of *Mystacides.* The swarming of leptocerids, as far as it is known today, falls into two groups. The first group is exemplified by *Athripsodes* and *Ceraclea,* which swarm close to the water and perform a horizontal zig-zag pattern. The second group is exemplified by *Mystacides* and *Oecetis,* which congregate and swarm high above the water in a zig-zag pattern with amplitudes in vertical line.

Regarding the classification of leptocerids (Wiggins 1977), *Athripsodes* and *Ceraclea* are considered to have evolved earlier than *Mystacides* and *Oecetis.* A reliable selective pressure on the swarming features of *Mystacides* and *Oecetis* could then be that swarming places near the water and near the shore were already occupied by established species of *Athripsodes* and *Ceraclea* or their ancestors. To go further out from the shore than e.g. *C. nigronervosa* and *C. fulva* do, would probably be a disadvantage, and therefore *Mystacides* and *Oecetis,* or their ancestors, were forced to use the space above *Athripsodes* and *Ceraclea,* and to evolve a swarming pattern suitable for these sites. In a few observations where *M. azureus* was the only swarming species, the individuals made some kind of horizontal zig-zagging close to the water before a swarm was really established.

The swarming behaviour of the phryganeids *A. obsoleta* and *P. bipunctata* (Solem 1976) and the leptocerids dealt with, are distinctly different. However, observations of *Rhadicoleptus alpestris* (Kolenati) (Limnephilidae) (Solem unpubl.) and hydropsychids (Gruhl 1960, Schumacher 1969, Benz 1975, Statzner 1978) show that they make swarming clouds high above the ground and have up and down movements like *Mystacides* and *Oecetis.*

A strong connection between swarming and mating of *A. obsoleta* and *P. bipunctata* was questioned by Solem (1976). For the leptocerids, Gruhl (1960) and the present study agree that there is a high frequency of mating when there is a high swarming activity. Gruhl (1960) emphasized that females of *Mystacides* and *Leptocerus* (a name that earlier included *Athripsodes* and *Ceraclea)* searched for swarming males. The differences in the swarming patterns between leptocerids and phryganeids may account for a stronger connection between swarming and mating among leptocerids than among phryganeids. However, it must be mentioned that we lack a great deal of information about what leptocerid adults do at 'resting' places.

References

Benz, G. 1975. Über die Tranzschwärme der Köcherfliege *Hydropsyche pellucidula* Curtis (Trichoptera: Hydropsychidae). *Mitt. schweiz. entomol. Ges. 48*, 147–157.

Cummins, K. W. 1964. Factors limiting the micro-distribution of larvae of the caddisflies *Pycnopsyche lepida* (Hagen) and *Pycnopsyche guttifer* (Walker) in a Michigan stream. *Ecol. Monogr. 34*, 271–295.

Dahl, C. 1965. Studies on swarming activity in Trichoceridae (Diptera) in southern Sweden. *Opusc. entomol. Suppl. 27*, 1–68.

Grant, P. R. & Mackay, R. J. 1969. Ecological segregation of systematically related stream insects. *Can. J. Zool. 47*, 691–694.

Gruhl, K. 1960. Die Tanzgesellschaft der *Hydropsyche saxonica* McLach. (Trichoptera). *Mitt. dtsch. entomol. Ges. 19*, 76–83.

Macan, T. T. 1973. *Ponds and Lakes.* 148 pp. Allen & Unwin Ltd., London.

Mackay, R. J. 1972. Temporal patterns of life history and flight behaviour of *Pycnopsyche gentilis, P. luculenta,* and *P. scabripennis* (Trichoptera: Limnephilidae). *Can. Entomol. 104*, 1819–1835.

Malicky, H. 1973. Trichoptera (Köcherfliegen). *Handb. Zool. 4* (2), 1–114.

Morgan, N. C. 1956. The biology of *Leptocerus aterrimus* Steph. with reference to its availability as a food for trout. *J. Anim. Ecol. 25*, 349–365.

Mori, S. & Matutani, K. 1953. Daily swarming of some caddisfly adults and their habitat segregations. *Zool. Mag. Tokyo 62*, 191–198.

Resh, V. H. 1976. Life histories of coexisting species of *Ceraclea* caddisflies (Trichoptera: Leptoceridae): The operation of independent functional units in a stream ecosystem. *Can. Entomol. 108*, 1303–1318.

Schumacher, H. 1969. Das Schwärmverhalten von *Hydropsyche borealis* Martynov (Insecta, Trichoptera). *Zool. Anz. Suppl. 33*, 555–558.

Solem, J. O. 1973. The bottom fauna of lake Lille-Jonsvann, Tröndelag, Norway. *Norw. J. Zool. 21* (3), 227–261.

Solem, J. O. 1976. Studies on the behaviour of adults of *Phryganea bipunctata* and *Agrypnia obsoleta* (Trichoptera). *Norw. J. Ent. 23*, 23–28.

Statzner, B. 1978. The effect of flight behaviour on the larval abundance of Trichoptera in the Schierenseebrooks (North Germany). *Proc. 2nd Int. Symp. Trichoptera* (in press).

Wesenberg-Lund. C. 1943, *Biologie der Süsswasserinsekten.* Gyldendalske Boghandel. 682 pp.

Wiggins, G. B. 1977. *Larvae of the North American caddisfly genera (Trichoptera).* University of Toronto Press, Toronto and Buffalo. 401 pp.

Received 2 March 1978

Influence of temperature on the sex ratio of Trichoptera in light-trap catches in western Norway

TROND ANDERSEN

Andersen, T. 1978. Influence of temperature on the sex ratio of Trichoptera in light-trap catches in western Norway. *Norw. J. Ent.* Vol. 25 pp. 149–151. Oslo. ISSN 0029-1897.

During August 1972 Trichoptera was collected in a light trap on Osterøy in western Norway. In total, 2263 specimens belonging to 39 species were trapped. During the coldest nights only males were caught, while the proportion of females increased to about fifty percent during the warmest nights. The Sperman rank-correlation coefficient was used to estimate the relation between the percentage of females and the night temperature. Significant positive correlation ($p < 0.001$) was found between the night temperature and the percentage of females in the total catches; the same applied to the three dominant species.

Trond Andersen, Zoological Museum, University of Bergen, N-5014 Bergen-Univ., Norway.

The uneven sex ratio of Trichoptera in light-trap catches has been commented on by many workers (Corbet, Schmid & Augustin 1966, Crichton 1960, Marshall 1939, Solem 1977, Ulfstrand 1970). Though an excess of males has been reported from emerging adults of some Trichoptera species (Morgan 1956, Svensson 1974, Tobias 1967, Tobias & Tobias 1971), the uneven sex ratio in light-trap catches probably reflects differences in behaviour and hence in trapability. Göthberg (1973) and Svensson (1972) showed that the location of the trap in relation to the breeding locality is of great importance, the males ranging more widely than the females.

During August 1972 Trichoptera was collected in a light trap at a slow flowing river on Osterøy in western Norway. The aim was to study the effect of the weather conditions on the catches. The present paper examines the influence of the night temperature on the sex ratio.

Study area, method, and material

The data were collected at the River Fitjo (UTM:32VLN098155) on Osterøy in Hordaland, western Norway. The river is about four metres wide and half a metre deep, the bottom is covered with fine sand and some larger stones. Large areas are covered with *Equisetum fluviatile* L., *Sparganium angustifolium* Michx., *Potamogeton natans* L. and *Nuphar luteum* (L.).

The light trap used was a Robinson trap fitted with a mercury vapour bulb (Philips HPL 125W). The trap was placed in an open position on the bank. The trap was operated from 2 August to 1 September 1972. During this period the actual temperature and the minimum temperature were read regularly at 0900 hrs. and 2100 hrs. every day, Table I.

In total, 2263 specimens belonging to 39 species were collected. The three most dominant species were *Limnephilus flavicornis* (Fabricius, 1787), *Polycentropus flavomaculatus* (Pictet, 1834), and *Oxyethira flavicornis* (Pictet, 1834), accounting for 27.3%, 13.1%, and 11.4%, respectively.

Results

The quantity of the light-trap catches was found to be greatly influenced by the temperature during the night. Only single specimens were caught when the minimum temperature fell below +3°C. The correlation between the catches and the minimum temperatures of nights with a minimum above +3°C is shown in Fig. 1 ($r = 0.741$, $n = 19$, $p < 0.001$). The number of specimens is expressed as $\log_{10}(n + 1)$ (Williams 1937). The catches were doubled by a rise of 2.7°C in the minimum temperature ($Q_{10} = 12.92$).

In the total catch the proportion of females was 42.2%. Of *L. flavicornis* (F.), *P. flavomaculatus* (Pict.), and *O. flavicornis* (Pict.), the proportion of females was 43.6%, 25.6%, and 60.9%, respectively. The percentage of females caught during a night seemed to rise with the night temperature (Fig. 2.) The night temperature is expressed as the average between the

Table I. Temperatures, total catch and catch of Limnephilus flavicornis (F.), Polycentropus flavomaculatus (Pict.) and Oxyethira flavicornis (Pict.) at Fitjo during August 1972.

	Temperature 21^{00} hrs.	Minimum temperature	Night temperature	Total catch			Limnephilus flavicornis (F.)		Polycentropus flavomaculatus (Pict.)		Oxyethira flavicornis (Pict.)	
Date	°C	°C	°C	n	$\log_{10}(n+1)$	% ♀	n	% ♀	n	% ♀	n	% ♀
2- 3	14.7	8.0	11.35	113	2.056	43.4	33	57.6	18	44.4	2	0.0
3- 4	9.4	1.0	5.20	0	0.000	-	0	-	0	-	0	-
4- 5	10.2	7.4	9.05	15	1.204	13.3	4	0.0	0	-	0	-
5- 6	9.6	-0.4	4.60	0	0.000	-	0	-	0	-	0	-
6- 7	15.2	13.6	14.40	301	2.480	42.9	77	55.8	38	20.8	11	63.6
7- 8	15.4	9.2	12.30	164	2.217	61.0	30	53.3	30	56.7	38	94.7
8- 9	18.4	12.6	15.50	400	2.603	55.8	109	65.1	97	32.0	31	83.9
9-10	13.4	9.4	11.40	265	2.424	45.3	43	30.2	8	50.0	31	61.3
10-11	10.6	8.6	9.60	45	1.662	22.2	12	25.0	0	-	7	28.6
11-12	9.6	6.4	8.00	54	1.740	5.6	4	0.0	0	-	31	3.3
12-13	8.3	0.3	4.30	0	0.000	-	0	-	0	-	0	-
13-14	8.3	1.6	4.95	1	0.301	0.0	0	-	0	-	0	-
14-15	9.8	2.4	6.10	2	0.477	0.0	0	-	0	-	0	-
15-16	11.6	4.4	8.00	59	1.778	42.4	13	53.8	5	0.0	23	43.5
16-17	12.0	8.4	10.20	153	2.187	44.4	49	44.9	10	0.0	13	76.9
17-18	9.2	3.4	6.30	15	1.204	6.7	3	0.0	0	-	9	0.0
18-19	6.1	-1.4	2.35	0	0.000	-	0	-	0	-	0	-
19-20	10.6	8.0	9.30	96	1.986	28.1	33	27.3	11	18.2	15	53.3
20-21	9.7	1.5	5.60	0	0.000	-	0	-	0	-	0	-
21-22	7.7	-1.2	3.25	0	0.000	-	0	-	0	-	0	-
22-23	8.1	7.6	7.85	76	1.886	17.1	30	10.0	1	0.0	3	33.3
23-24	9.8	7.8	8.80	59	1.778	16.9	31	12.9	1	0.0	0	-
24-25	10.2	7.4	8.80	38	1.591	36.8	19	42.1	0	-	0	-
25-26	7.8	-0.6	3.60	2	0.477	0.0	0	-	0	-	0	-
26-27	5.6	1.0	3.30	0	0.000	-	0	-	0	-	0	-
27-28	7.2	3.4	5.30	50	1.707	8.0	24	0.0	0	-	3	0.0
28-29	6.6	1.2	3.90	1	0.301	0.0	0	-	0	-	1	0.0
29-30	13.0	8.5	10.75	198	2.298	53.0	60	53.3	46	8.7	36	91.7
30-31	12.0	7.0	9.50	73	1.869	30.1	21	33.3	26	0.0	4	100.0
31- 1	11.2	9.8	10.50	83	1.924	36.1	22	54.5	6	0.0	0	-

temperature at 2100 hrs. and the minimum temperature. The percentage of females cannot be assumed to be normally distributed; the Sperman rank-correlation coefficient is therefore used to estimate the relation between the percentage of females and the night temperature.

The Sperman rank-correlation coefficient showed significant correlation between the night temperature and the percentage of females in the total catches ($r_s = 0.895$, $n = 23$, $p < 0.001$). The same applied to each of the three dominant species: *L. flavicornis* (F.) ($r_s = 0.762$, $n = 19$, $p < 0.001$), *P. flavomaculatus* (Pict.) ($r_s = 0.786$, $n = 13$, $p < 0.01$) and *O. flavicornis* (Pict.) ($r_s = 0.654$, $n = 16$, $p < 0.01$).

Discussion

As a rule there is an excess of males in light-trap catches of Trichoptera (Svensson 1972), The proportion of males of the Limnephilidae species

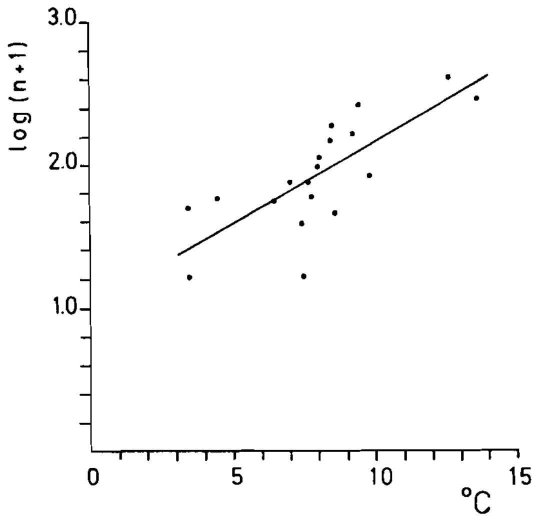


Fig. 1. Correlation between total catch, $\log_{10}(n+1)$, and minimum temperature for nights with a minimum above +3°C at Fitjo from 2 August to 1 September 1972.

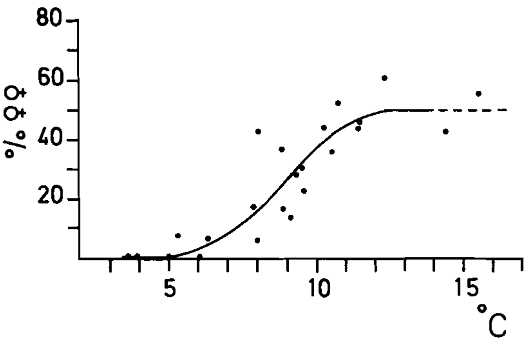


Fig. 2. Relationship between the percentage of females in the total catches and the night temperature at Fitjo from 2 August to 1 September 1972.

often reaches 70 percent. However in some species, such as the *Hydropsyche* spp., *Lepidostoma hirtum* (Fabricius, 1775) and many Hydroptilidae species, females are usually caught in excess (Crichton 1960, Ulfstrand 1970).These factors reflect differences in trapability between the two sexes due to variations in behaviour between different species or groups of species.

Independently of this, there seems to be a difference between the two sexes in their reaction to the night temperature, common to a number of Trichoptera species. At Fitjo only males were caught during nights with a temperature below 5°C, and during nights with a temperature below 7.5°C the proportion of females did not exceed ten percent of the catches. When the night temperature rose above 7.5°C the percent of females increased rapidly and during nights with a temperature above 10.5°C the proportion of females varied between forty and sixty percent. The relationship between the percentage of females and the night temperature is probably better expressed by a sigmoid curve rather than a straight line. Without trying to calculate an equation which fits the data, such a curve is suggested in Fig. 2. None of the nights were particularly warm, so the material does not contain information on the proportion of females during such nights. It is not inconceivable that the percentage of females would have decreased again if the night temperature had risen further.

References

Corbet, P. S., Schmid, F. & Augustin, C. L. 1966. The Trichoptera of St. Helen's Island, Montreal. I. The species present and their relative abundance at light. *Can. Ent. 98*, 1284–1298.

Crichton, M. I. 1960. A study of captures of Trichoptera in a light trap near Reading, Berkshire. *Trans. R. Ent. Soc. Lond, 112*, 319–344.

Göthberg, A. 1973. Dispersal of lotic Trichoptera from a north Swedish stream. *Aquilo Ser. Zool. 14*. 99–104.

Marshall. A. C. 1939. A qualitative and quantitative study of the Trichoptera of western Lake Erie (as indicated by light trap material). *Ann. Ent. Soc. Am. 32*, 665–688.

Morgan, N. C. 1956. The biology of *Leptocerus aterrimus* Steph. with reference to its availability as a food for trout. *J. Anim. Ecol. 75*, 349–365.

Solem, J. O. 1977. Mire invertebrate fauna at Eidskog, Norway. VIII. Trichoptera. *Norw. J. Ent. 24*, 113–115.

Svensson, B. W. 1972. Flight periods, ovarian maturation, and mating in Trichoptera at a South Swedish stream. *Oikos 23*, 370–383.

Svensson, B. W. 1974. Population movements of adult Trichoptera at a South Swedish stream. *Oikos 25*, 157–175.

Tobias, W. 1967. Zur Schlüpfrhytmik von Köcherfliegen (Trichoptera). *Oikos 18*, 55–75.

Tobias, W. & Tobias, D. 1971, Köcherfliegen und Steinfliegen einiger Gewässer in Sör Varanger (Nord-Norwegen) (Trichoptera, Plecoptera). *Senckenbergiana biol. 52*, 227–245.

Ulfstrand, S. 1970. Trichoptera from River Vindelälven in Swedish Lapland. A four-year study based mainly on the use of light-traps. *Ent. Tidskr. 91*, 46–63.

Williams, C. B. 1937. The use of logarithms in the interpretation of certain entomological problems. *Ann. Appl. Biol. 24*, 404–414.

Received 22 December 1977

On the biology of ants (Hym., Formicidae) in Trøndelag, Norway

PER SVEUM

Sveum, P. 1978. On the biology of ants (Hym., Formicidae) in Trøndelag, Norway. *Norw. J. Ent.* Vol. 25, pp. 153–155. Oslo. ISSN 0029-1897.

Formicidae were collected with pitfall traps in seven habitat types at Jonsvatnet, Sør-Trøndelag county. The habitat choices of the 10 collected species are discussed, and an unexpected activity in *Myrmica* queens is reported. Five species are reported new to Nord-Trøndelag and six species are reported new to Sør-Trøndelag.

Per Sveum, Marie Sørdals vei 15, N-7000 Trondheim, Norway.

The present material was sampled by The Royal Norwegian Society of Science and Letters, the Museum, as part of a study of the invertebrate fauna in different vegetational types in Sør-Trøndelag county. As Collingwood's (1974) list of Norwegian ants shows, the ant fauna has previously been scarcely investigated in this part of Norway.

Material and methods

The study was carried out in four different localities at Jonsvatnet near Trondheim from mid-May to mid-October 1974. Each locality contained one or more of the seven different habitats studied (see description below). The material comprised 17,126 specimens and was mainly collected in pitfall traps containing 4% formaldehyde (one trap per habitat per locality), but also in a few bigger, yellow, waterfilled containers designed for flying insects. The traps were emptied at irregular intervals throughout the summer. A sample comprises the specimens obtained when one trap is emptied once. No considerations were taken about the situation of the traps compared with ant tracks and ants nests. In the list of new records, at the end of this paper, a small material collected by The Royal Norwegian Society of Sciences and Letters, the Museum at Leka in Nord-Trøndelag county, and a few specimens collected by Mr. Per Straumfors (PS) and myself (SV) are included. The nomenclature used in this paper follows that of Collingwood (1974).

Habitats

I. Damp meadow. This habitat has a thick humus layer which is rich in nutrients. The vegetation is tall and dense and provides a stable climate just above the soil surface.

II. Dry meadow. This comprises small treeless areas where the humus layer is thin and dry. The vegetation is short and sparse and gives bad protection against sun and wind. As a result the moisture and temperature varies a great deal near the ground during day and night.

III. Spruce forest with bilberry. This is a common type of vegetation in Norway. The decomposition of dead coniferous twigs and needles, bilberry leaves, and mosses is slow. The result is the formation of an acidic raw humus layer. The underlying soil layers are poor in nutrients. The humidity is high, as the dense spruce forest is shady and calm.

IV. Low herb spruce forest. Much like the former but with more herbs than ericaceous species. The vegetation varies from short to tall. The soil is richer in nutrients than in the former type, and the humus layer is thinner and less acidic.

V. Pine forest with lichens and heather. This is found on rocky ground with a thin raw humus layer, poor in nutrients. The dead plant material is slowly decomposed, and the soil is acid. The habitat is shady, calm, and damp above the soil layer.

TABLE I. The distribution of species in the different habitats.
T = number of samples, S = number of specimens.

	I		II		III		IV		V		VI		VII		
Species	T	S	T	S	T	S	T	S	T	S	T	S	T	S	Σ S
Myrmica ruginodis Nyl.	13	24	64	331	7	10	29	52	38	210	41	180	25	71	878
M. sulcinodis Nyl.									5	12	7	9			21
M. scabrinodis Nyl.	1	30	6	7							39	171	8	11	219
M. lobicornis Nyl.			3	13					4	5					18
Leptothorax acervorum Fab.							2	2	10	12	2	2			16
Camponotus herculeanus L.					2	2	2	2					1	1	5
Formica aquilonia Yarr.	18	50	56	634	127	10402	53	3022	46	530	71	748	64	408	15794
F. exsecta Nyl.											14	59			59
F. lemani Bond.	7	11	17	33			1	1	12	14	14	29	9	17	105
F. gagatoides Ruzs			5	5							3	4	2	2	11
Σ S		115		1023		10414		3079		783		1202		510	17126
No. of species	4		6		3		5		6		8		6		

VI. Ombrotrophic bog. This bog type is distributed all over the country. There is no ordinary soil layer, as the *Sphagnum* mosses, lichens, and heather grow in height and form a thick acidic peat layer. The nutrients are solely contributed through the precipitation. The climate varies a lot during day and night.

VII. Minerotrophic fen. The peat layer contains more nutrients than in the former, and the plants are taller. As a result the ground is more sheltered and the climate is more stable. The nutrients are contributed through the continuously circulating ground water.

Results and discussion

Species

As can be seen from Table I, *Myrmica ruginodis* and *Formica aquilonia* were captured in all habitats. Holgersen (1943) considered *M. ruginodis* as rare on mires and in dark forest in Rogaland, south-western Norway, This seems to be right as regards dark forest (habitat III), but not for fen in Trøndelag. The high frequency of captures of *F. aquilonia* is probably due to high tolerance in foraging area rather than nesting habitats. Nests of the *Formica rufa* group species are normally situated on the edge of a forest (Douwes 1976).

M. sulcinodis was captured in habitats V and VI. The upper strata where this species forms its nests are dry in these habitats. This corresponds well with Holgersen's results (1943).

M. scabrinodis was captured in habitats I, II, VI, and VII. Bolton & Collingwood (1975) considered it to be adapted to a wide range of localities. This is also suggested by the present records. In habitat I the species was only captured once (31 May 1974); however, as many as 30 specimens were taken. I can find no reasonable explanation for this sudden occurrence and disappearance.

M. lobicornis occurred in habitats II and V, which indicates a wide adaptation in the area. Bolton & Collingwood (1975), Larsson (1943), and Douwes (1976) considered it to belong to a wide variety of habitats.

Leptothorax acervorum was captured in small numbers in habitats IV, V, and VII. Holgersen (1943), Larsson (1943), and Douwes (1976) considered this species as xerophilous, but Holgersen also put forward the proportion 5:1 for dry:wet habitats. The present material is too small to consider this proportion.

Camponotus herculeanus was captured only three times in habitats IV and VII. This species has been regarded as xerophilous, belonging to rocky ground (Holgersen 1943, Larsson 1943), The present material may, although rather small, indicate a wider adaptation. I have myself captured it several times on mires near Mo i Rana, Northern Norway.

Formica exsecta which was only captured in habitat VI is usually regarded as xerophilous, often associated with Juniperus (Collingwood 1974). Holgersen (1973) points out that *F. exsecta* is a real exception on mires in Rogaland, but Douwes (1976) also regards it as a mire species, certainly with a question mark. The present observation indicates at least that the species forages on mires. Collingwood (1976) reported it from mire habitats in Eidskog, Hedmark; however, without further remarks on the species.

The subgenus *Serviformica* is represented by two species: *Formica lemani* and *F. gagatoides. F. lemani* was captured in all habitats, except III. This may be due to bad light conditions in the habitat. *F. gagatoides* has been considered as xerophilous (Holgersen 1943b).

In the present material it was captured in habitats II, VI, and VII: this suggests a hygrophilous adaptation as well. Forsslund (1947) reported it once from a mire habitat.

Queens and males

As can be seen from Table II, the reproductive specimens captured were widely distributed all over the sample period. All the queens belonging to *Myrmica* were dealated, implying that they had been fertilized. According to Bolton & Collingwood (1975), the nuptial flight for *Myrmica* species in Britain occurs in August. O'Rourke (1950), reported the nuptial flight for *M. ruginodis* and *M. rubra* in Narvik, Northern Norway on 19 August.The present material is too small to draw conclusions, but it may suggest the following alternatives: Some queens participate in foraging, or the nuptial flight may occur earlier in the year than August, or the captured queens are queens from the year before which had not yet established a colony. However, the two males were captured in late August (Table II), and this may indicate nuptial flight in this month and so invalidate the second hypothesis. In laboratory experiments, Brian (1974) found that queens in small colonies of *M. rubra* restricted their activity to nursing; thus the first hypothesis may be invalidated. The third hypothesis should be tested by further work.

A single alate queen of *Formica aquilonia* was captured in the middle of June. Three alate queens of the same species were captured with a net on 4 July 1977 in the same area. This is consistent with observations of nuptial flight in *Formica rufa* group species in Britain (Bolton & Collingwood, 1975).

Table II. Distribution of sexuals in the sampling period. F = one queen. M = one male

Species	May	June	July	Aug.	Sept.
Myrmica ruginodis Nyl.	F	3F	3F	6F	2F
M. rubra L.	F				
M. sulcinodis Nyl.		F	F		F
M. scabrinodis Nyl.	F	F	F	F+M	F
M. lobicornis Nyl.				M	
Formica aquilonia Yarr.		F			

New records

According to Collingwood's (1974) list the following records are new to Nord-Trøndelag, NT, and Sør-Trøndelag, ST. *Myrmica rubra:* NT, Leka 5 May 1974. *M. ruginos:* NT, Leka 5 May 1964 Egge, Steinkjer 30 April 1972. (leg. PS), ST, Jonsvatnet, Trondheim 1974. *M scabrinodis:* ST, Jonsvatnet, Trondheim 1974. *M. lobicornis:* NT, Leka 25 June 1974. ST, Jonsvatnet, Trondheim 1974. *Campotonus herculeanus:* ST, Jonsvatnet, Trondheim 1974. *Formica lugubris:* ST, Kyvatnet, Trondheim 2 Nov. 1975 (leg. SV.) Jonsvatnet, Trondheim 1974. *F. truncorum:* NT, Leka 5 June 1974. *F. exsecta:* NT, Leka 6 June 1974. ST, Jonsvatnet, Trondheim 1974.

Acknowledgements. – I should like to thank Mr. B. Larsson for information about the habitats and for putting the material at my disposal, Mr. C. A. Collingwood for checking some of the identifications and for valuable criticism and linguistic improvements, and Mr. J. O. Solem for valuable help with the manuscript. Finally I should like to thank Mr P. Straumfors for contributing specimens.

References

Bolton, B. & Collingwood, C. A. 1975. Hymenoptera Formicidae. *Handb. ident. Brit. ins. VI: 3 (c),* 34 pp.

Brian, M. V. 1974. Brood rearing behaviour in small cultures of the ant Myrmica rubra. *Anim. Behav. 22* 879–889.

Collingwood, C. A. 1974. A revised list of Norwegian ants (Hymenoptera Formicidae). *Norsk ent. Tidsskr. 21* 31–35.

Collingwood, C. A. 1976. Mire invertebrate fauna at Eidskog, Norway. III. Formicidae (Hymenoptera Aculeata). *Norw. J. Ent. 23,* 185–187.

Douwes, P. 1976. Sveriges myror – illustrerade bestämningstabeller över arbeterna. *Entomologen 5* 37–54.

Forsslund, K.-H, 1974. Svenska Myror 1–10. *Ent. tidskr. 68,* 67–80.

Holgersen, H. 1943a. Ant studies in Rogaland (South-western Norway). *Avhandl. Det Norske Vid.-Akad. Oslo, Mat.-Naturv. Klasse 1943 nr. 7,* Oslo.

Holgersen, H. 1943b. Formica gagatoides Ruzs in Norway. *Tromsø Mus. Årsh. 64* 1–17.

O'Rourke, F. J. 1950. Myrmecological notes from Narvik, northern Norway. *Norsk ent. Tidskr. 8* 47–50.

Larsson, Sv. G. 1943. Myrer. *Danm. Fauna 49,* 190 pp. København.

Received 29 March 1978

Herbivorous insects of the mountain birch (*Betula pubescens* ssp. *tortuosa*) in eastern Finnmark (Norway) and northern Lapland (Finland)

SEPPO KOPONEN & LASSE ISO-IIVARI

Koponen, S. & Iso-Iivari, L. 1978. Herbivorous insects of the mountain birch (*Betula pubescens* ssp. *tortuosa)* in eastern Finnmark (Norway) and northern Lapland (Finland). *Norw. J. Ent.*Vol. 25, pp. 157–163. Oslo. ISSN 0029-1897.

Great differences in abundance and biomass of the studied herbivore groups (symphytan, lepidopteran, and dipteran larvae and coleopteran adults and larvae) as well as of dominant species were found at eleven sites from Petsikko fell (69°26'N.) to Kongsfjord on the Arctic Ocean (70°44'N.). The two northernmost isolated birch shrub formations in Varangerpeninsula seemed to differ, based on the fauna, from other sites in Norway and Finland situated in the continuous birch forest zone. Data on consumption and the effect of certain geographical and biological factors on the occurrence of herbivores are given; especially altitude of site was important. The differences between the study year (1973) and results from corresponding studies during the previous year (1972) are discussed.

Seppo Koponen & Lasse Iso-Iivari, Department of Zoology, University of Turku, SF-20500 Turku 50, Finland.

Herbivores and herbivory of the mountain birch (*Betula pubescens* ssp. *tortuosa)* in the forest tundra (sensu IBP, e.g. Rosswall & Heal 1975) have been the main object of Finnish IBP studies at Kevo, northern Finland, and in adjacent areas (Haukioja & Koponen 1975, Kallio 1975). Data on herbivorous insect fauna of the birch in northernmost Fennoscandia from the study period 1971–73 have been published by Koponen (1973a, b, 1974), Haukioja et al. (1973), Haukioja & Koponen (1975), and Haukioja & Iso-Iivari (1977). Mention should also be made of papers from the earlier period by Nuorteva (1963, 1966), Tenow (1972), and Kallio & Lehtonen (1973).

The aim of the present paper is to give information about certain groups of herbivorous insects of the mountain birch in eastern Finnmark and northern Lapland, 1973, collected at the same study sites and using the same method and study period as in the study of Haukioja et al. (1973) the previous year.

Study area, material, and methods

The study area is situated north of the limit of continuous pine forest, and the two northernmost sites are north of the limit of mountain birch forest (Fig. 1). The line of sites runs from the top of Petsikko fell (69°26'N., 27°15'E.) to the coast of the Arctic Ocean, Kongsfjord (70°44'N., 29°18'E.). The birch formations at Alaköngäs, Kongsfjorddal, and Kongsfjord are sparse birch shrubs; at other sites there grows mountain birch 'forest'. The study sites were as follows.

1. Petsikko. Birch forest on the top of Petsikko fell, about 300 m a.s.l., average height of trees 3.0 m.
2. Leppälä. Birch forest with western exposition, 130 m a.s.l., trees 4.8 m.
3. Ailigas. Birch forest with northeastern exposition on the northern slope of Ailigas fell, about 110 m a.s.l., trees 4.5 m.
4. Alaköngäs. Sparse birch shrub formation with slight northern exposition. Some of the bushes were eaten by *Oporinia* in 1965, about 135 m a.s.l., height of shrubs 3.3 m.
5. Skipagurra. Birch forest near the river Tana, western exposition, about 30 m a.s.l., trees 4.7 m.
6. Luoftjok. Birch forest on a hill terrace, southern exposition, about 60 m a.s.l., trees 4.3 m.
7. Leirpollskogen. Tall birches on the shore of the river Julelva near the Arctic Ocean (Tanafjord), 35 m a.s.l., trees 5.8 m.
8. Gavzavarre. Birch forest with southeastern exposition near the northern limit of conti-

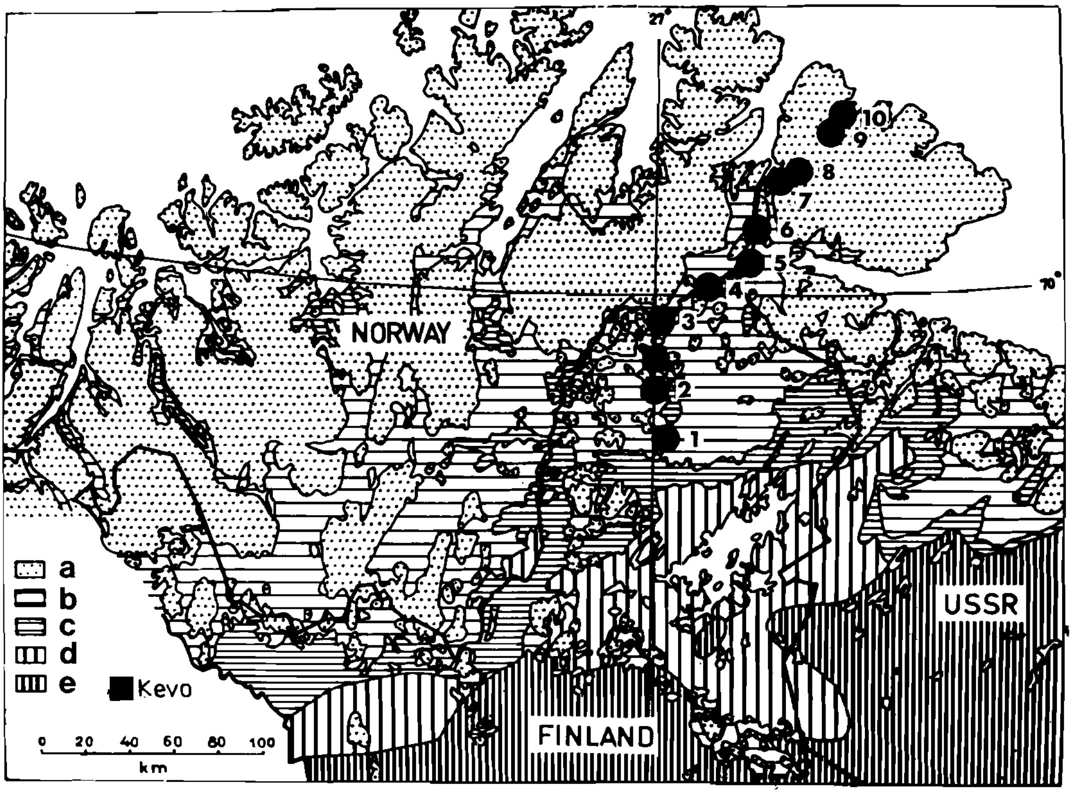


Fig. 1. The study sites and biotic zones in northernmost Fennoscandia. The study localities outside of Kevo are 1. Petsikko, 2. Leppälä, 3. Ailigas, 4. Alaköngäs, 5. Skipagurra, 6. Luoftjok, 7. Leirpollskogen, 8. Gavzavarre, 9. Kongsfjorddal, 10. Kongsfjord. Biotic zones are as follows: a. tundra and barren fells, b. birch bushes and birch forests, c. birch forests and small groves of pines, d. pine forests, e. coniferous forests (pine and spruce). Zones redrawn from Atlas of Finland, 1960.

nuous birch forest, about 160 m a.s.l., trees 3.3 m

9. Kongsfjorddal. Birch shrubs in the valley of the river Gaednajokka, 90 m a.s.l. A very severe site surrounded by tundra. Average height of shrubs 3.0 m.
10. Kongsfjord. Small birch shrubs on the east slope of coastal mountains beside the Arctic Ocean, about 30 m a.s.l., height of shrubs 1.8 m.

In addition to these sites, information from the IBP study site at Kevo is used in the present paper. This is situated on the northern slope of a hill, 130–160 m a.s.l. (Koponen 1973b). The average height of birches is 4.3 m. All these 11 study sites were also used in the 1972 study (Haukioja et al. 1973).

Birch branches chosen at random were quickly pushed into a large net, cut off, stored in a plastic sack, and studied in the laboratory at the Kevo Subarctic Research Institute. Each sample included 40 birch twigs, and the samples were taken from a height of up to 2.5 m.The study period was from 25 June to 27 August 1973, and samples were taken once a week.

Dry weight figures for birch leaves were taken after 24 hours drying at 105°C, and the insects were weighed live. The dry weight of insects was calculated using correlation equations obtained in laboratory studies.

The herbivore material from birch foliage comprised about 4100 individuals (Symphyta and Lepidoptera larvae and herbivorous Coleoptera).

A special check of galls of *Massalongia* spp. was made from 23 July to September; 300 birch leaves were checked from each sample.

Leaf material used for investigating feeding marks in order to estimate consumption was

Table I. Diversity of herbivore fauna at the studied sites. Index = 100 x N groups/ N individuals; 11 herbivore groups altogether (Table II excluding Massalongia).

Sites	N groups	Index
Petsikko	10	0.8
Leppälä	10	1.4
Kevo	7	2.5
Ailigas	10	3.6
Alaköngäs	9	2.3
Skipagurra	9	6.8
Luoftjok	9	3.4
Leirpollskogen	9	5.3
Gavzavarre	10	3.9
Kongsfjorddal	6	3.5
Kongsfjord	4	2.5

collected during the period 3–10 September 1973. The average number of leaves in these samples was 3800 leaves.

The herbivore material together with the feeding mark analyses were compared with certain geographical (N-coordinate of site, E-coordinate, distance from the Arctic Ocean, height above sea level) and biological (height of trees, thickness of birch forest, degree of polycormy, weight of leaf, water percentage of leaf) data of each site using multiple regression analysis.

Results and discussion

Faunal structure

The most abundant free-living birch herbivore group of the area, Homoptera (especially Psyllina, see Koponen 1973b), was excluded from the present study because of the method used.

Some data on the diversity of studied herbivore fauna caught at the study sites are given in Table I. Low figures for observed taxa were found at Kongsfjord, Kongsfjorddal, and Kevo. The highest value according to the simple index of diversity used was found at Skipagurra, where the total individual number was lowest. The two lowest index values were obtained at Petsikko and Leppälä, the southernmost sites, with a very high dominance of *Dineura viridorsata*.

The abundance of herbivorous insects is shown in Table II. Petsikko and Leppälä had the highest numbers (49% of the total herbivore individuals), and Skipagurra the lowest. Great differences in the abundance of species were found in different areas. *Dineura viridorsata* was the most abundant at the southernmost sites, with the exception of Ailigas, and rather infrequent near the Arctic Ocean. For other Tenthredinidae larvae the opposite was true. The most serious pest in the area, *Oporinia*

Table II. Abundance of herbivorous insects at the studied sites, 1973 (total individual number/100 g dried leaves).

Herbivores	Sites											
	1	2	K	3	4	5	6	7	8	9	10	Mean
Symphyta larvae	58.4	35.4	14.5	4.6	19.7	6.1	13.3	3.1	2.3	10.6	7.4	16.0
Dineura viridorsata	52.1	31.4	13.3	3.3	15.9	3.4	10.5	1.4	0.4	2.9	2.7	12.5
Other Tenthredinidae	5.4	3.7	1.2	1.1	3.4	2.4	2.7	1.4	1.3	6.7	4.6	3.1
Cimbicidae	0.8	0.2	-	0.1	0.2	0.2	0.1	0.1	0.2	-	0.1	0.2
Pamphiliidae	0.1	0.1	-	0.1	0.2	0.1	-	0.2	0.4	1.0	-	0.2
Lepidoptera larvae	13.7	2.5	1.9	6.7	4.6	1.9	1.4	1.2	2.4	0.4	3.7	3.7
Oporinia autumnata	1.2	-	-	-	0.1	0.1	0.1	-	-	-	-	0.1
Other Macrolepidoptera	0.7	0.4	0.3	0.2	0.5	0.2	0.2	-	0.1	-	-	0.2
Microlepidoptera	11.8	2.1	1.6	6.4	4.1	1.6	1.1	1.2	2.3	0.4	3.7	3.3
Coleoptera adults	1.4	5.4	4.6	4.5	0.6	0.9	1.6	6.1	11.0	0.2	-	3.3
Coeliodes spp.	-	3.1	3.7	3.6	0.4	0.8	1.3	2.5	4.9	-	-	1.9
Polydrosus ruficornis	1.3	2.1	0.9	0.7	-	-	-	3.4	4.9	0.1	-	1.2
Others	0.1	0.1	0.1	0.1	0.2	0.1	0.2	0.2	0.2	0.1	-	0.1
Coleoptera larvae	1.2	0.7	0.1	0.5	-	-	0.2	0.1	0.3	-	-	0.3
Total	74.6	43.8	21.1	16.2	24.9	8.9	16.5	10.4	16.0	11.2	11.1	23.2
Dry weight of leaves (g)	1714	1651	1339	1743	1595	1483	1601	1644	1585	1522	1426	1573
Diptera:												
Massalongia rubra	345.3	83.9	132.7	38.0	217.4	130.5	366.7	73.8	35.8	69.3	376.9	170.0

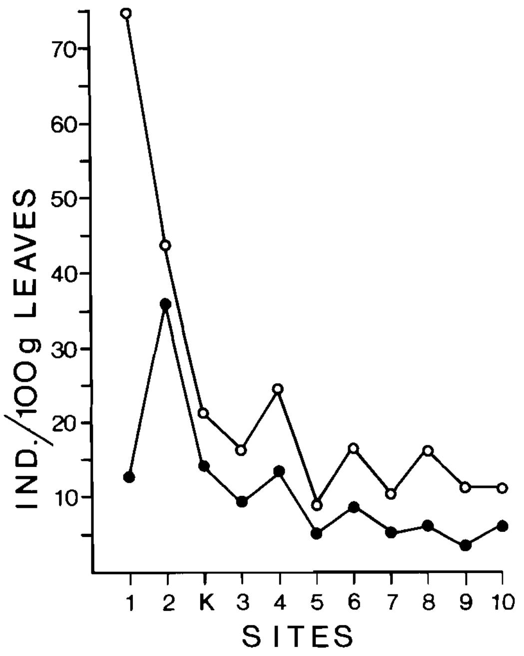


Fig. 2. The total individual numbers of herbivores (Symphyta and Lepidoptera larvae and Coleoptera) per 100 g dried birch leaves at the different sites in 1973 (open circles) and in 1972 (closed circles).

autumnata (Tenow 1972, Kallio & Lehtonen 1973), was still very uncommon in 1973 as it was in 1972 (Haukioja et al. 1973); only at Petsikko was it more common (1.6% of herbivore individuals). A high proportion of microlepidopteran larvae was also found at Petsikko, especially the genus *Eriocrania* (Koponen 1974). Curculionidae beetles (*Coeliodes* spp. and *Polydrosus ruficornis)* had the highest numbers at Gavzavarre. Other herbivorous beetles (mainly Chrysomelidae) were uncommon at the study sites.

The total individual numbers per 100 g dry leaves are shown in Fig. 2. Numbers in 1973 were higher at all sites than in 1972. The difference between years was rather small, with the exception of Petsikko, where the individual number for 1973 was six times the number for 1972 (caused mainly by *D. virididorsata*).

The number of insects included in Table II per hectare (mean for the study period) varied from 40,000 to 400,000 (a rough estimation, Haukioja & Koponen 1975). The density of *D. virididorsata* at the maximum site, Petsikko, was about 250,000 ind./hectare.

The abundance of *Massalongia rubra* was very high, and great differences were found between sites. *M. rubra* galls were partly referred to as 'Homoptera' feedings in the 1972 study (Haukioja et al. 1973) based on Nuorteva's (1966) data. Haukioja & Koponen (1975) discussed the numbers and consumption of *M. rubra* at Kevo in 1973. Besides *M. rubra* inhabiting midvein galls, another species, *M. betulifolia,* also lives at study sites. This recently described species (Harris 1974) lives in galls situated in lamina (Askew & Ruse 1974); at most sites it was less abundant than *M. rubra.* In many localities *Massalongia* spp. seemed to be the most abundant and important herbivores of the birch in late summer (Koponen 1974, Haukioja & Koponen 1975).

The correlation coefficients for the main herbivore groups and for geographical and biological factors are shown in Table III (running multiple regression analysis). High correlations were noted especially for *Dineura virididorsata* (distance from the Arctic Ocean and N°), Cimbicidae (altitude), Macrolepidoptera larvae, excluding *Oporinia* (altitude, distance from sea, and N°), mining microlepidopteran larvae (altitude), and Coleoptera larvae (altitude, distance from sea, and N°). All these correlations are statistically significant ($p<0.01$). The only biological factor significant at this level was the density of birch trees and the occurrence of Pamphiliidae (note, however, the small number of pamphilid larvae). Adult Coleoptera, Tenthredinidae (excl. *Dineura)*, and *Massalongia rubra* showed lower correlation coefficients with the tested factors.

Altitude of site alone explained (according to correlation analysis) the occurrence of many herbivore groups at a high level: Coleoptera larvae at 62%, miners 60%, *Oporinia* 58%, and Cimbicidae 57%. The mining genus *Eriocrania* was explained by altitude of site at as high a level as 65% (Koponen 1974). N-coordinate explained the occurrence of Macrolepidoptera larvae (excl. *Oporinia)* at 67%, and the distance from the Arctic Ocean the occurrence of *D. virididorsata* at 66%.

The proportion of the dominant group, Symphyta, in 1972 and 1973 is shown in Fig. 3. In 1973 the percentages of Symphyta were somewat lower at all sites (except Leirpollskogen) than in 1972. The proportion of herbivorous Coleoptera in 1973 was about the same or a little higher than in 1972, and in Lepidoptera larvae there was no clear tendency (Haukioja et al. 1973). The abundance of Symphyta larvae and Coleoptera

Table III. Correlations for occurrence of herbivores and geographical (alt = altitude of site, dist = distance from the Arctic Ocean, N-co = N-coordinate, E-co = E-coordinate) and biological (height = height of trees, thickn = thickness of forest, polych = degree of polychormy, weight = weight of leaf, water = % of water in leaf) factors of the sites using multiple regression analysis. • = p <0.05, ••= p <0.01, •••= p <0.001.

	alt	dist	N-co	E-co	height	thickn	polych	weight	water
Symphyta larvae	.78••	.77••	-.74••	-.53	-.17	-.01	.27	.59	-.44
Dineura virididors.	.79••	.82••	-.80••	-.60	-.10	-.07	.24	.66•	-.44
Other Tenthredinid.	.20	.03	.11	.30	-.62•	.43	.41	-.23	-.15
Cimbicidae	.76••	.52	-.58	-.33	-.21	-.25	.02	.51	-.38
Pamphiliidae	-.00	-.35	.45	.49	-.22	.83••	-.10	-.59	-.11
Lepidoptera larvae	.76••	.61•	-.62	-.46	-.31	-.29	.32	.39	-.23
Oporinia autumnata	.76••	.53	-.57	-.31	-.25	-.14	.16	.38	-.33
Other Macrolepidop.	.81••	.75••	-.82••	-.70•	-.07	-.23	.13	.69•	-.40
Microlepidoptera	.73•	.58	-.59	-.44	-.32	-.30	.33	.35	-.20
Coleoptera adults	.17	.01	-.05	-.12	.38	-.08	-.62•	.23	-.20
Coeliodes spp.	.08	.15	-.17	-.33	.47	-.06	-.41	.27	.00
Polydrosus ruficor.	.23	-.11	.08	.09	.21	-.10	-.70•	.15	-.36
Others	-.00	-.36	.26	.23	.21	.18	-.73•	-.00	-.40
Coleoptera larvae	.79••	.75••	-.74••	-.57	.00	-.05	.10	.71•	-.21
Diptera:									
Massalongia rubra	.10	.03	-.03	.11	-.51	-.52	.31	.13	-.14

was clearly reversed; there was a highly significant (p<0.001) negative correlation in their occurrence. In general, the situation of herbivore fauna was very similar in 1973 and 1972; Symphyta clearly dominated in both years (quite equal percentages, see Fig. 3); only at Ailigas and Kongsfjord were Lepidoptera larvae abundant, and at Leirpollskogen and Gavzavarre, Coleoptera adults.

If the present material together with rather similar data from earlier studies in the northernmost parts of Finnish Lapland and from eastern Finnmark (Koponen 1973b, Haukioja et al. 1973, Haukioja & Koponen 1975) is compared with mountain birch in other areas, remarkable differences in fauna composition can be found. For example, the low abundance of Symphyta in Sogndal, western Norway, is a striking phenomenon (Hågvar 1976). However, this material was from the year 1967, when there was a mass outbreak of Geometrid larvae (*Oporinia autumnata* and *Operophtera* spp.) in Sogndal, and this makes comparisons with the present data difficult. A general feature in Sogndal, especially at the highest sites (vegetation and environmental factors resembling the present study area), was surprisingly small species and individual numbers of herbivores, with the exception of *O. autumnata*. In southern Greenland, the dominance of Lepidoptera larvae was very clear, and Symphyta and herbivorous Coleoptera were not found in the material collected from *Betula pubescens* and *B. glandulosa* at Narssaq, 1976 (Koponen 1978).

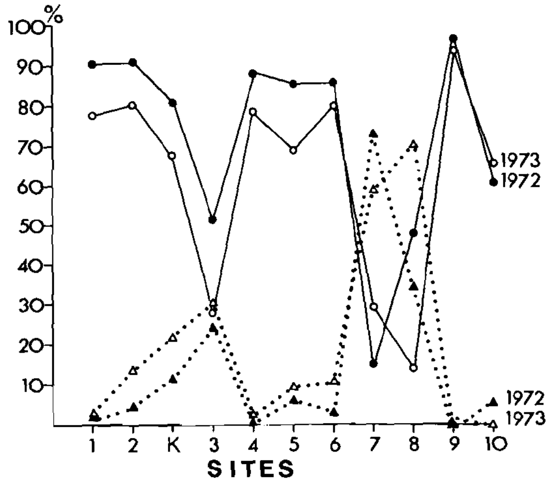


Fig. 3. Percentages of Symphyta larvae (solid lines) and herbivorous Coleoptera (dotted lines) of the total individual number of studied herbivores (Symphyta, Lepidoptera, Coleoptera) at different sites in 1973 and 1972.

Table IV. Total biomass of herbivorous insects at the studied sites, 1973 (mg dw / 100 g dried leaves).

Herbivores	Sites										
	1	2	K	3	4	5	6	7	8	9	10
Symphyta larvae	158.96	64.38	15.53	21.41	47.51	33.23	29.40	13.05	9.21	32.67	17.58
Dineura viridiorsata	88.25	36.12	8.21	4.30	19.45	4.03	11.34	1.20	0.22	1.51	1.79
Other Tenthredinidae	20.79	16.60	7.32	4.06	17.67	10.92	10.30	8.79	4.13	24.88	14.69
Cimbicidae	49.21	11.51	-	12.78	7.84	17.91	7.76	0.87	0.59	-	1.10
Pamphiliidae	0.71	0.15	-	0.27	2.55	0.37	-	2.19	4.27	6.28	-
Lepidoptera larvae	34.81	7.84	1.04	5.01	19.53	5.20	6.68	1.30	12.23	0.48	6.03
Oporinia autumnata	13.34	-	-	-	0.91	1.34	0.64	-	-	-	-
Other Macrolepidoptera	15.68	6.99	0.57	2.79	14.62	2.60	5.00	-	8.58	-	-
Microlepidoptera	5.79	0.85	0.47	2.22	4.00	1.26	1.04	1.30	3.65	0.48	6.03
Coleoptera adults	3.41	7.67	5.62	4.64	0.76	1.27	2.00	9.11	15.06	0.92	-
Coeliodes spp.	-	2.45	2.80	2.78	0.37	0.45	1.09	1.96	3.88	-	-
Polydrosus ruficornis	3.10	4.83	2.99	1.49	-	-	-	6.17	9.99	0.17	-
Others	0.31	0.39	0.58	0.37	0.39	0.82	0.91	0.98	1.19	0.75	-
Coleoptera larvae	0.37	1.18	0.15	1.42	-	-	0.17	0.26	0.21	-	-
Total	197.55	81.07	22.34	32.48	67.80	39.70	38.25	23.72	36.71	34.07	23.61
Diptera:											
Massalongia rubra	23.68	6.32	•	2.13	15.67	4.71	22.23	3.93	1.64	2.81	12.49

Biomass

Biomass is shown in Table IV. Three different groupings of study sites could be observed on the basis of total herbivore biomass. The bulk of sites had a low biomass (about 20–40 mg dr. w/100 g dr. leaves), Alaköngäs and Leppälä had higher (70–80 mg) and Petsikko as much as 200 mg/100 g dry leaves (*Massalongia* excluded). The biomass value at Kevo, the IBP site, was the lowest observed. The herbivore biomass (Hymenoptera and Lepidoptera larvae, and herbivorous Coleoptera) at Petsikko was nearly 1 kg dr. w/hectare and at Kevo about 100 g /ha.

Symphyta larvae comprised the majority of the herbivore biomass (*Massalongia* excl.), except at Gavzavarre. The biomass figures in 1973 and 1972 were quite similar (Haukioja et al. 1973). The biomass of *Eriocrania* spp. and of other mining insects has been discussed by Koponen (1974), and the biomass and productivity of *Dineura viridiorsata* by Haukioja & Iso-Iivari (1977). Statistically significant correlation coefficients for biomass were noted in many groups: e.g. *Dineura* (66% explaining level by altitude), Lepidoptera larvae (64% by altitude), miners (62% by altitude), and *Oporinia* (58% by altitude). A biological factor, the degree of polycormy, explained the biomass of 'other Coleoptera' (mainly Chrysomelidae) at a level of 65%.

When comparing the total biomass for 1973 and 1972, two different areas can be found. In Norway, the biomass was more stable both between years and between study sites, and the total biomass figures were low. In Finland, there were great differences between years and sites, and the biomass values were high. However, Kevo and Ailigas resembled the situation of Norwegian sites. Both these sites are situated on a slope facing north. The biomass figure and the individual number per leaf biomass shown in Fig. 2 fits rather well.

Three species (*Dineura viridiorsata, Polydrosus ruficornis* and *Oporinia autumnata*) comprised more than the half of the herbivore biomass at the three southernmost sites: Petsikko 53.1%, Leppälä 50.6%, and Kevo 50.2% (*Massalongia* spp. naturally excluded). The importance of these species diminished northwards, and at the two northernmost isolated sites their proportion in biomass was at Kongsfjorddal 4.9% and at Kongsfjord 7.6%. The percentage of biomass of *Dineura* alone was highest at Petsikko (44.7%) and lowest at Gavzavarre (0.6%).

Consumption

The percentages of leaves bearing evidence of feeding in the material from September 1973 are shown in Table V. The highest proportions of

Table V. Percentages of leaves eaten by different herbivores, September 1973.

Sites	un-touched	holes	Dineura	Massalongia rubra-galls	n
Petsikko	1.8	55.7	83.8	59.9	3648
Leppälä	8.2	30.0	75.3	43.4	3148
Kevo	10.5	62.0	38.3	34.9	8753
Ailigas	27.9	29.8	21.0	41.2	3565
Alaköngäs	11.3	20.2	58.7	55.4	3252
Skipagurra	44.1	16.0	16.4	34.6	2544
Luoftjok	18.3	28.1	36.0	53.4	2788
Leirpollskogen	26.0	49.1	11.0	34.0	3361
Gavzavarre	20.6	71.3	5.7	22.6	3538
Kongsfjorddal	57.1	16.5	19.8	12.5	4247
Kongsfjord	49.2	14.6	8.7	35.5	3021

untouched leaves were found at the two northernmost sites and at Skipagurra, the locality with tall and healthy trees at low altitude. *Dineura* feeding was highest, of course, at the two southernmost sites. The percentage of *Dineura* feeding was higher in 1973 than in 1972 at all sites, except Kevo.

The leaves with mid-vein galls of *Massalongia rubra* (partly referred to as 'Homoptera' feeding in 1972, Haukioja et al. 1973) were common at all sites, except Kongsfjorddal. They were more common in 1973 than in 1972. The galls of *M. betulifolia* in leaf lamina were not included in this leaf checking material.

The feeding mark data and the data from insect collecting agree rather well, e.g. hole-eating and number of Curculionidae at Gavzavarre, indicating the usefulness of the feeding mark method. However, data about occurrence of *Massalongia* that were checked in summer (Table II) and in September (Table V) differed greatly. This was caused by the phenology of *Massalongia;* they are abundant in late summer and autumn.

The correlation coefficients for feeding marks are shown in Table VI. High correlations were found for some groups. For *Dineura* feeding the level explained by the distance from the Arctic Ocean was 76% and that for *Eriocrania* mines by the same distance 72%, see also Koponen (1974).

Table VI. Correlations for certain feeding marks and geographical factors of the sites; the leaf checking material of September 1973. For explanations, see Table III.

Feeding mark	alt	dist	N-co	E-co
Dineura	$.75^{**}$	$.87^{***}$	$-.84^{**}$	$-.74^{*}$
M. rubra galls	.44	.62	$-.70^{*}$	$-.68^{*}$
Eriocrania mines	$.85^{**}$	$.85^{**}$	$-.83^{*}$	$-.69^{*}$
holes	.52	.16	-.22	-.13
un-touched	$-.67^{*}$	$-.69^{*}$	$.76^{*}$	$.74^{*}$

Acknowledgements. – This work was supported by the Nordic Council for Ecology and the Emil Aaltonen Foundation. We wish to thank Prof. Paavo Kallio for working facilities at the Kevo Subarctic Research Station, and the persons of the herbivory research group at Kevo for help during the work. The English text was kindly checked by Mr. Christopher Grapes, B. A.

References

Askew, R. R. & Ruse, J. M. 1974. The biology of some Cecidomyiidae (Diptera) galling the leaves of birch (Betula) with special reference to their chalcidoid (Hymenoptera) parasites. *Trans. R. ent. Soc. Lond. 126,* 129–167.

Hågvar, S. 1976. Altitudinal zonation of the invertebrate fauna on branches of birch (Betula pubescens Ehrh.). *Norw. J. Ent.23,* 61–74.

Harris, K. M. 1974. Massalongia betulifolia sp. n. (Diptera: Cecidomyiidae) described from leaf galls on Betula pendula Roth and B. pubescens Ehrhart. *Entomologist's Gaz. 25,* 137–139.

Haukioja, E. & Iso-Iivari, L. 1977. Local and annual variation in secondary production by Dineura virididorsata (Hym., Tenthredinidae). *Rep. Kevo Subarctic Res. Stat. 13,* 26–32.

Haukioja, E. & Koponen, S. 1975. Birch herbivores and herbivory at Kevo. pp. 181–188 in Wielgolaski, F. E. (ed.) *Fennoscandian Tundra Ecosystems 2 (Ecol. Studies 17).* Springer, Berlin, Heidelberg & New York.

Haukioja, E., Koponen, S. & Ojala, H. 1973. Local differences in birch leaf consumption by invertebrates in northern Norway and Finland. *Rep. Kevo Subarctic Res. Stat. 10,* 29–33.

Kallio, P. 1975. Kevo, Finland. pp. 193–223 in Rosswall, T. & Heal, O. W. (eds.) *Structure and Function of Tundra Ecosystems (Ecol. Bull. 20).* Swedish Natural Science Council, Stockholm.

Kallio, P. & Lehtonen, J. 1973. Birch forest damage caused by Oporinia autumnata (Bkh.) in 1965–66 in Utsjoki, N Finland. *Rep. Kevo Subarctic Res. Stat. 10,* 55–69.

Koponen, S. 1973a. On the mining insects of the mountain birch in northernmost Fennoscandia. *Rep. Kevo Subarctic Res. Stat. 10,* 14–19.

Koponen, S. 1973b. Herbivorous invertebrates of the mountain birch at Kevo, Finnish Lapland. *Rep. Kevo Subarctic Res. Stat. 10,* 20–28.

Koponen, S. 1974. On the occurrence and ecology of Eriocrania spp. (Lep., Eriocraniidae) and other mining insects of the birch in northernmost Fennoscandia in 1973. *Rep. Kevo Subarctic Res. Stat. 11,* 52–64.

Koponen, S. 1978. Notes on herbivorous insects of the birch in southern Greenland. *Rep. Kevo Subarctic Res. Stat. 14,* 13–17.

Nuorteva, P. 1963. The influence of Oporinia autumnata (Bkh.) (Lep., Geometridae) on the timber line in subarctic conditions. *Ann. Ent. Fenn. 29,* 270–277.

Nuorteva, P. 1966. Leaf development and leaf pathogens on subarctic birches after a calamity of Oporinia autumnata (Bkh.) (Lep., Geometridae). *Ann.Zool. Fenn. 3,* 270–286.

Rosswall, T. & Heal, O. W. 1975. The IBP tundra biome – an introduction. pp. 7–16 in Rosswall, T. & Heal, O. W. (eds.) *Structure and Function of Tundra Ecosystems (Ecol. Bull. 20).* Swedish Natural Science Council, Stockholm.

Tenow, O. 1972. The outbreaks of Oporinia autumnata Bkh. and Operophthera spp. (Lep., Geometridae) in the Scandinavian mountain chain and northern Finland 1862–1968. *Zool. Bidrag, Uppsala Suppl. 2,* 1–107.

Received 14 February 1978

Notes on the Scandinavian fauna of social Aculeates (Hym., Vespidae and Apidae s.s.)

ASTRID LØKEN

Løken, A. 1978. Notes on the Scandinavian fauna of social Aculeates (Hym., Vespidae and Apidae s.s.). *Norw. J. Ent.* Vol. 25, pp. 165–169. Oslo. ISSN 0029-1897.

Recent records of six species of Vespidae and ten species of Apidae s.s. occurring in Scandinavia are listed and to some extent commented upon. In Sweden, *Bombus lapidarius* (L.) and *B. distinguendus* Morawitz range north to Torne Lappmark. *Psithyrus vestalis* (Seidl.) is new to northern Europe.

Astrid Løken, Zoological Museum, University of Bergen, N-5014 Bergen-Univ., Norway.

Social wasps and bumble bees identified by me in recent years include specimens that widen the picture of the distribution of several species in Scandinavia (Erlandsson 1971, Løken 1964, 1966, 1973). The specimens were collected during my fieldwork in northern Sweden 1974 and 1976, or accidently found in Norway and Sweden by various collectors. In addition, a few individuals traced in trap material from Messaure in Lule Lappmark 1974 belong to species not previously mentioned for that area (Svensson 1974, D. S. Peters 1974 a, b). I have also received some records by personal communication.

The nomenclature follows Løken (1964, 1978). The species list below is in general restricted to locality, sex, and the name of the collector. If not otherwise mentioned, the specimens are kept in Zoological Museum, University of Bergen. The abbreviations of the names of the provinces follow those generally accepted, cf. for instance Løken (1973). The abbreviations of the names of the collectors are according to the ZOO-TAX'list:

ADTn – Trond Andersen
ALAs – Lars A. L. Andersson
ANHs – Hugo Andersson
BNGs – Simon Bengtsson
BEN– – Robert B. Benson
BJO– – John Breen
BRDs – Lars Brundin
DOMn – Sisel Dommersnes
DYRn – Njål Dyrrdal
EDVn – Ole Edvin
FJAn – Arne Fjellberg
FJSn – Arild Fjeldså
GNLs – Daniel Gaunitz
GGUn – Guro Gjellestad
GJNn – Lita Greve Jensen
GKJn – Johanna Gullaksen
HGØn – Jan Haugsbø
LMAn – Maja Larsen
LøAn – Astrid Løken
MEBn – Bjarne A. Meidell
MRCn – Asbjørn Mørch
MüKs – Karl Müller
NTEn – Tore Nielsen
RRKn – Ragnhild Rosendahl Knudsen
TjTs – Tord Tjeder
TLIn – Inger Meidell Tambs-Lyche
ØSVn – Svein Ødegården
ØYHn – Magnar Øyhovden

Abbreviation of institutions:
ZIL – Zoological Institute, Lund
ZMB – Zoological Museum, Bergen
ZMO – Zoological Museum, Oslo

Vespidae

Vespula (Dolichovespula) norwegica (Fabricius)

Sweden. Jmt.: 25 km NW Föllinge ☿ (LøAn); Hotagen ☿ (RRKn); Toskströmmen NE Hotagen ☿ (RRKn). Ång.: Innerfällmo 60 km NW Örnsköldsvik ☿ (LøAn). Vb.: 10 km N Burträsk ☿ (LøAn). Nb.: NW Junosuando ☿ (LøAn); N Sundom ☿ (LøAn).

Vespula (Dolichovespula) saxonica (Fabricius)

Norway. Ø: Våler: Vannsjø ♀ (MRCn). HEs: Elverum: Sætre a nest (BJO); Ringsaker: Grupen 2 ☿☿ (ØSVn). Bv: Hol: Geilo 800 m ♀ (BEN). VE: Nøtterøy: Hella and Herstad 6 ☿☿ (ADTn); Sandar: Årø ☿ (GJNn). HOy: Sveio: Førde a nest (MEBn); Tysnes: Ånuglo 2 ☿☿ (Feltkurs); Bergen 4 nests GGUn, GJNn, HGØn, LøAn); Haus: Kallekleiv a nest (GGUn); Bruvik: Eikemo ♂ (GJNn); Meland: Brakstad 2 nests (GJNn); Radøy: Syltavåg 2 ☿☿ (ØYHn). HOi: Kvinnherad: Rosendal ☿ (Feltkurs); Varaldsøy ♀ (Feltkurs); Voss: N Vossevangen a nest (DOMn). All nests were constructed in protected localities.

Sweden. Ång: 25 km SE Kramfors ☿ (RRKn). Nb: Edefors 60 km NW Boden ♀ (TLIn). Ås.Lpm: Dorotea ☿ (LøAn). Ly.Lpm: Sorsele by ♂ (GNLs) ZIL. Lu. Lpm: Messaure in traps 1974: 17–24 June 5 ♀♀, 24 June –1 July ♀, 1–8 July 2 ♀♀, 8–15 July ☿ (MüKs); Porjus in traps 1976: 10–24 July ☿, 24–30 July ☿, 31 July –15 August ☿, 20 August –10 September 4 ☿☿ (MüKs). T. Lpm: Abiskojokk ♂ 10 August 1909 (BNGs) ZIL.

Records from Ly. Lpm: Ammarnäs 2 ♀♀ (GNLs) ZIL were revised to the 'zetterstedti' form of *V. norwegica*; likewise 3 ♀♀ from Lu. Lpm: Virihaure: Una Titir and Staloluokta respectively (Brinck & Wingstrand 1951). A female from Ly. Lpm: Sorsele: Vännäs 19 July 1928 (GNLs) ZIL (Gaunitz 1929) was revised to *V. adulterina* (Buysson).

Vespula (Dolichovespula) sylvestris (Scopula)

Norway. Os: Fåberg: Jørstadmoen ♀ (ØSVn). Bv: Hol: Geilo 800 m ♀ (BEN) and Vikastølen 1000 m 2 ☿☿ (LøAn). VE: Tjøme: Hvasser ♀ (GJNn) and Kjære ♀ (FJAn). HOy: Vikebygd: Dommersnes a nest (DOMn); Sund: Telavåg ♀ (LøAn); Haus: Kallekleiv a nest (GGUn); Meland: Brakstad ☿ (GJNn). HOi: Kvinnherad: Gjermundshavn ♀ (Feltkurs) and Varaldsøy ♀ (Feltkurs); Kvam: Steinestø ♀ (NTEn); Voss: Mjølfjell ♀ (EDVn). Sogn & Fjordane (SFi): Aurland: Flåm ♀ (GJNn), Aurlandsvangen a nest (LøAn).

Sweden. Lu. Lpm: Messaure in traps 1974: 17–24 June 3 ♀♀ and 24 June –1 July ♀ (MüKs).

Vespula (Pseudovespula) adulterina (Buysson)

Norway. Bv: Hol: N Haugastøl 1130 m a.s.l. ♀ (LøAn). HOy: Os: Nordstrøno ♀ (GKJn); Bergen: Hetlevik 2 ♀♀ (LMAn). Nsi: Krokstrand ♀ (FJSn).

Sweden. Ly.Lpm: Vännäs ♀ (GNLs) ZIL. T.Lpm: Abisko 4 ♂♂ (BRDs) ZIL; Karesuando ♀ (LøAn).

Finland. Lk: Pallastunturi (close to the Swedish border almost 68°N) ♀ (LøAn).

Vespula (s.s.) *germanica* (Fabricius)

Norway. VE: Tjøme: Kjære a nest (FJAn). HOy: Bergen: Botanical Garden 2 ♀♀ 2☿☿. HOi: Skånevik: Skånevik a nest (DYRn).

Vespula (s.s.) *rufa* (Fabricius)

Norway. Fø: Sør-Varanger: Fiskevann 2 ♀♀, Gjøkvann ♀, Skogfoss ♂ and Ødevann ♀ (NTEn), Ivargammevann ♀ and Svanvoll ♀ (Passvik ekspedisjonen) ZMO.

Vespula (s.s.) *austriaca* (Panzer)

Norway. On: Lesja: Nordmannsetri ♀ (GJNn). VE: Tjøme: Kjære ♀ (FJAn). Ry: Hå: Ogna ♀ (NTEn); Klepp: Øksnevad ♀ (NTEn). HOy: Stord: Storsøy ♀ (Feltkurs); Os: Nordstrøno 2 ♀♀ (GKJn). HOi: Kvinnherad: Staffvann ♀ (Feltkurs). Nsi: Saltdal: Kjemågå ♀ (FJSn). Fø: Sør-Varanger: Fiskevann 2 ♀♀ and Grenseneset ♀ (NTEn), Ivargamme ♀ (Passvik ekspedisjonen) ZMO.

Sweden. Lu.Lpm: Malmberget ♀ (LøAn) and Randijaur 25 km NW Jokkmokk ♀ (LøAn).

Apidae s.s.

Bombus (Alpigenobombus) wurfleini spp. *mastrucatus* Gerstaecker

Norway. Nnø: Ankenes: Katterat 22 km ESE Narvik 375 m a.s.l., July 1972 ☿ visiting *Trifolium repens* L. (B. Svensson in litt.)

Sweden. Lu.Lpm: Malmberget 9 June 1974 ♀ perforating the corolla of *Lathyrus pratensis* L. (LøAn).

Bombus (Kallobombus) soroeensis (Fabricius)

Norway. HEn: Engerdal: Sorken 670 m a.s.l., ☿ (LøAn).

Sweden. Med: Böle 30 km SSW Sundsvall ☿ (RRKn); Stavreviken 25 km N Sundsvall ☿ (LøAn). Ång: Gräsmyr 40 km S Umeå 2 ♀ ♀ ☿ (LøAn); Oreälv 4 ☿☿ (LøAn). Vb: Burträsk 3 ☿☿ (LøAn); Ekorrsele 35 km NW Vindeln 3 ♀♀ 18 ☿☿ (LøAn & RRKn); Hednäs 15 km W Vindeln 3 ☿☿ (LøAn); Hjoggböle ☿ (LøAn); Hällnäs ☿ (RRKn); Ljusvattnet ♀ (LøAn); Sjöbotten ♀ (TLIn); 20 km Skellefteå ☿ (TLIn); Strycksele 2 ♀♀ 11 ☿☿ (LøAn & TLIn); 15 km ENE Vindeln ☿ (LøAn); 13 km ESE Vindeln 2 ♀♀ (TLIn); Åmsele ☿ (LøAn). Ås.Lpm: Häggsjömoen 35 km SE Åsele 3 ☿☿ (LøAn & RRKn); Överissjö 20 km SE Åsele ☿ (RRKn); Tegelträsk 40 km SE Åsele ☿ (RRKn); Ly.Lpm: S. Mårdsele 30 km ESE Lycksele 3 ☿☿ (LøAn). Lu. Lpm: Messaure in trap ♀ (MüKs); Puottaure 75 km WNW Boden ☿ (RRKn); Purmuvaara NE Dokkas ☿ (LøAn).

Bombus (Pyrobombus) cingulatus Wahlberg.

Sweden. Dlr: Floda ☿ (TjTs); Leksand ♀ (TjTs); 35 km WNW Mora ♂ (RRKn); Oreälven 40 km NE Mora ♀ (TjTs); Storsätern 30 km NW Idre ☿ (LøAn). Jmt: SE Föllinge ☿ (RRKn); 15 km W Föllinge ♂ (LøAn); NW Föllinge 2 ☿☿ (LøAn); 30 km NW Föllinge ☿ (RRKn); N Överturinge ♂ (LøAn); 35 km SE Östersund ♂ (RRKn). Vb: Andersfors W Burträsk ☿ (LøAn); Burträsk ☿ (LøAn); Ljusvattnet 3 ♀♀ ☿ 6♂♂ (LøAn & TTIn); Strycksele ♀ (LøAn); 15 km ENE Vindelen ☿ (RRKn); Övre Ekorrsele 20 km SE Lycksele 2 ♂♂ (RRKn). Nb: Haparanda ☿ (TLIn); Huuki 30 km N Pajala ☿ (RRKn); Kassa 20 km SE Pajala 3 ♀♀ 5 ☿☿ (LøAn & TLIn); Kolari 25 km NE Pajala ☿ ♂ (LøAn); W Lakaträsk ☿ (LøAn); Luppio ♀ (TLIn); Luppioberget 15 km SE Övertorneå ☿ (LøAn); N Sundom 22 km N Luleå 2 ♂♂ (LøAn); Trundöen 20 km NE Piteå (LøAn) 2 ♂♂. Ås.Lpm: Ytterissjö 30 km SE Åsele ♂ (RRKn). Ly.Lpm: Arvträsk 17 km E Lycksele 2 ♀♀ 3 ♂♂ (LøAn & TLIn); 30 km W Malå ♂ (RRKn). P.Lpm: SE Abborträsk ♀ (LøAn); W Bjørnheden 30 km SE Arjeplog ☿ (LøAn), Lu.Lpm: 25 km S Messaure 7 ♀♀ 4 ☿☿ ♂ (LøAn & TLIn); Nattavaara ☿ (RRKn); Porjus in trap 10–24 July 1976 ☿ ♂ (MüKs); Vuollerim 2 ♂♂ (LøAn). T.Lpm: 50 km SE Karesuando ♂ (RRKn); W Masungbyn ♂ (LøAn).

Bombus (Pyrobombus) lapponicus (Fabricius)

Sweden. Hjd: Ljungdalen 2 ♂♂ (RRKn). Jmt: Hotagen ☿ (RRKn). Nb: 20 km SW Muonio ♀ (RRKn). P.Lpm: 25 km SSE Arvidsjaur ♂ (RRKn); W Björnheden 20 km SE Arjeplog ♀ (LøAn); E Östansjö 50 km SSE Arjeplog ♀ ☿ (LøAn). Lu.Lpm: Ripats ☿ (TLIn); Vaikijaur 6 km N Jokkmokk ☿ (TLIn); Porjus in traps 1976: 20 June–9 July ☿ 20 August–10 September 1976 ♀ (MüKs). T. Lpm: 65 km SE Karesuando ☿ (RRKn); W Masungbyn ☿ (LøAn); Maunu 15 km NW Karesuando 3 ☿☿ (LøAn); Nikkaluokta 50 km W Kiruna 5 ♀♀ 8 ☿☿ (LøAn & TLIn); Paittasjärvi 25 km ESE Karesuando 3 ♀♀ 3 ☿☿ (LøAn & TLIn); Saivomuotka 40 km SE Karesuando 2 ♂♂ (RRKn).

Bombus (Melanobombus) lapidarius (L.)

Norway, TEi: Kviteseid: Morgedal – Brekke ♀ (GJNn).

Sweden. Dlr: Floda: Mossel 2 ♀♀ ☿ (TjTs); N Mora ☿ (RRKn); NE Älvdalen 3 ☿☿ (RRKn). Hls: Arbrå 2 ☿☿ (LøAn & RRKn); Vallsta 2 ♀♀ (LøAn); Viksjöfors 2 ☿☿ (LøAn & RRKn). Med: Vivsta 12 km N Sundsvall 3 ☿☿ (RRKn). Jmt: 25 km W Strömsund ☿ (RRKn); Skärvågnen 15 km NW Föllinge ☿ (LøAn). Ång: Ava NW Rundviksverken 2 ☿☿ (LøAn); Gräsmyr 40 km SW Umeå ☿ (LøAn); Lögdeå 2 ☿☿ (LøAn & RRKn); Rundviksverken 2 ☿☿ (LøAn & RRKn); Västanbäck 70 km N Sollefteå ☿ (RRKn); W Sidensjö ♀ ☿ (LøAn & RRKn). Vb: Hällnäs ♀ (LøAn); NE Vindeln ☿ (RRKn). Ås.Lpm: Tegelträsk 2 ☿☿ (LøAn). Ly.Lpm: Malå 5 ☿☿ (LøAn & RRKn); Vindelgransele 2 ☿☿ (LøAn & RRKn). T.Lpm: Vittangi 2 ☿☿ (RRKn); Abisko 68° 22′N, July 1974 ☿ (Svensson in litt.).

Bombus (Alpinobombus) hyperboreus Schønherr

Sweden. Jmt: Ulvåtjärn 14 km SE Enafors 3 July 1977 ♀ (ALAs).

Bombus (Megabombus) hortorum (L.)

Sweden. Lu.Lpm: Messaure in trap 17–24 June 1974 ♀ (MüKs); Porjus in trap 31 July–15 August 1976 ☿ (MüKs). T.Lpm: Karesuando 2 ♀♀ (LøAn & RRKn).

Bombus (Thoracobombus) sylvarum (L.)

Sweden. Dlr: Floda: Mossel ♀ (TjTs); Leksand: Sångån ♀ (TjTs). Hls: Ovanåker 2 typical ♀♀ and a melanotic ♀ (LøAn & RRKn); Vallsta 2 typical ☿☿ and a melanotic ☿ (LøAn & RRKn).

Bombus (Subterraneobombus) distinguendus Morawitz

Sweden. Ång: Gräsmyr 40 km SE Umeå 2 ♀♀ (LøAn & RRKn). Vb: Burträsk ☿ (TLIn); Hjoggböle 20 km S Skellefteå ♀ (TLIn); Sjöbotten 18 km SSE Skellefteå 5 ♀♀ ☿ (LøAn & RRKn). Nb: Haparanda ♀ (LøAn); Muodoslompolo ♀ (LøAn); 8 km NNE Pajala 2 ♀♀ (LøAn & RRKn); 25 km S Övertorneå ♀ (LøAn). Lu.Lpm: Malmberget 3 ♀♀ (TLIn). T.Lpm: Karesuando 2 ♀♀ visiting *Caragana arborescens* Lam. (LøAn & TLIn).

Psithyrus (Ashtonipsithyrus) vestalis (Geoffroy in Fourcroy)

Sweden. Sk: Lund 12 August 1973 ♀ (AHNs) ZIL. New to Sweden.

Discussion

Vespidae

Vespula norwegica, the most abundant social wasp in Norway (Løken 1964), is undoubtedly densely distributed throughout the entire mainland of Scandinavia. The fact that Erlandsson (1971) did not list the species for the Swedish provinces mentioned above or for Blekinge, Västmanland, Hälsingland, Medelpad and Härjedalen might be due to lack of voucher specimens in the examined collections. As many of us know, the commonest species may be poorly represented in museum collections.

V. norwegica produces dimorphic infrasubspecific forms, viz. a typical form with laterally red spots on the first and second gastral abdominal tergite more or less pronounced, and a dark form, viz. the 'zetterstedti' form without red spots. The available Swedish material (kept ZMB and ZIL) agrees with a phenotypical study of Norwegian populations (Løken 1964), i.e. the two forms occur throughout Scandinavia. A possible variation in the distribution of the frequency of the forms is not yet studied. A preliminary analysis of nests reveals, however, that the typical and the 'zetterstedti' form can be produced in the same colony. For instance, in the Haugastøl area, 1000 m to 1140 m a.s.l. and situated at the northern edge of the mountainous plateau Hardangervidda, a total of 12 nests were analyzed, of which seven contained specimens of both forms.

The Norwegian records of *V. saxonica* listed above were restricted to southern Norway. They do not change the general picture of the distribution of the species, being confined to the southeastern lowlands and the coast north to Sognefjorden at about 60°N, but emphasize a greater abundance of populations than previously known (Løken 1964, 1965, 1966). The species in Sweden is listed for all provinces except Gotska Sandön (Erlandsson 1971). The records above indicate a wide distribution in Lappland which justifies the suggestion by Løken (1964) that the only two specimens so far observed in northern Norway (in Troms) refer to populations immigrating from Sweden.

The records of *V. adulterina* emphasize a wider distribution of the cuckoo wasp than that of the host *V. saxonica.* The discrepancy was indicated by Løken (1964), suggesting that *V. norwegica* could also be the host of this inquiline. To my knowledge however, a colony of *V. norwegica* has not yet been observed being usurped by *V. adulterina*. In fact in Scandinavia there is no reliable record of any species having its colony invaded by this parasite (Løken, 1964).

The information gained about another inquiline, viz. *V. austriaca,* demonstrates that the species occurs throughout the range of the host *V. rufa* (L.) (Erlandsson 1971, Løken 1964, D. S. Peters 1974a); both these were recently recorded in Sør-Varanger in northernmost Norway.

Apidae s.s.

The worker from Katterat in Ankenes 68°24'N listed above is the northernmost record of *B. wurfleini mastrucatus* (Løken 1973, Fig. 50). Flowers of *Aconitum septentrionale* Koelle with the helmet perforated as typical for *B. wurfleini* (Løken 1949) were observed in Norway by me near 68°N. The plant, an attractive foodplant for this bumble bee, grows north up to Ankenes. *B. wurfleini* may therefore have a fairly continuous distribution north up to this area.

The information gained about *B. soroeensis* accords with the distribution suggested by Løken (1973, Fig. 51). The specimens from Swedish Lappland are of particular interest, indicating a wide and local occurrence of the species in the taiga.

Although the numerous records of *B. cingulatus* do not widen the general picture of this taiga element (Løken 1973, Fig. 60) the great abundance of the species locally occurring in high frequency is surprising. There are no records of nest, and the biology is poorly known.

The arcto-alpine *B. lapponicus* is represented by two subspecies, viz. *B. l. lapponicus* invading Scandinavia from northeast and *B. l. scandinavicus* Friese immigrating from south. The subspecies are distinguished by differences in the colour pattern of the coat. A phenotypical study of the recent material (2 ♀♀ 11 ☿☿ ♂collected Lu.Lpm: Malmberget–Gällivare 1974 and 12 ♀♀ 10 ☿☿ 3 ♂♂ collected in the surroundings of T.Lpm: Karesuando 1974, 1976 in addition to 12 ♀♀ 21 ☿☿ 6 ♂♂ listed above) agrees with the general picture of the distribution of the individual subspecies tentatively indicated by Løken (1973, Fig. 63). Perhaps the intergrading area extends slightly further east in Torne Lappmark. Svensson (1973, 1977) and Svensson & Lundberg (1977) give the two taxa specific rank, claiming a difference in the chemical composition of the male pheromone produced in the mandibular gland and some morphological differences in the males in addition to features not yet published. I hesitate to discuss the ranking of the eastern and the southern immigrant until all the evidence is presented.

The information gained about *B. lapidarius* reveals that the southern species is occurring much further north than previously known (Løken 1973, Fig. 65). It has apparently a wide and local distribution throughout the lowlands of Northern Sweden and is even recorded in Abisko 68°22'N. The species is, however, not yet observed in Norrbotten. Pekkarinen & Teräs (1977) have corrected the northern distribution of *B. lapidarius* in Finland presented by Løken (1973) and claim that the species is not recorded north of Uleåborg. Thus the question remains whether the Scandinavian and the Finnish population are linked north of the Gulf of Bothnia (Løken 1973, p. 200).

The recent records reveal that *B. distinguendus* is ranging further north than shown by Løken (1973, Fig. 91), passing 68°N in Torne Lappmark. According to Pekkarinen & Teräs (1977) the species is not observed north of Uleåborg in Finland. A number of records from localities situated along the Swedish side of the river constituting the border to Finland (Nb: Haparanda, Karungi, Pajala, 8 km NNE Pajala, Muodoslompolo. T.Lpm.: Karesuando 68°25') would, however, indicate that the Scandinavian population is linked to the Finnish population north of the Gulf of Bothnia.

The female of *Psithyrus vestalis* collected in Skåne was traced during revision of *Psithyrus* collections kept in Lund. The species is new to Sweden as records hitherto published as *P. vestalis* apply to *P. bohemicus* (Seidl) (Ander 1965). Revision of collections reveals the same confusion of the two taxa in the neighbour countries, i.e. *P.vestalis* is not observed in Norway and Denmark. The nearest occurrence is Mecklenburg in Germany where the cuckoo bumble bee is reaching north to Rügen (G. Peters 1967). The host *B. terrestris* (L.) is widely distributed in Denmark and southern Scandinavia (Løken 1973, Fig. 57) and thus ranges further north than the inquiline. The host does not occur in Finland, consequently neither does the inquiline. The specimen above is the first reliable record of *P. vestalis* in northern Europe.

Acknowledgments.– My sincere thanks go to Inger Meidell Tambs-Lyche and Ragnhild Rosendahl Knudsen for assisting me in the tedious fieldwork in 1974 and 1976, respectively. Lars A. L. Andersson and Bo G. Svensson have kindly allowed me to include a few unpublished records. The fieldwork in 1976 was supported by A/S Norsk Varekrigsforsikrings Fond.

References

Ander, K. 1965. Über die Verbreitung der Hummeln in Schweden (Hym., Apidae). *Opusc.ent. 30,* 135–139.

Erlandsson, S. 1971. Catalogus Insectorum Sueciae XIX. Hymenoptera: Aculeata. *Ent. Tidskr. 92,* 87–94.

Gaunitz, D. 1929. Gadd- och guldsteklar från Sorsele, Lycksele lappmark. *Ent. Tidskr. 50, 196–202.*

Løken, A. 1949. Bumble bees in relation to *Aconitum septentrionale* in Central Norway (Øyer). *Nytt Mag. Naturv. 87,* 1–60.

Løken, A. 1964. Social wasps in Norway (Hymenoptera, Vespidae). *Norsk ent. Tidsskr. 12,* 195–218.

Løken, A. 1965. A nest of *Vespula saxonica* (Fabr.) (Hym., Vespidae). *Norsk ent. Tidsskr. 13,* 36–40.

Løken, A. 1966. Ekskursjonsberetning. Insekter og arachnoider samlet under det 13. Nordiske Entomologmøtets ekskursjon til Flåm (SFi: Aurland 13–16 august 1965. *Norsk ent. Tidsskr. 13,*371–386.

Løken, A. 1973. Studies on Scandinavian bumble bees (Hymenoptera, Apidae). *Norsk ent. Tidsskr. 20,* 1–218.

Pekkarinen, A. & Teräs, I. 1977. Suomen kimalaisista ja loiskimalaisista. *Luonnon Tutkija 81,* 1–24.

Peters, D. S. 1974a. Getingar (Vespoidae) i Messaureområdet. *Norrbottens Natur 30, 75.*

Peters, D. S. 1974b. Humlor (Hymenoptera: Apoidea) i Messaureområdet. *Norrbottens Natur 30,* 76.

Peters, G. 1967. Ein Frühsommeraspekt der Hummelfauna von Mönchgut auf Rügen (Hymenoptera: Bombus et Psithyrus). *Dtsch. Ent. Z., N. F. 14,* 125–137.

Svensson, B. G. 1973. Morphological studies on the two Scandinavian subspecies of *Bombus lapponicus* Fabricius (Hym. Apidae). *Ent. Tidskr. 94,*140–147.

Svensson, B. G. 1974. Bin (Hymenoptera, Apoidea) fångade i fällor vid Messaure ekologiska station, Lule lappmark, med anmärkning om humlornas fenologi. *Ent. Tidskr. 95,* 122–125.

Svensson, B. G. 1977. Pheromones in male bumble bees – a taxonomical tool, exemplified by *Pyrobombus lapponicus* Fabr. (Hym., Apidae). *Proc. 8th Int. Congr.I.U.S.S.I.,*p 317.

Svensson, B. G. & Hans Lundberg, 1977. Distribution of bumble bee nests in subalpine/alpine area in relation to altitude and habitat (Hymenoptera, Apidae). *Zoon 5,* 63–72.

Received 10 March 1978

Spatial attack pattern of the bark beetle *Tomicus piniperda* L. (Col., Scolytidae)

ARNE C. NILSSEN

Nilssen, A. C. 1978. Spatial attact pattern of the bark beetle *Tomicus piniperda* L. (Col., Scolytidae). *Norw. J. Ent.* Vol. 25, pp. 171–175. Oslo. ISSN 0029-1897.

The spatial attack pattern of *Tomicus* (=*Blastophagus*) *piniperda* L. on a standing pine stump was investigated by means of R, the distance to the nearest neighbour. The stump was marked horizontally into eight sections, and in seven of the eight sections the departure from randomness in the direction of uniformity was significant or highly significant. Three possible mechanisms responsible for such a uniform attact pattern are discussed; bark structure, short-range repellent pheromones, and sonic interactions. To the author sonic interactions seem most probable.

Nilssen, A. C., Institute of biology and geology, University of Tromsö, N-9001 TROMSÖ, Norway.

Sex attraction and aggregation pheromones are now, with a few possible exceptions, known to occur throughout the family Scolytidae (Borden et al. 1975). If these pheromones are attractive at high concentrations and work effectively even at short distances, aggregations within small areas may be expected.

Recently it has been discovered, however, that repellent mechanisms start functioning when the host selecting individuals come too close together in the bark. Thus *Dendroctonus pseudotsugae* has short-range anti-aggregative pheromone resulting in a masking of the aggregative pheromones (Rudinsky 1969, Rudinsky et al. 1973). Some pheromones may also be multifunctional, that is, the behavioural effect depends upon their concentration (Rudinsky 1973).

Further, a great number of bark beetle species are shown to have stridulation organs (Barr 1969, Schönherr 1970). Studies of American species of the genera *Ips* and *Dendroctonus* demonstrate that different species and sexes produce by means of these organs specific signals associated with stress, rivalry, and attraction (Rudinsky et al. 1976 and included references).

With this advanced system of attractant and repellent mechanisms, it seems that the gallery-establishing sex of certain bark beetles species attack the bark surface with a more regular spatial pattern than could be expected without such intraspecific territorial behaviour. For the present, a uniform attack pattern has been demonstrated for *Dendroctonus ponderosae* (Shepherd 1965), *Scolytus ventralis* (Berryman 1968), and *D. pseudotsugae* (Hedden & Gara 1976). The latter authors present a hypothesis involving bark distribution, sonic interaction, and short-range repellent pheromones controlling the attack spacing.

According to Perttunen et al. (1970), the orientation of *Tomicus* (=*Blastophagus*) *piniperda* L. to its host tree occurs in response to constituents of the phloem tissue. The authors could not prove for certain the existence of secondary attraction pheromones for this species. However, later Schönherr (1972) and Francke & Heeman (1976) have made the existence of such pheromones seem likely.

It has been known for a long time that *T. piniperda* has stridulatory organs and is sound producing (Barr 1969, Schönherr 1970). It is likely that the acoustic signals of this species serve the same function as those of the *Ips* spp. and *Dendroctonus* spp. where the phenomenon has been intensively studied; namely to operate attractantly or repellently on other individuals depending upon the quality of the sounds and the situation.

Thus, as *T. piniperda* possibly has a system of both attractant and repellent mechanisms, it becomes an interesting question whether the females attack the bark surface with a regular (uniform) pattern. The intention of the present study is to establish whether this is the case, and if so, to elucidate the causal relationships.

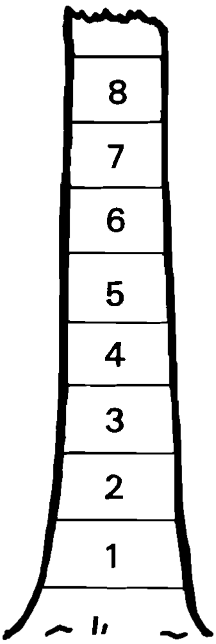


Fig. 1. The investigated pine stump was marked into eight sections, each of 20 cm height.

Table I. Results of the statistical analysis of the attack pattern of Tomicus piniperda in the eight sections of the stump. The symbols are the same as those used in Clark & Evans (1954).

Section	N	Galleries/m^2	$\bar{r}_A$	R	C	P
8 (top)	34	211	5.10	1.48	5.33	<0.001
7	39	239	4.53	1.43	5.06	<0.001
6	36	218	3.85	1.16	1.79	n.s.
5	33	198	4.35	1.21	2.18	<0.05
4	42	249	4.18	1.31	3.87	<0.001
3	46	269	4.17	1.37	4.84	<0.001
2	51	288	3.60	1.25	3.36	<0.001
1 (base)	63	335	3.30	1.24	3.52	<0.001

N: Number of attacks in each section.

$\bar{r}_A$: The mean of the distances (cm) to nearest neighbour attack.

R: The measure of the degree to which the observed distribution departs from random expectation with respect to the distances to nearest neighbour.

C: The standard variate of the normal curve.

P: Probability level.

Material and methods

A standing tree stump of about 1.8 m height, heavily attacked by *T. piniperda,* was investigated. The origin of the stump was a Scots pine (*Pinus silvestris* L.), wind-thrown by a storm during the winter 1974–75. The stump was situated at the edge of a wood and was exposed to the sun mainly from E and S. The stump had no branches, and no other phytophagous bark insects than *T. piniperda* could be found.

The main investigation was undertaken in June 1975 at Forsheim Research Station in Skjomen, Nordland county in northern Norway (68°18′N, 17°18′E). The investigation was repeated in 1977.

All the bark of the stump was peeled, and the stump was marked horizontally into eight sections, each of 20 cm height (Fig. 1).

The whole system of attack holes and galleries was accurately mapped on a large sheet of transparent plastic. Thus the area of each section and the distance to the nearest neighbour of each entrance hole could be measured in the laboratory. The method of distance to nearest neighbour (Clark & Evans 1954) was used in the statistical treatment of the material.

Results

All the attacking females had begun the construction of the egg galleries, and most galleries were 7–12 cm long. This indicates that the females had almost finished the egg-laying (Eidmann & Nuorteva 1968). Among a total number of 344 galleries only two turned downwards; the remainder all turned more or less perfectly upwards the stump.

The results of the measurements and the statistical treatment of the figures are shown in Table I.

In all the sections the value of R was above 1.0, that is the value of perfect randomness. In seven of the eight sections the departure from randomness in the direction of uniformity was significant or highly significant. The position of the attack holes in four of the sections is shown in Fig. 2. In 1977 comparable studies resulted in R-values as high as 1.42 at at much lower attack density ($\bar{r}_A = 8.83$).

Table I indicates that the number of attack holes per section decreases with the height. However, at the same time the area of each section also decreases, and because of this, the figures of each section were recalculated to

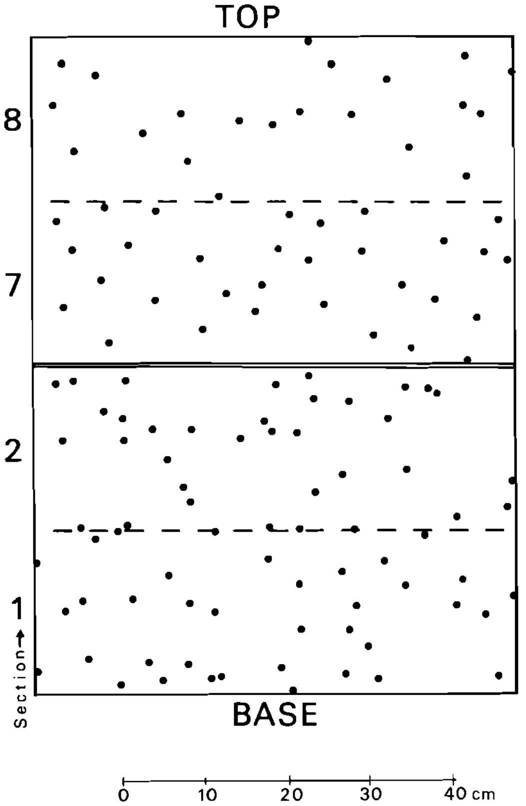


Fig. 2. The distribution of the attack holes by *Tomicus piniperda* in the two uppermost and the two lowest sections of the stump. The area mapped here does not cover the whole circumference of the stump.

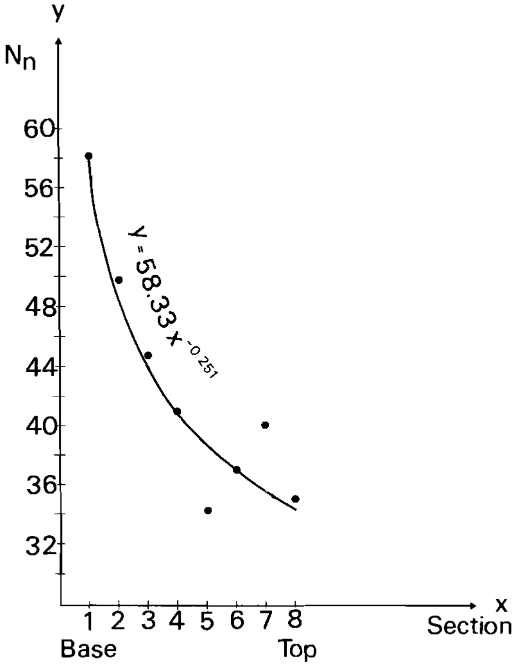


Fig. 3. The relation between the attack density and the height above the base. N_n = number of attacks in each section, recalculated to represent a standard area. The curvilinear (logarithmic) regression analysis (the line drawn in the figure) gave $r = -0.93$ ($p < 0.001$), whereas a linear regression analysis gave $r = -0.87$ ($p < 0.01$). Thus the values fit the curved line better than a straight one.

represent a standard area (the mean area of all eight sections). These recalculated figures are shown as a function of the height in Fig. 3. The negative correlation between the number of holes and the height is highly significant ($p < 0.001$). That the density of holes decreases with the height implies that the mean distance between the holes increases, which is also indicated by the values of $\bar{r}_A$ in Table I.

Discussion

The advantages of a uniform attack pattern and consequently an even distribution of galleries seem obvious. Such spacing secures maximal utilization of the available resources and minimizes intraspecific competition at the same time. Intraspecific competition in *T. piniperda* has been studied in more detail by Eidmann & Nourteva (1968) and Beaver (1974).

Both exposure to the sun and the bark structure and thickness influence the spatial attack pattern of bark beetles. Shepherd (1965) and Safranyik & Vithayasai (1971) hypothesized that a regular distribution of crevices controlled the attack pattern of *Dendroctonus ponderosae*.

In the present study the distribution of the crevices seems unlikely to be responsible for the regular attack pattern of *T. piniperda*.

Most of the crevices present in the investigated stump were on the lowest part and typically had the shape of longitudinal furrows. If the furrows represent favourable attack points, this should rather give a spatial concentration of attacks and a trend towards contagious distribution.

The bark surface gradually became more even and smooth higher up, and a less aggregated (more uniform) distribution might be expected. This does appear as a slight tendency in the present data. Thus the attack pattern of *T.*

piniperda seems to be more regular in the two uppermost sections than in the two sections at the base (Fig. 2), which is reflected in the higher value of R in the two uppermost parts of the stump (Table I).

Although the crevices probably contribute to aggregation of attacks rather than to a regular distribution, a statistically significant departure from randomness in the direction of regularity was found in seven of the eight sections. In the two uppermost sections especially, this regularity was more perfect than that found for *D. pseudotsugae* (Hedden & Gara 1976).

As stated in the introduction, two other mechanisms may be responsible for a uniform attack pattern among bark beetles, namely sonic interactions and short-range repellent pheromones. It is unknown whether *T. piniperda* produce anti-aggregative pheromones. In all situations, however, such pheromones alone are unlikely to be responsible for the high regularity of the attack spacing. Pheromones are probably effective only over the surface of the bark and may be influenced by wind, temperature, and humidity.

Sonic interactions are in all probability a much better communication system to create such an attack pattern, especially in areas of high attack density (see also Hedden & Gara 1976). Thus Rudinsky & Michael (1973) argue that the only rapid and exact communication likely from insects inside the bark to those outside it is sonic, and found further that the observed distances at which phonoresponse was evoked correspond to the typical density of attack by the investigated *Dendroctonus* spp.

T. piniperda is monogamous, and the gallery-establishing females have not yet been found to stridulate (Barr 1969, Schönherr 1970). If this is the case, the males have the task of defending the area around the entrance hole provided that stridulation sounds are involved.

In any case, a thorough study of possible sound production of the females is called for. Stridulation was not previously recognized in that sex which establishes the gallery (Barr 1969, Schönherr 1970), but Rudinsky & Michael (1973) reported the production of sound by the gallery-establishing sex, the female of four *Dendroctonus* species, and suggested that sonic communication is a spacing mechanism during host invasion. Later on, Oester & Rudinsky (1975) recorded stridulation from the host-selecting males in three *Ips* species.

The present investigation shows in addition that the mean distance to closest neighbouring attack increases with increasing height up the stump. The explanation of this is not evident, but one possibility is outlined here. The structure and the thickness of the bark change up the stump, and it is not unlikely that this difference in the bark quality can bring about a difference in sound transmission through the bark and thereby cause a change in the critical distance to the nearest neighbour. It is also possible, however, that the higher density near the base reflects only that *T. piniperda* prefers a more rough and corky bark surface for its attacks.

Many species of Scolytidae are sound producing (Barr 1969, Schönherr 1970). It would thus be worth-while to study the spatial attack pattern of further species of bark beetles, and especially to compare the attack distributions of stridulating with those of non-stridulating species, and to study the influence of population level.

Acknowledgements. – I wish to thank cand. real. Johan Andersen and cand. real. Per Grotnæs for help with the statistical treatment, and students Inger Marie Fremming and Yngve Eilertsen for assistance during field work.

References

Barr, B. A. 1969. Sound production in Scolytidae (Coleoptera) with emphasis on the genus *Ips*. *Can. Ent. 101,* 636–672.

Beaver, R. A. 1974. Intraspecific competition among bark beetle larvae (Coleoptera: Scolytidae). *J. Anim. Ecol. 43,* 455–467.

Berryman, A. A. 1968. Distribution of *Scolytus ventralis* attacks, emergence, and parasites in Grand fir. *Can. Ent. 100,* 57–68.

Borden, J. H., VanderSar, T. J. & Stokkink, E. 1975. *Secondary attraction in the Scolytidae.* An annotated bibliography. Pest Management Paper No. 4. Simon Fraser University, Canada.

Clark, P. J. & Evans, F. C. 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. *Ecology 35,* 445–53.

Eidmann, H. H. & Nuorteva, M. 1968. Der Einfluss der Siedlungsdichte und anderer Faktoren auf die Anzahl der Nachkommen von *Blastophagus piniperda* L. (Col., Scolytidae). *Ann. ent. fenn. 34,* 135–148.

Francke, W. & Heemann, V. 1976. Das Duftstoff-Bouquet des Grossen Waldgärtners *Blastophagus piniperda* L. (Coleoptera: Scolytidae). *Z. ang. Ent. 82,* 117–119.

Hedden, R. L. & Gara, R. I. 1976. Spatial attack pattern of a Western Washington Douglas-fir beetle population. *Forest Sci. 22,* 100–102.

Oester, P. T. & Rudinsky, J. A. 1975. Sound production in Scolytidae: Stridulation by 'silent' *Ips* bark beetles. *Z. ang. Ent. 79,* 421–427.

Perttunen, V., Oksanen, H. & Kangas, E. 1970. Aspects of the external and internal factors affecting the olfactory orientation of *Blastophagus piniperda* (Coleoptera: Scolytidae). *Contrib. Boyce Thompson Inst. 24,* 293–297.

Rudinsky, J. A. 1969. Masking of the aggregation pheromone in *Dendroctonus pseudotsugae* Hopk. *Science 166,* 884–885.

Rudinsky, J. A. 1973. Multiple functions of the Southern pine beetle pheromone Verbenone. *Environ. Entomol. 2,* 511–514.

Rudinsky, J. A. & Michael, R. R. 1973. Sound production in Scolytidae: Stridulation by female *Dendroctonus* beetles. *J. Insect Physiol. 19,* 689–705.

Rudinsky, J. A., Morgan, M., Libbey, L. M. & Michael, R. R. 1973. Sound production in Scolytidae: 3-Methyl-2-cyclohexen-1-one released by the female Douglas fir beetle in response to male sonic signal. *Environ. Entomol. 2,* 505–509.

Rudinsky, J. A., Ryker, L. C., Michael, R. R., Libbey, L. M. & Morgan, M. E. 1976. Sound production in Scolytidae: Female sonic stimulus of male pheromone release in two *Dendroctonus* beetles. *J. Insect Physiol. 22,* 1675–81.

Safranyik, L. & Vithayasai, C. 1971. Some characteristics of the spatial arrangement of attacks by the Mountain pine beetle, *Dendroctonus ponderosae* (Coleoptera: Scolytidae), on Lodgepole pine. *Can. Ent. 103,* 1607–1625.

Schönherr, J. 1970. Stridulation einheimischer Borkenkäfer.*Z. ang. Ent. 65,* 309–312.

Schönherr, J. 1972. Pheromon beim Kiefern-Borkenkäfer "Waldgärtner", *Myelophilus piniperda* L. (Coleopt., Scolytidae) *Z. ang. Ent. 71,* 410–413.

Shepherd, R. F. 1965. Distribution of attacks by *Dendroctonus ponderosae* Hopk. on *Pinus contorta* Dougl. var. *latifolia* Engelm. *Can. Ent. 97,* 207–215.

Received 2 March 1978

The biology and life history of *Araneus cucurbitinus* Clerck (Araneae, Argiopidae) in south-eastern Norway

PER BAKKEN

Bakken, Per. 1978. The biology and life history of *Araneus cucurbitinus* Clerck (Araneae, Argiopidae) in south-eastern Norway. *Norw. J. Ent.* Vol. 25, pp. 177–182. Oslo. ISSN 0029-1897.

The biology of *A. cucurbitinus* was studied both in the field and the laboratory. In the field, females produced 5–6 egg cocoons from mid-July to mid-September. The number of eggs per cocoon and the hatching percent are described. The developmental time for the eggs varied with the temperature, from about 27 days at 15°C to about 10 days at 25°C. The spider had 7 juvenile instars and became adult at the eighth. A linear relationship exists between the logarithm of the carapace width and the instars, with a regression coefficient of 0.99. Most of the population had an annual life cycle, but a varying minor part was found to be biennial.

Per Bakken, Zoological Institute, University of Oslo, Norway.
Present address: *Statens forurensingstilsyn, Postboks 8100 Dep., Oslo 1, Norway.*

Araneus cucurbitinus Clerck (Araneae, Argiopidae) is a common European spider, which is numerous in most parts of its range. Few detailed studies have been done on this species, and except for the short descriptions in systematical works and a study of the mating (Blanke 1973), very little of its biology is known. For this reason the present investigation was carried out to describe the life cycle and some aspects of the biology of the species in south-eastern Norway.

Study area

The field studies were carried out in an apple orchard in Sem, Asker, south-eastern Norway. The study area used for examination of changes in population density and size distribution during the growth season, was 8 × 42 m, containing a total of 64 trees in three rows. The dominating apple sorts were Torstein and Red Torstein.

Spiders for laboratory studies were collected in another area nearby. This area, which was ca. 65 × 55 m, was dominated by the apple sorts Ingrid Marie and Gravenstein.

Material and methods

Some of the specimens used in the laboratory studies were collected in the field while others came from laboratory cultures.

Laboratory cultures were started by putting 1–3 well-fed adult females in a cage, 21.5 × 30.0 × 26.5 cm, with fine-meshed netting on the top and two of the sides. The females were given 24 hours to settle and spin the web before twice as many males as females were put into the cage. Courtship and mating were usually observed shortly afterwards. The males were kept in the cage until they died, after they had mated several times with the same or different females. The spiders had a constant supply of fruitflies from *Drosophila* cultures within the cage. This was found important to prevent the females from killing and eating the males. The cages were kept at a constant temperature of 21°C, 70% R. H., and 16 hours photoperiod. A total of 21 females were used for culture purposes. For 10 of the females, the time from mating to the production of their first egg cocoon was noted, likewise the time between the production of the following cocoons.

The egg masses were removed from the cage the same day they were produced, put separately in small petri dishes, and kept at constant temperatures of either 16°, 21° or 26°C, 70% R. H., and 16 hours photoperiod. The time from when the eggs were deposited until the first specimen hatched was noted as the hatching time.

To find the number of eggs per cocoon, 25 cocoons were opened and the number of eggs were counted. These cocoons were randomly selected regardless of whether they were from an early or late production.

Table I. Time in days between each cocoon production. M = Mating, N = Number of females observed.

	Average	Range	N
M - 1. cocoon	8.6	3 - 15	10
1. - 2. cocoon	8.8	4 - 12	10
2. - 3. cocoon	9.7	7 - 12	10
3. - 4. cocoon	10.4	5 - 18	9
4. - 5. cocoon	7.4	5 - 9	4
5. - 6. cocoon	9.7	9 - 11	3

During the first two instars no specimen was removed from the petri dishes where the cocoon had been placed. After the first moult the spiderlings were offered small, live nematocera and Aleyrodina every other day. As soon as the spiderlings had reached the third instar, they were separated to prevent cannibalism and put into individual glass tubes, 10 × 1.5 cm. From now on they were offered *Drosophila melanogaster* once or twice a week.

The width of carapace was used as an indicator of the instar (Hagstrum 1971). The carapace width of living, unanaesthetized spiders was measured to the nearest 0.03 mm, not later than two days after a moult.

The variation in population density during the season was found by counting every specimen on 12 of the 64 trees. During 1975, 17 counts were made from May to October, and in 1976 15 counts from April to September. The trees on which the spiders were counted were the same each time and in both years. The searching time on each tree was 15 to 30 minutes, shortest time during the spring and longest during the summer to compensate for the increase of the surface due to growth and foliage.

The size distribution within the population was found by regular half-monthly, random collections during April, May, June, July, and September 1976. The specimens were brought alive to the laboratory. Measurements of the carapace gave an indication of the instar of each specimen.

The sex ratio is based on the collection of 77 specimens, found in the field from mid May to end of June, i.e. the time before adult males died. The specimens were either collected as adults or the sex was noted after the final moult in the laboratory.

Results

Egg production

In the field, the females produced eggs over a long period of time. The first egg cocoon was observed in the field on 13 July 1976, and as late as 29 September the same year an adult female was observed with four unhatched cocoons. The female normally remained at the same place where she produced her first cocoon. It was therefore possible to find out how many broods she produced. Under field conditions no female was observed with more than five cocoons. Some of these cocoons contained newly produced eggs while others contained spiderlings in the second instar. The laboratory results gave an average of 4.8 egg cocoons per female with an individual variation from three to six. The time from mating to the construction of the first cocoon, and the time between the following productions, are given in Table I.

The number of eggs per cocoon varied from 30 to 159, with a median value of 52. One female produced a total of 488 eggs in five masses. The first three of these contained considerably more eggs than the last two.

The developmental time for the eggs at the three temperatures used in the laboratory study is given in Fig. 1. The differences found are significant at 0.05-level (Students t-test).

Six of the 11 egg cocoons used to find the hatching percent had 100% hatching, while the lowest percent was 42.3. The average was 89.9.

Instars

The laboratory studies showed that both males and females normally had 7 juvenile instars and became mature in the 8th. There was, however, an individual variation in the number of instars from 6 to 9.

The first instar spiderling, the deutova, is morphologically different from the following instars. The cephalothorax and the legs are yellow-white and transparent, the abdomen is brown, and the whole body is naked. The mouth parts and the spinnerets are rudimentary and non-functional. In this instar the spiderling usually stays within the cocoon. After the first moult, great morphological changes take place. Although the size of the carapace is only slightly larger than the previous instar, the spiderling now becomes a true spider with hair, spines,

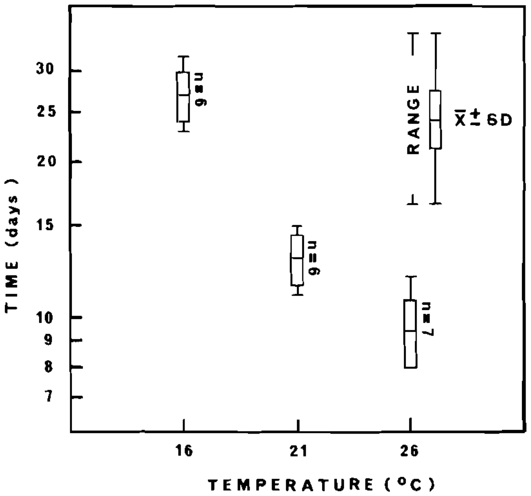


Fig. 1. The developmental time for eggs from *A. cucurbitinus* at three temperatures.

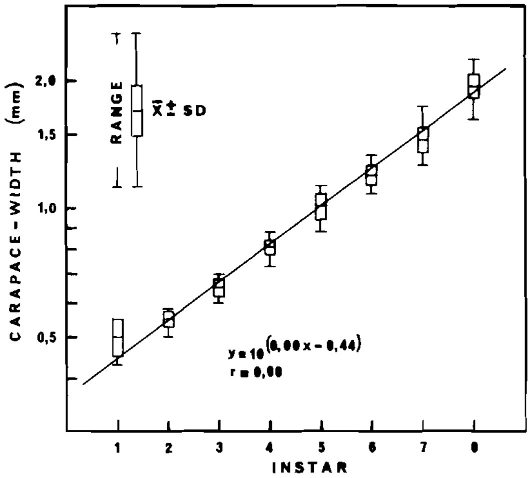


Fig. 2. The growth of carapace width from first instar spiderlings to adults.

claws and with the ability to feed and spin. The abdomen has got the characteristic green colour, and the cephalothorax and the legs are light brown and no longer transparent. It was not possible to distinguish the sex by morphological characters as long as the spiders were juvenile. However, males in the last juvenile instar, the subadult males, could be separated from the rest by their swollen palps.

The increase in carapace width from instar to instar is shown in Fig. 2. The carapace width for the first six instars was measured on laboratory specimens. Since most of them would not develop further without a period of low temperature, the carapace width for subadults and adults was measured on specimens taken from the field which completed their development under laboratory conditions. Since there were no significant differences in the carapace width in adult males and females, they are treated as a unit. There was only minor overlapping in the carapace widths from one instar to the next, and the differences were all significant on 0.05-level (Students t-test).

A linear relationship was found between the logarithm of the carapace width (Y) and the instar (X), as shown by the regression coefficient r = 0.99 (Fig. 2).

A comparison between the carapace width of laboratory specimens in the third, fourth, fifth, and sixth instars and specimens collected in the field in the same instars is given in Table II. There were no significant differences in the third and the fourth instars, but at the last two instars the laboratory specimens were significantly larger at 0.05-level (Students t-test).

The results from the study of the sex ratio revealed that 38 specimens, or near 50% of the adults, were males, indicating a sex ratio near 1.

Population density and size distribution

The population density during the growth season showed two distinct peaks in 1975, one in the spring and one in the autumn (Fig. 3). The results in 1976 were somewhat different in that the spring peak that year was divided. The autumn peak was, however, similar to that of the previous year, and in both years this peak was the larger.

As shown by the size distribution during 1976 (Fig. 4), the spring peak consisted of specimens from the second to the subadult instar, while the

Table II. The carapace width in mm ± SD, of Araneus cucurbitinus, measured on specimens collected in the field and on specimens from the laboratory culture. N = Number of specimens measured.

	Field specimens	N	Lab.specimens	N
3.Instar	0.65 ± 0.02	18	0.65 ± 0.03	44
4.Instar	0.82 ± 0.05	29	0.81 ± 0.03	39
5.Instar	0.95 ± 0.09	17	1.01 ± 0.07	37
6.Instar	1.15 ± 0.07	38	1.20 ± 0.07	25

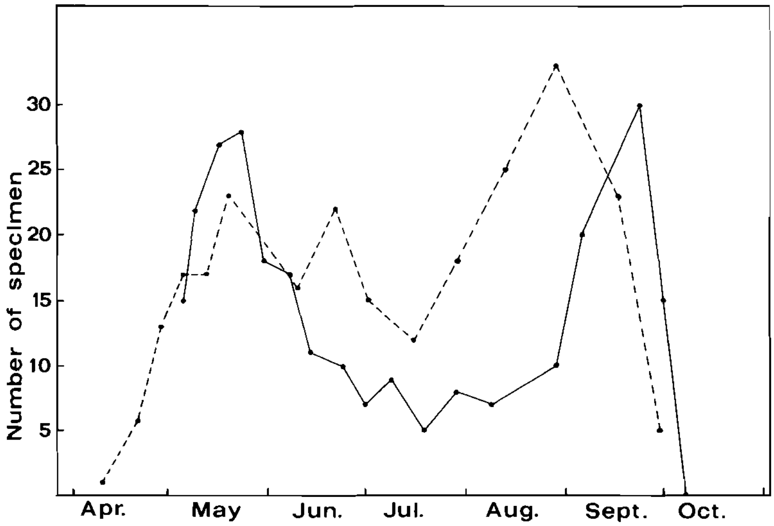


Fig. 3. Variation in *A. cucurbitinus* population during the season. Total number of specimens on 12 trees.
1975, -----
1976 ——

autumn peak contained specimens from the second to the sixth instar in addition to a few adult females. From July and for the rest of the season, no subadults were found in the field, and subadults and adults were not found just after the winter period, i.e. April.

Adult males were found in the field over a relatively short period, from 27 May to 8 July 1975, and from 25 May to 6 July in 1976. Adult females lived much longer and were found from 7 June to 23 September 1975 and from 1 June to 29 September 1976.

Life history

By using both the field and the laboratory results it is now possible to picture the life history of *A. cucurbitinus*. Adults of both sexes are present in the field over a period of about five weeks. The mating, which is described by Blanke (1973), normally takes place in June, and the males die shortly afterwards.

The females produce their first egg cocoon in the middle of July. This is somewhat later than expected in view of the laboratory results (Table I). The reason for this delay is probably due to the less favourable temperature in the field than in the laboratory. Kessler (1971) states that the temperature during the egg ripening period is important: the cooler the weather, the longer the egg ripening period.

Both field and laboratory results showed that a female can produce 5–6 cocoons. This is somewhat more than found by Blanke (1973). In view of the laboratory results (Table I) it was expected that the last egg masses would be produced from the middle to the end of September, in agreement with field observations, since the field conditions were not as favourable as in the laboratory.

Since the autumn peak of the population density curve was dominated by newly hatched spiderlings, the time of the peak gives information as to when most of the hatching takes place. The difference in the time of the peak in 1975 and 1976 is probably due to the warmer summer up to August in 1976. As shown in Fig. 1, the development time for the eggs is highly dependent on the temperature. An increase in the temperature by only five degrees, from 16° to 21°C, reduced developmental time to the half.

Late in September, which is the time just before overwintering, the population contains specimens in all but one instar (Fig. 4), deutova, and unhatched eggs.

The population density of *A. cucurbitinus* decreases in October (Fig. 3). This indicates that the spider either stays in lower vegetation near the ground during the winter or migrates out of the area to more suitable overwintering places. Hågvar & Hågvar (1975) have found the spider on branches of spruce in November, January, February, and March.

From the size distribution just before (September) and just after (April/May) the winter period, it seems likely that the spider can survive this period in all instars from the second to the sixth. Whether the eggs could stand a period exposed to low temperatures was not considered, but no egg cocoons were found in the field during early spring.

Most of the specimens will be adults in the early summer of the following year, which means that these have an annual life cycle. There are, however, indications that part of the population is biennial. From the end of July and the rest of the season there are representatives of three generations in the field: adult females, their offspring, and a third group of half-grown specimens from fourth to sixth instars which must have already lived through one winter period (Fig. 4).

Discussion

The total number of instars is larger than expected. Bonnet (1930) states a normal number of 5–6 instars for a spider the size of *A. cucurbitinus*, although he has made reservations to this general rule. The feeding conditions are important. If they are poor this will result in a slower speed of growth and an increased number of instars. As shown in Table II, the field conditions must be worse than those in the laboratory. The time needed to reach the adult stage will also affect the size and thereby the number of instars.

Juberthie (1954) states that *Araneus cucurbitinus* has an annual life cycle. The size distribution during the season (Fig. 4) is, however, similar to that of *Araniella displicata* (=*Araneus displicata*) in Nova Scotia (Dondale 1961), a species closely related to *Araneus cucurbitinus* (Wiehle 1931). Dondale drew the conclusion that *A. displicata* was biennial in Nova Scotia. Peck & Whitcomb (1970) have criticized Dondale's conclusion on the grounds that he overlooked the possibility of successive broods within a single year. This seems to hold true for *A. cucurbitinus* in southern Norway; most of the population have an annual cycle but a varying minor part is biennial.

The combination of at least two factors is of importance for this result. First, the spider has a relatively large number of instars which means a large total developmental time even under optimal conditions. Second, there is a long time interval between the first and the last brood. This leads to a relatively short growth season for specimens from a late brood the first year compared to those from an early one. Laboratory studies (Bakken, in prep.) also indicate that if a specimen reaches the fourth or higher instar before winter, i.e. the eggs hatch in July/August, it will be adult the following summer. On the other hand, specimens from a late brood will only reach the second or the third instar before the first winter period and they will not complete development during the following spring and summer. The laboratory studies also indicate that these specimens must have another period of chilling before they can be adults. Specimens from a late brood will, due to this, not become adults in June of the following year and must overwinter a second time. In 1976 about 18% of the total field sample from April, May, and June

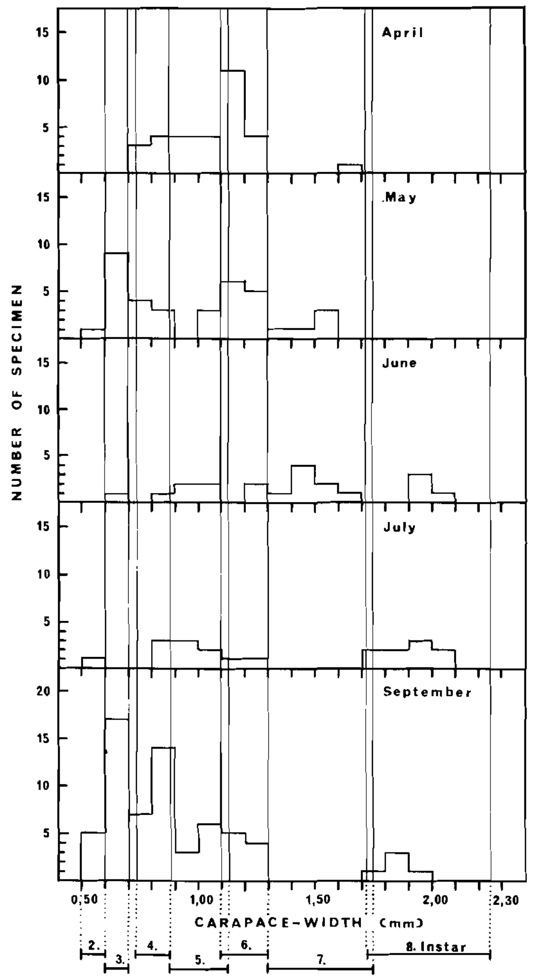


Fig. 4. Size distribution within the *A. cucurbitinus* population during the growth season 1976.

contained specimens in second or third instar, that is, specimens with a biennial life cycle.

The present results do not affect the statement of Juberthie (1954) about an annual life cycle in France. It is probable that the life cycle in southern Norway, as described above, must be looked upon as a result of the northern climate. A similar phenomen is reported for *Dolomedes fimbratus,* which is annual in northern Italy, partly annual in France, and biennial in northern Europe (Bonnet 1930, Palmgren 1939). *Araneus diadematus* has also been reported annual in France (Bonnet 1930) and biennial in Germany and Denmark (Wiehle 1931, Nielsen 1928).

There is a lack of information about the life cycle for spiders with a wide geographical distribution, but developmental delays as a result of cooler climate and shorter growth season are well known for many insect species.

Acknowledgements – I would like to thank Dr. Lauritz Sømme for valuable advice and critical reading of the manuscript, and Mrs. Roushan Birkeland for improving the English.

References

Blanke, R. 1973. Neue Ergebnisse zum Sexualverhalten von *Araneus cucurbitinus* Cl. (Araneae, Araneidae). *Forma et functio, 6,* 279–290.

Bonnet, P. 1930. La mue, l'automie et la régénération chez les araignées avec une étude des Dolomédes d'Europe. *Bull. Soc. Hist. nat. Toulouse, 159,* 237–700.

Bonnet, P. 1938. La proportion sexuelle chez les araignées. *Bull. Soc. Hist. nat. Toulouse, 72,* 241–256.

Dondale, C.D. 1961. Life histories of some common spiders from trees and shrubs in Nova Scotia. *Can. J. Zool. 39,* 777–787.

Hagstrum, D.V. 1971. Carapace width as a tool for evaluating the rate of development of spiders in the laboratory and the field. *Ann. ent. Soc. Am. 64,* 757–760.

Hågvar, E.B., Hågvar, S. 1975. Studies on the invertebrate fauna on branches of spruce (*Picea abies*) (L.) during winter. *Norw. J. Ent. 22,* 23–30.

Juberthie, C. 1954. Sur les cycles biologiques des araignées. *Bul. Sos. Hist. nat. Toulouse. 39,* 299–318.

Kessler, A. 1971. Relation between egg production and food consumption in species of the genus *Paradosa* (Lycosidae, Araneae) under experimental conditions of food-abundance and food-shortage. *Oecologia 8,* 93–109.

Nielsen, E. 1928. *De danske edderkoppers biologi.* Levin & Munkegaards. Köbenhavn. 723 pp + 5 plansjer.

Palmgren, P. 1939. Ökologische und physiologische Untersuchungen über die Spinne *Dolomedes fimbriatus* (Cl.). *Acta Zool. fenn. 24* 1–42.

Peck, W.B., Whitcomb, W.H. 1970. Studies on the biology of a spider, *Chiracanthium inclusum* (Hentz). *Bull. Ark. agric. Exp. Stn. 753,* 1–76.

Wiehle, H. 1931. Araneidae, pp. 1–136 in Dahl. F (Ed.) *Die Tierwelt Deutschlands und der angrenzenden Meerstelle. 23,* G. Fiscer, Jena.

Received 16 March 1978

contained specimens in second or third instar, that is, specimens with a biennial life cycle.

The present results do not affect the statement of Juberthie (1954) about an annual life cycle in France. It is probable that the life cycle in southern Norway, as described above, must be looked upon as a result of the northern climate. A similar phenomen is reported for *Dolomedes fimbratus,* which is annual in northern Italy, partly annual in France, and biennial in northern Europe (Bonnet 1930, Palmgren 1939). *Araneus diadematus* has also been reported annual in France (Bonnet 1930) and biennial in Germany and Denmark (Wiehle 1931, Nielsen 1928).

There is a lack of information about the life cycle for spiders with a wide geographical distribution, but developmental delays as a result of cooler climate and shorter growth season are well known for many insect species.

Acknowledgements – I would like to thank Dr. Lauritz Sømme for valuable advice and critical reading of the manuscript, and Mrs. Roushan Birkeland for improving the English.

References

Blanke, R. 1973. Neue Ergebnisse zum Sexualverhalten von *Araneus cucurbitinus* Cl. (Araneae, Araneidae). *Forma et functio, 6,* 279–290.

Bonnet, P. 1930. La mue, l'automie et la régénération chez les araignées avec une étude des Dolomédes d'Europe. *Bull. Soc. Hist. nat. Toulouse, 159,* 237–700.

Bonnet, P. 1938. La proportion sexuelle chez les araignées. *Bull. Soc. Hist. nat. Toulouse, 72,* 241–256.

Dondale, C.D. 1961. Life histories of some common spiders from trees and shrubs in Nova Scotia. *Can. J. Zool. 39,* 777–787.

Hagstrum, D.V. 1971. Carapace width as a tool for evaluating the rate of development of spiders in the laboratory and the field. *Ann. ent. Soc. Am. 64,* 757–760.

Hågvar, E.B., Hågvar, S. 1975. Studies on the invertebrate fauna on branches of spruce (*Picea abies*) (L.) during winter. *Norw. J. Ent. 22,* 23–30.

Juberthie, C. 1954. Sur les cycles biologiques des araignées. *Bul. Sos. Hist. nat. Toulouse. 39,* 299–318.

Kessler, A. 1971. Relation between egg production and food consumption in species of the genus *Paradosa* (Lycosidae, Araneae) under experimental conditions of food-abundance and food-shortage. *Oecologia 8,* 93–109.

Nielsen, E. 1928. *De danske edderkoppers biologi.* Levin & Munkegaards. Köbenhavn. 723 pp + 5 plansjer.

Palmgren, P. 1939. Ökologische und physiologische Untersuchungen über die Spinne *Dolomedes fimbriatus* (Cl.). *Acta Zool. fenn. 24* 1–42.

Peck, W.B., Whitcomb, W.H. 1970. Studies on the biology of a spider, *Chiracanthium inclusum* (Hentz). *Bull. Ark. agric. Exp. Stn. 753,* 1–76.

Wiehle, H. 1931. Araneidae, pp. 1–136 in Dahl. F (Ed.) *Die Tierwelt Deutschlands und der angrenzenden Meerstelle. 23,* G. Fiscer, Jena.

Received 16 March 1978

◆

Lepidoptera from Sigdal and adjacent districts, western Buskerud, Norway

TROND ANDERSEN, ARILD FJELDSÅ & ASBJØRN MØRCH

Andersen, T., Fjeldså, A. & Mørch, A. 1978. Lepidoptera from Sigdal and adjacent districts, western Buskerud, Norway. *Norw. J. Ent.* Vol. 25, pp. 183–186. Oslo. ISSN 0029-1897.

A list of 81 species of Lepidoptera of the sub-orders Zeugloptera, Dacnonypha, Homoneura, Monotrysia and the ditrysian superfamilies Zygaenoidea, Tineoidea, and Gelechoidea from western Buskerud is given. 53 of the species are previously not recorded from the area.

Trond Andersen & Arild Fjeldså, Zoological Museum, N-5014 Bergen – Univ., Norway.

During the years 1968 to 1974 the late Asbjørn Mørch did extensive field work on the lepidopterous fauna of various parts of southern Norway. His collecting activity was particularly thorough in Sigdal and other municipalities in western Buskerud, and his aim was to compile a lepidopterous fauna of this district. After his death his collection of Lepidoptera was donated to the Zoological Museum, University of Bergen, and it was thus the duty of two of us to enumerate the Lepidoptera from Sigdal and adjacent districts based on his collecting. This paper covers the sub-orders Zeugloptera, Dacnonypha, Homoneura, Monotrysia and the distrysian superfamilies Zygaenoidea, Tineoidea, and Gelechoidea.

The only long list of Lepidoptera of the families mentioned above previously given for western Buskerud is included in a list of insects from Ål in Hallingdal (Strand 1899). Single records were published by Strand (1901, 1902, 1904) and Opheim (1962, 1965, 1968, 1971, 1977 a, b); the latter papers include revisions of material already published by Strand. Some recent captures were compiled by Opheim (1970, 1973, 1975). Other information on this region has appeared as dots in distribution maps (Nordström et al. 1961), and as records given for western Buskerud in tabular form (Opheim in press). Records from the present material were communicated to Opheim and thus are included in the latter publications. According to these publications reliable records of altogether 53 species in the present material are lacking for western Buskerud.

The localities are given in Table I. In the case of most captures the year is deleted, but appears from the following light trap periods: Prestfoss June 1968; Hollerud 7–11 July 1970, 10–20 Aug. 1970, 30 Aug.–medio Sept. 1971; Juvet 19–27 June 1969.

All species are identified by A. Fjeldså. Three nomenclatural or systematically confused taxa must be elucidated.

Nematopogon schwarziellus (Zeller, 1839) (syn. *Nemophora schwarziella* sensu Benander, 1953). The question of the identity of *Adela schwarziella* Zeller 1839, is perhaps open (Heath & Pelham-Clinton 1976), but the synonymy of contemporary British and Continental authors (Bradley et al. 1972, Heath & Pelham-Clinton 1976, Wojtusiak 1971) is confusing. They list *N. schwarziella* (in the sense used here) as a synonym of *N. panzerellus* (Fabricius, 1794), a species not occurring in Norway or Britain. The type of *Alucita panzerella* Fabricius is *Nemophora panzerella* sensu Lewin, 1945 and Benander, 1953.

Argyrestia sorbiella (Treitschke, 1833). *Argyrestia submontana* (Frey, 1856) was published as Norwegian by Feichtenberger (1965). Further material referred to *A. submontana* by I. Svensson exists in various collections. Habitually specimens of *A. sorbiella* from Juvet are large, somewhat metallic, with broad pattern elements of various bronze tones, and thus refer to *A. submontana* sensu Svensson. *A. sorbiella* and supposedly *A. submontana* were studied in 1974 for the purpose of genital identification. In the males the extra-genital Y-shaped structure of 8th sternite varied, but did not correlate to exterior characters. Habitual variation was thus interpret-

Table I. Localities.

Locality	Municipality	UTM-reference	m a.s.l.
Haglebu	Sigdal	32VNM099899	820
Hollerud	Sigdal	32VNM183803	540
Juvet	Sigdal	32VNM205798	480
Prestfoss	Sigdal	32VNM3557	140
Strandefjorden	Hol	---------	450
Ustaoset	Hol	---------	990

ed as infrasubspecific. The composition of bread series from *Sorbus aucuparia* L. and *S. meinichi* Lindem. confirmed this assumption. In the present author's opinion, the Norwegian specimens are *A. sorbiella*, disregarding phaenotypical range.

Pseudatemelia sp. (syn. *Tubuliferola josephinae* Knaben, 1957, p. 155, Fig. 2, nec. *Topeutis josephinae* Toll, 1956 ♀ – part. (genit.)). Awaiting a type examination of *Topeutis* (*Tubuliferodes*) *josephinae* Toll, the species recorded here is the one with laterally almost straight-sided antevaginal plate entirely lacking median-posterior minute scobinae, but with long posterior setae.

Micropterigidae

Micropterix aureatella (Scopoli, 1763) Juvet 19–27 June.

Eriocraniidae

Heringocrania unimaculella (Zetterstedt, 1839) Hollerud Apr. 1971 1♂. *Eriocrania semipurpurella* (Stephens, 1835) Hollerud Apr. 1971 1♀.

Hepialidae

Hepialus humuli (Linnaeus, 1758) Hollerud, Juvet, Prestfoss 20–24 June, numerous specimens. *H. hecta* (Linnaeus, 1758) Juvet 26 June 1969. *H. fusconebulosus* (DeGeer, 1778) Hollerud, Juvet 22 June – 11 July, numerous males.

Nepticulidae

Trifurcula weaveri (Stainton, 1855) Juvet 19–27 June 1♂. *Stigmella betulicola* (Stainton, 1856) Juvet 19–27 June 3♂. *S. lapponica* (Wocke, 1862) Juvet 19–27 June 1♂.

Incurvariidae

Nematopogon swammerdamellus (Linnaeus, 1758) Prestfoss 1 June 1♂. *N. schwarziellus* (Zeller, 1839) Juvet 19–27 June 2 ♂ 1 ♀. *Lampronia praelatella* (Denis & Schiffermüller, 1775) Prestfoss 1 June 1 ♀. *L. vetulella* (Zetterstedt, 1839) Haglebu, Ustaoset 14–17 June. *L. rubiella* (Bjerkander, 1781) Juvet 19–27 June 1 ♂. *L. rupella* (Denis & Schiffermüller, 1775) Juvet 19–27 June 1 ♂.

Zygaenidae

Adscita statices (Linnaeus, 1758) Strandefjorden 19 June 1970 1 ♂.

Psychidae

Taleporia tubulosa (Retzius, 1783) Juvet 19–22 June, several males. *Psyche casta* (Pallas, 1767) Hollerud, Juvet 19 June–11 July, numerous males.

Tineidae

Scardia tessulatella (Zeller, 1846) Hollerud 7–11 July, males. *Morophaga choragella* (Denis & Schiffermüller, 1775) Juvet 22 June 1 ♂. *Triaxomera fulvimitrella* (Sodoffsky, 1830) Juvet 19–27 June. *Nemapogon cloacellus* (Haworth, 1828) Hollerud, Juvet, Prestfoss 19 June–20 Aug. *N. picarellus* (Clerck, 1759) Juvet 19–27 June. *Haplotinea insectella* (Fabricius, 1794) Hollerud 7–11 July 1 ♂. *Tinea semifulvella* Haworth, 1828 Prestfoss 22–28 June, several specimens. *T. trinotella* Thunberg, 1794 Juvet 19–22 June 1 ♂. *Monopis weaverella* (Scott, 1858) Hollerud 7–11 July 1 ♂. *M. spilotella* (Tengström, 1848) Juvet, Prestfoss 19 June – 27 July.

Gracillariidae

Caloptilia syringella (Fabricius, 1794) Prestfoss June, hibernated. *Calybites auroguttella* (Stephens, 1835) Prestfoss 1 June 1 ♂. *Parornix loganella* (Stainton, 1848) Juvet 19–22 June 1 ♂. *P. scoticella* (Stainton, 1850) Juvet, Prestfoss 1–27 June, several specimens. *Phyllonorycter junoniellus* (Zeller, 1846) Juvet 19–27 June. *P.*

rajellus (Linnaeus, 1758) (syn. *rajella* (Zeller, 1839), nec. Bradley, 1971) Juvet 19–27 June.

Glyphipterigidae

Anthophila fabriciana (Linnaeus, 1767) Hollerud 10–20 Aug.

Yponomeutidae

Blastotere glabratella (Zeller, 1847) Juvet, Prestfoss 1–27 June, numerous specimens. *B. bergiella* Ratzeburg, 1840 Juvet 19–27 June, several specimens. *Argyresthia brockeella* (Hübner, 1813) Hollerud, Prestfoss 17 July–20 Aug., numerous specimens. *A. goedartella* (Linnaeus, 1758) Hollerud, Prestfoss 17 July–20 Aug., numerous specimens. *A. pygmaeella* (Denis & Schiffermüller, 1775) Hollerud 10–20 Aug. *A. sorbiella* (Treitschke, 1833) Juvet 19–27 June. *A. conjugella* Zeller, 1839 Hollerud, Juvet 19 June – 11 July, several specimens. *A. semifusca* (Haworth, 1828) Hollerud 10–20 Aug. *Yponomeuta evonymellus* (Linnaeus, 1758) Prestfoss 27 July 1968 2 ♂. *Y. vigintipunctatus* (Retzius, 1783) Prestfoss 1 June 1 ♂. *Swammerdamia caesiella* (Hübner, 1796) (nec. Friese, 1960 et auct., syn. *heroldella* Hübner, 1825) Juvet, Prestfoss 19–28 June. *S. compunctella* (Herrich-Schäffer, 1855) Prestfoss 22–28 June. *Paraswammerdamia conspersella* (Tengström, 1848) Haglebu 10 July 1968 2 ♂. *Cedestis subfasciella* (Stephens, 1834) Hollerud 7–11 July. *Ypsolopha parenthesella* (Linnaeus, 1761) Hollerud 10–20 Aug. *Plutella xylostella* (Linnaeus, 1761) (syn. *maculipennis* Curtis, 1832) Prestfoss 1 June. *Rhigognostis senilella* (Zetterstedt, 1839) Juvet 19 June 1 ♀, hibernated.

Coleophoridae

Coleophora serratella (Linnaeus, 1761) (nec. Benander, 1939 et auct., syn. *fuscedinella* Zeller, 1849) Juvet 19–27 June. *C. alticolella* Zeller, 1849 Prestfoss 1 June, several specimens. *C. virgaureae* Stainton, 1857 Hollerud, Prestfoss 7–17 July.

Oecophoridae

Pleurota bicostella (Clerck, 1759) Haglebu 10 July 1968. *Schiffermuelleria similella* (Hübner, 1796) Hollerud 7–11 July. *S. stipella* (Linnaeus, 1758) Hollerud, Juvet 19 June–11 July, numerous specimens. *Borkhausenia fuscescens* (Haworth, 1828) Hollerud 7–11 July 2 ♂. *Endrosis sarcitrella* (Linnaeus, 1758) Hollerud 7–11 July. *Pseudatemelia sp.* Juvet 19–27 June 2 ♂ 1 ♀. *Depressaria badiella* (Hübner, 1796) Hollerud 10 Aug.–9 Sept. 1 ♂. *D. weirella* Stainton, 1849 Hollerud 10–20 Aug. *Depressariodes ciniflonella* (Lienig & Zeller, 1846) Hollerud 9 Sept. 1 ♂. *Agonopterix heracliana* (Linnaeus, 1758) (syn. *applana* (Fabricius, 1777)) Hollerud. Prestfoss Apr.–1 June, 10 Aug.–9 Sept. *A. annexella* (Zeller, 1868) (syn. *ciliella* auct.) Prestfoss Apr. 1971 1 ♂. *A. liturella* (Denis & Schiffermüller, 1775) Prestfoss 27 July 1968 1 ♂. *A. broennoeensis* (Strand, 1920) Hollerud 9 Sept. 1 ♂. *A. liturosa* (Haworth, 1811) Hollerud 10–20 Aug., numerous specimens. *A. ocellana* (Fabricius, 1775) Hollerud 10–20 Aug.

Gelechiidae

Teleiodes notatella (Hübner, 1813) Prestfoss 1 June. *T. proximella* (Hübner, 1796) Juvet, Prestfoss 1–27 June. *Bryotropha senectella* (Zeller, 1839) Hollerud, Juvet 7 July–20 Aug. *B. terrella* (Denis & Schiffermüller, 1775) Hollerud 7–11 July. *Chionodes viduella* (Fabricius, 1794) Haglebu 17 June 1968 1 ♂. *C. lugubrella* (Fabricius, 1794) Hollerud 7–11 July 2 ♂. *C. luctuella* (Hübner, 1793) Prestfoss June 1 ♂. *Syncopacma cinctella* (Clerck, 1759) Juvet 19–27 June. *Acompsia cinerella* (Clerck, 1759) Hollerud, Juvet, Prestfoss 19 June–11 July. *Anacampsis blattariella* (Hübner, 1796) Prestfoss 27 July 1968.

Blastobasidae

Holcocera binotella (Thunberg, 1794) Hollerud 7 July 1 ♂.

References

Benander, P. 1953. Microlepidoptera. Micropterygina och Tineides aculeatae. *Svensk Insektfauna 10,* 72 pp.

Bradley, J. D., Fletcher, D. S. & Whalley, P. E. S. 1972. Lepidoptera, *in* Kloet, G. S. & Hincks, W. D. (ed.): *Ch. List Br. Ins. sec. ed. 2,* 153 pp.

Feichtenberger, E. 1965. Die norwegische Lepidopterenfauna am Polarkreis, mit Bezug auf die der Ostalpen. *Zeitschr. wien. ent. Ges. 50,* 80–118.

Heath, J. & Pelham-Clinton, E.C. 1976. Incurvariidae, pp. 277–300, *in* Heath, J. (ed.): *The Moths and Butterflies of Great Britain and Ireland 1*, 343 pp. The Curven Press Ltd., London.

Knaben, N. 1957. Lepidoptera-nytt. *Norsk ent. Tidsskr. 10*, 153–156.

Lewin, A. 1945. Beskrivning av en ny Nemophora-art, jämte bestämningstabell för släktet. *Opusc. ent. 10*, 150–152.

Nordström, F., Opheim, M. and Sotavalta. O. 1961. De fennoskandiska svärmarnas och spinnarnas utbredning. *Lunds Univ. Årsskr. N.F. avd. 2, 57 No. 4*, 87 +LXVIII pp.

Opheim, M. 1962. Notes on the genus Depressaria Haw. (Lepidoptera). *Norsk ent. Tidsskr. 12*, 19–21.

Opheim, M. 1965. The Norwegian species of Niditinea Petersen, 1957 and Tinea Linnaeus, 1758 (Lep., Tineidae). *Norsk ent. Tidsskr. 13*, 52–60.

Opheim, M. 1968. Nye Lepidoptera for Norge. *Atalanta norveg. 1*, 98–101.

Opheim, M. 1970. Nye Lepidoptera for Norge. *Atalanta norveg. 1*, 176–180.

Opheim, M. 1971. The Norwegian species of Momphidae (Lepidoptera). *Atalanta norveg. 1*, 204–217.

Opheim, M. 1973. Lepidoptera from birds' nests in Norway. *Atalanta norveg. 2*, 43–51.

Opheim, M. 1975. Nye lokaliteter for norske Lepidoptera samt sjeldnere funn VIII. *Atalanta norveg. 2*, 111–119.

Opheim, M. 1977a. Revision of microlepidoptera in the collections of Zoological Museum, Oslo. I. *Atalanta norveg. 3*, 5–15.

Opheim, M. 1977b. Revision of microlepidoptera in the collections of Zoological Museum, Oslo. II. *Atalanta norveg. 3*, 33–35.

Opheim, M. (in press). *The Lepidoptera of Norway, Check-List, Part III.* Norsk Lepidopterologisk Selskap, Trondheim.

Strand, E. 1899. Bidrag til Hallingdals og Lyngørs insektfauna. *Nyt Mag. Naturv. 22*, 1–62.

Strand, E. 1901. Beitrag zur Schmetterlingsfauna Norwegens. *Nyt Mag. Naturv. 39*, 25–72.

Strand, E. 1902. Bemerkungen über einige Norwegische Tephrochlystien und Tineinen. *Kgl. n. Vid. Selsk. Skr. 1901 No. 8*, 1–8.

Strand, E. 1904. Beitrag zur Schmetterlingsfauna Norwegens III. *Nyt Mag. Naturv. 42*, 109–179.

Toll, S. 1956. Versuch einer naturlichen Gruppierung der europäischen Oechophoridae auf Grund der Genitalapparate, samt Beschreibung von zwei neuen Arten (Lepidoptera). *Ann. Zool. Warsaw. 1*, 171–193.

Wojtusiak, J. 1972. Adelidae. Motyle – Lepidoptera, częçé 27, zeszyt 9. *Klucze do oznacz. owad. pol. No. 76*, 52 pp.

Received 29 April 1978

Nucleating agents in the haemolymph of third instar larvae of *Eurosta solidagensis* (Fitch) (Dipt., Tephritidae)

LAURITZ SØMME

Sømme, L. 1978. Nucleating agents in the haemolymph of third instar larvae of *Eurosta solidagensis* (Fitch) (Dipt., Tephritidae), *Norw. J. Ent.* Vol. 25, pp. 187–188. Oslo. ISSN 0029-1897.

The presence of nucleating agents has been demonstrated in the haemolymph of the frost resistant, third instar, overwintering larvae of *Eurosta solidagensis* (Fitch). The substances are partly destroyed by heating. The results explain the poor ability of these larvae to supercool in spite of their high content of glycerol and sorbitol.

Lauritz Sømme, Zoological Institute, University of Oslo, P.O. Box 1050, Blindern, Oslo 3, Norway.

The goldenrod gallfly *Eurosta solidagensis* overwinters in the third larval stage in stem galls on goldenrod (*Solidago canadensis*). The larvae are frost resistant, and can survive for 18 days at −55°C (Salt 1957), or more than 64 days at −30°C (Sømme 1964). Their frost resistance may be explained by the accumulation of glycerol and sorbitol in the haemolymph (Salt 1961); glycerol and sorbitol in combination with trehalose form a multi-cryoprotectant system (Morrisey & Baust 1976).

Morrisey & Baust (1976) observed that the supercooling points of third instar *E. solidagensis* larvae increased from −17° in August to −10° in November and −9°C in midwinter. They pointed out that this increase is converse to the cryoprotectant levels, since the supercooling points usually decrease with increased glycerol concentrations (e.g. Sømme 1964, Asahina 1969). As suggested by Baust & Morrisey (1977) nucleator efficiency in *E. solidagensis* is apparently enhanced to ensure freezing. Following pupation and the loss of cryoprotectant substances in the spring, the supercooling points dropped to −23° (Morrisey & Baust 1976).

High supercooling points in frost resistant beetles and wasp queens have recently been explained by the presence of nucleating agents in the haemolymph. Zachariassen & Hammel (1976) demonstrated that these substances are present in a number of frost resistant, adult beetles, causing them to freeze at temperatures around −7°C. In the beetle *Phyto depressus*, which also contains nucleating agents, the supercooling points are only slightly influenced by high glycerol concentrations (Zachariassen 1977). Similarly, Duman & Patterson (1978) found that the mean supercooling point of −4.6°C of overwintering, frost resistant *Vespula maculata* queens could be explained by nucleating agents. This species also has a high level of glycerol. The nature of the nucleating agents is not known, but they are destroyed by heat (Zachariasson & Hammel 1976, Duman & Patterson 1978), and by proteolytic enzymes (Duman & Patterson 1978).

The high supercooling points, in spite of high levels of cryoprotectant substances in *E. solidagensis* larvae, strongly suggest that a similar mechanism to avoid high degrees of supercooling is present. The present study was initiated to see if nucleating agents could be found in the haemolymph of these larvae.

Material and methods

Stem galls of goldenrod plants were collected in the vicinity of Lethbridge, Alberta, Canada in October 1977. They were mailed to Oslo, and stored at 3°C till the end of February. At this time the galls were opened, and the third instar *E. solidagensis* larvae removed for experimental purposes.

The presence of nucleating agents in the haemolymph was demonstrated by the method described by Zachariassen & Hammel (1976) and Zachariassen (1977). Samples of haemolymph were taken from a cut in the dorsal side of the larvae, and diluted to 5 percent with a 0.9

Table 1. Supercooling points of overwintering, third instar E. solidagensis larvae, and of haemolymph diluted to 5% in 0.9% NaCl.

	n	$\bar{x} \pm$ SD
Intact larvae	8	− 10.1 ± 1.13
5% haemolymph in 0.9% NaCl	7	− 9.8 ± 1.43
Heated, 5% haemolymph in 0.9% NaCl	7	− 13.4 ± 0.99
0.9% NaCl solution	11	− 17.4 ± 1.95

percent NaCl solution. 5 μl samples of the diluted haemolymph solution were placed in capillary tubes, which were sealed at both ends with petroleum jelly. Their supercooling points were measured by copper-constantan thermocouples, connected to a recording potentiometer. To study the effect of heat, samples of 5 percent haemolymph in 0.9 percent NaCl solution were heated to 100°C for one minute, centrifuged, and supercooling points measured in 5 μl samples of the supernatant.

Supercooling points of intact larvae were measured by the same method as for haemolymph samples. The cooling rate in both cases was kept at 1° to 2°C per minute (Salt 1966).

Results and discussion

The results are presented in Table I. As previously reported (Sømme 1964, Morrisey & Baust 1976), the overwintering, third instar larvae of *E. solidagensis* have supercooling points around − 10°C. The supercooling points of haemolymph samples in 0.9% NaCl were almost identical. Since the supercooling points of the NaCl solution itself were considerably lower, the results strongly suggest the presence of nucleating agents in the haemolymph. As in the insects studied by Zachariassen & Hammel (1976) and Duman & Patterson (1978), the supercooling points of the haemolymph samples were lowered by heating. Some nucleating effect was still present, since the new supercooling points were still above those of the NaCl solution.

The present results explain the apparent controversy pointed out by Morrissey & Baust (1976), namely that the supercooling points increase with the accumulation of cryoprotectant substances in *E. solidagensis* larvae. Since the third instar larvae initially have lower supercooling points (Morrissey & Baust 1976), it must be assumed that the nucleating agents are synthesised during the autumn, parallel to the accumulation of glycerol and sorbitol. During pupation the nucleators disappear, resulting in a considerable increase in ability to supercool.

While previous studies on haemolymph nucleating agents were performed on adult insects (Zachariassen & Hammel 1976, Duman & Patterson 1978), the present study demonstrates for the first time their presence in insect larvae. As pointed out by Zachariassen & Hammel (1976) and Duman & Patterson (1978), the importance of these substances is probably to induce extracellular freezing at relatively high temperatures, by which the risk of lethal intracellular freezing is greatly reduced.

Acknowledgements – Special thanks to Mr. William L. Pelham for collecting the goldenrod galls, and to Mrs. Inger Tambs-Lyche for technical assistance in the laboratory.

References

Asahina, E. 1969. Frost resistance in insects *Adv. Insect Physiol. 6*, 1–49

Baust, J.G. & Morrisey R.E. 1977. Strategies of low temperature adaptation *15th Int. Congr. Ent. Wash. D.C. Aug. 1976*, 173–184.

Duman, J.G. & Patterson J.L. 1978. The role of ice nucleators in the frost tolerance of overwintering queens of the bald faced hornet. *Comp. Biochem. Physiol. 59A*, 69–72.

Morrisey, R. E. & Baust, J. G., 1976. The ontogeny of cold tolerance in the gall fly, *Eurosta solidagensis. J. Insect Physiol. 22*, 431–437.

Salt, R.W. 1957. Natural occurrence of glycerol in insects and its relation to their ability to survive freezing. *Can. Ent. 89*, 491–494.

Salt. R.W. 1961. Principles of insect cold-hardiness. *Ann. Rev. Ent. 6*, 55–74.

Salt, R.W. 1966. Factors influencing nucleation in supercooled insects. *Can. Ent. 95*, 1190–1202.

Sømme, L. 1964. Effects of glycerol on cold-hardiness in insects. *Can. J. Zool. 42*, 87–101.

Zachariassen, K.E. 1977. Effects of glycerol in freeze-tolerant Phyto depressus L. (Col., Phytidae). *Norw. J. Ent. 24*, 25–29.

Zachariassen, K.E. & Hammel, H.T. 1976. Nucleating agents in the haemolymph of insects tolerant to freezing. *Nature 262*, 285–287.

Received 28 April 1978.

Contribution from the Norwegian IBP/PT-UM sections.

Pit-fall catches of surface-active arthropods in some high mountain habitats at Finse, south Norway. I. Aim, methods, and habitat descriptions

EIVIND ØSTBYE, SIGMUND HÅGVAR, KAREN MARIE HAANDE, PER STEINAR HAANDE, JAN MELÅEN & ARVID SKARTVEIT

Østbye, E., Hågvar, S., Haande, K. M., Haande, P. S., Melåen, J. & Skartveit, A. 1978. Pit-fall catches of surface-active arthropods in some high mountain habitats at Finse, south Norway. I. Aim, methods, and habitat descriptions *Norw. J. Ent.* Vol. 25, pp. 189–193. Oslo. ISSN 0029-1897.

Pit-fall catching for surface-active arthropods in five high mountain habitats was carried out in the snow-free seasons of 1969, 1970, and 1971. A presentation is made of the aims of the study, methods used, and descriptions of the investigated habitats with respect to meteorology and plant sociology. The habitats, situated between 1220 and 1350 m a.s.l., were: a pioneer ground, a eutrophic meadow, an oligotrophic dry heath, a snow bed, and a tussock or mesotropic mire habitat.

Eivind Østbye & Jan Melåen, Zoological Institute, University of Oslo, Blindern, Oslo 3, Norway; Sigmund Hågvar, Norwegian Forest Research Institute, N-1432 Ås-NLH, Norway; Karen Marie & Per Steinar Haande, Hallingdal videregående skole, N-3550 Gol, Norway; Arvid Skartveit, Geophysical Institute, University of Bergen, N-5000 Bergen, Norway.

Little is known of the arthropod fauna of Norwegian alpine habitats. As a part of an analysis of a high mountain ecosystem, pit-fall traps were placed in five dominant habitats from the low- and mid-alpine zones at Finse (60°36'N, 7°30'E) (UTM 32V MN 11), on the NW part of the Hardangervidda mountain plateau. The traps were run during the snow-free seasons of three successive years. The main purposes were to study species composition of typical surface-active groups, seasonal changes in activity, and variation in catches between years.

The results are presented in four articles. This first includes a short presentation of the material and method, a description of the habitats, temperature and precipitation, and presentation of the zoological material at group level. A second article treats the catches at group level, with emphasis on Opiliones, Araneida, and Coleoptera (Hågvar et al. 1978). The third article treats the catches of Araneida at species level (Hauge et al. 1978), and a fourth the catches of Coleoptera at species level (Østbye et al., in prep.). Data on Araneida collected under stones in all five habitats are included in the third article.

A. Skartveit prepared the meteorological material and K. M. Haande and P. S. Haande contributed the botanical analyses. The zoological part of the investigation was performed by E. Østbye, S. Hågvar, and J. Melåen. The senior author was responsible for the planning of the study.

Methods

15 pit-fall traps were placed in three rows with 5 m between each trap and row; these formed a grid. The traps, 9.5 cm high plastic cups, diameter 7 cm in the upper, and 6.5 cm in the lower end, were dug into the soil up to their upper rim and protected against rain and dust with a plywood shield 15 × 15 cm placed approximately 3–5 cm above the surface. Care was taken not to disturb the microhabitat around the traps. As killing and conserving agent the traps were filled 1/3 with 10% formaldehyde.

The traps were in place soon after snow melt, usually in medio June, and were allowed to stand until the arrival of the first snow in the autumn, usually in late September. They were emptied every second week if possible. If not, the catches were corrected to a 'two week period', which is later referred to as the standard trapping time unit. Every year the traps were placed in exactly the same positions, which were not changed throughout the season. However, in 1969, the oligotrophic dry heath habitat and the tussock habitat were not exactly the sites de-

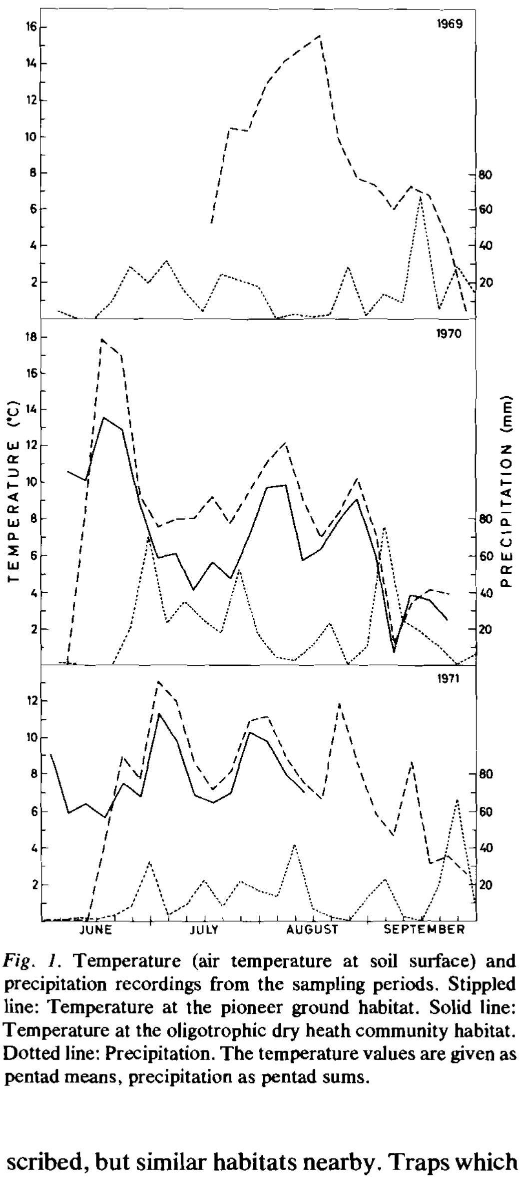


Fig. 1. Temperature (air temperature at soil surface) and precipitation recordings from the sampling periods. Stippled line: Temperature at the pioneer ground habitat. Solid line: Temperature at the oligotrophic dry heath community habitat. Dotted line: Precipitation. The temperature values are given as pentad means, precipitation as pentad sums.

scribed, but similar habitats nearby. Traps which were filled with water due to seasonal flooding, or which dried out, or became otherwise useless, were omitted from the calculations. In such cases, the catches from the reduced number of traps were adjusted to 'catches per 15 traps'.

The actual trapping periods were as follows: In 1969, the traps were set out 9 July and emptied on the following dates: 17 July, 3 August, 15 August, 2 September, 11 September, and 8 October. In 1970, they were set out on 16 June and emptied on 3 July, 13 July, 5 August, 15 August, 5 September, 15 September, and 29 September. In 1971, they were set out on 21 June in the pioneer ground, the eutrophic meadow, and the oligotrophic dry heath, on 29 June in the tussock habitat, and on 5 July in the snow bed. In the two first-mentioned habitats, they were emptied for the first time on 4 July, and in the third and fourth habitats on 11 July. After that, traps in all habitats were emptied on 2 August, 16 August, 3 September, and 20 September.

In all figures in the papers of this series, where catches per sampling period are presented, the values have been plotted for the middle of each sampling period.

The usefulness of the method for different purposes is treated in the second paper (Hågvar et al. 1978).

Material

The total material from the pit-fall traps in all the five habitats during the seasons consisted of 137,849 arthropod specimens. The following groups were represented: Opiliones, Araneida, Acarina, Collembola, Plecoptera, Thysanoptera, Mecoptera, Hemiptera, Trichoptera, Lepidoptera, Coleoptera, Diptera, and Hymenoptera.

Four typical predator groups, for which the method may be considered useful, will be treated more thoroughly, both at group and species level: Opiliones (one species only, *Mitopus morio* Fabr.), 10,818 specimens; Araneida, 4365 specimens; Carabidae (Col.), 1210 specimens; and Staphylinidae (Col.), 2168 specimens.

Meteorological observations

Mean temperatures, measured in air at soil surface, together with the precipitation are given in Fig. 1. Precipitation is given as pentad sums, and was measured at Finse (meteorological station 60°36'N, 7°30'E, 1224 m a.s.l.) except for 1969 when the recordings were made at Finse zoological station 1 km east of Finse. Finse meteorological station is approximately 1 km from the nearest, and 4 km away from the most distant sampling site.

Air temperatures were measured in two habitats, the pioneer ground in front of the glacier, and in the oligotrophic dry heath in the lower part of the gradient, thus representing the approximate climatic range of the succession gradient. Air temperatures are given as pentad means.

Fig. 2. An overview of the succession gradient, going from recently freed ground in front of the Blåisen glacier (background) down to the valley-bottom (foreground).

A broader description of the climate in this area is given in Lien et al. (1974), Østbye et al. (1975) and Skartveit (1976).

The habitats

The habitats cover parts of a north-sloped succession gradient in the Finse valley, ranging from recently freed ground in front of the Blåisen glacier, one of the largest outlets of the Hardangerjøkulen glacier, down to the valley-bottom at the Finsevatn lake. The gradient covers most of the dominant seral stages and ends in the presumed climax community of this area (Fig. 2). A preliminary description of the habitats studied is presented in an earlier paper (Hågvar & Østbye 1972).

A. *The pioneer ground* (Fig. 3). In front of the glacier on moraine and sedimentation flats with unstable soil, vegetation types of early seral stages are found.

The area in which the traps were situated had been exposed for not more than 200 years, and could not therefore be classified into definite alliances with regard to vegetation types. Where vegetation occurs, the field layer is sparse, while the bottom layer varies between predominance of *Stereocaulon alpinum* and *Racomitrium canescens*. Also typical, but less dominating, are the following plants: *Salix herbacea, Empetrum hermaphroditum, Polygonum viviparum, Oxyria digyna* and *Cetraria nivalis*.

Stones of different size groups cover approximately 30% of the habitat, and most can be turned by hand (Hågvar & Østbye 1972). The soil is relatively dry, due to the low water-holding capacity of morainic soils.

Fig. 3. The pioneer ground habitat.

The sampled habitat is located 800 m from the glacier at an altitude of 1350 m a.s.l. Pioneer ground habitat types in the Finse area cover approximately 35% of north-facing slopes and 1% in south-facing slopes. Half of the pioneer ground in north-facing slopes can be considered as being covered with vegetation (J. Schmidt & E. Østbye, in prep.).

B. *The eutrophic meadow* (Fig. 4). This habitat is characterized by eutrophic, chionophilous low herb meadow vegetation of the alliances *Potentilleto-Polygonion vivipari* Nordhagen 1936 +*Ranunculo-Poion alpinae* Gjærevoll 1956. This type of community demands high soil moisture, especially melt-water, and is recognized by densely luxuriant species such as *Erigeron uniflorum, Ranunculus acris, Sibbaldia procumbens, Gnaphalium supinum, Taraxacum croceum, Alchemilla vulgaris* group, *Oxyria digyna, Poa alpina,* and *Thalictrum alpinum*.

Fig. 4. The eutrophic meadow habitat.

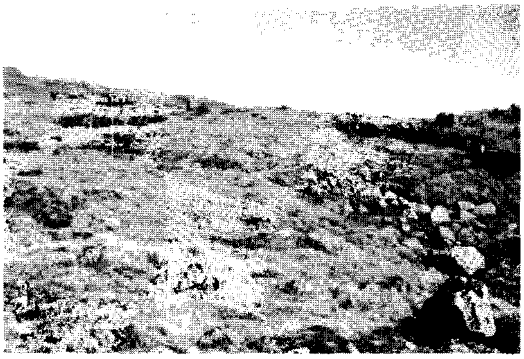


Fig. 5. The oligotrophic dry heath habitat.

Fig. 7. The tussock or mesotrophic mire habitat.

The area is relatively flat, and stones and barren rocks cover about 10% of the surface. Most of the stones can be turned by hand (Hågvar & Østbye 1972). The soil has a high humidity due to a steady inflow of melt-water from the nearby summer snow fields, and tussock formations are seen in some places.

The sampled habitat is located approximately one km from the glacier at an altitude of 1300 m a.s.l.

In this area this type of habitat has a coverage of approximately 3% of north-facing slopes versus 14% on south-facing slopes (J. Schmidt & E. Østbye, in prep.).

C. *The oligotrophic dry heath* (Fig. 5). In the Finse area, oligotrophic dry heath communities represent a dominant vegetational type. The most common alliance is Arctostaphyletocetrarion nivalis Dahl 1956, on which studies have been conducted. This type of community is found on ridges with a thin snow-cover in winter. The vegetation is oligotrophic and predominated by acidiphilous and xerophilous species. A growth with a dense lichen covering occurred in the higher parts of the study plot, and is called a 'lichen heath'. The most common species are *Cetraria nivalis, C. islandica, Cladonia mitis, C. ericetorum,* and *C. rangiferina.* Of the vascular plants *Carex bigelowii, Empetrum hermaphroditum, Festuca ovina, Juncus trifidus,* and *Luzula spicata* are characteristic species.

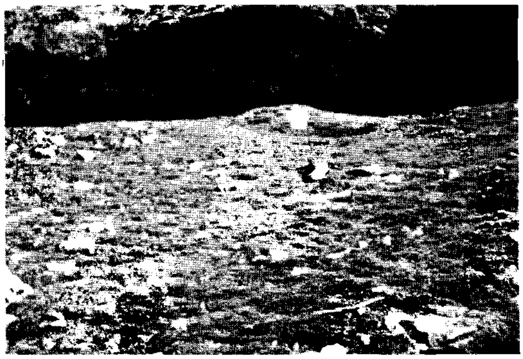


Fig. 6. The snow bed habitat.

The study area is relatively flat, and stones and boulders cover 5–10% of it. Most of the cover is represented by boulders and only a smaller part is covered by stones which can be turned by hand (Hågvar & Østbye 1972). The humidity of the soil is variable, being lowest on the 'lichen heaths'.

The sampled habitat is located approximately 2.5 km from the glacier at 1230 m a.s.l.

Oligotrophic dry heath communities, having the alliances *Arctostaphyleto-Cetrarion nivalis* Dahl 1956 and *Phyllodoco-Vaccinion myrtilli* Nordhagen 1936 as the dominant ones, have in this area a coverage of 32% in north-facing slopes and 55% in south-facing ones (J. Schmidt & E. Østbye, in prep.).

D. *The snow bed* (Fig. 6). This is a rather common type of habitat in this area, the vegetation type being of the alliance *Cassiopeto-Salicion herbacea* Nordhagen 1936. It is characterized by large amounts of snow accumulating during winter, and shows a distinct solifluction during the melting period. On such sites with a prolonged snow cover and unstable oligotrophic ground, the plant cover will be sparse. The study plot is a typical snow-bed community and is dominated by the tiny willow species *Salix* *herbacea*. The moss *Kiaeria starkei* forms a carpet in the bottom layer. Otherwise *Ranunculus glacialis* is characteristic.

The habitat is gently sloping and has a stone coverage of 15–20%. Most of the stones can be turned by hand (Hågvar & Østbye 1972). Information on soil conditions is given in Hågvar et al. (1974).

The sampled habitat is situated approximately 2.6 km from the glacier at an altitude of 1220 m a.s.l.

The investigated habitat is representative of snow-bed communities on north-facing slopes in the Finse area. Richer snow beds can be found in south-facing slopes. *Salix herbacea* snow beds have a coverage of approximately 23% on north-facing and 25% on south-facing slopes in the area (J. Schmidt & E. Østbye, in prep.).

E. *The tussock or mesotrophic mire habitat* (Fig. 7). This is characterized by an extensive tussock formation on oligotrophic dwarf-mire vegetation on ombrogenous, topogenous peat bogs. This alliance *Oxycocco-Empetrion hermaphroditii* Nordhagen 1936 has the following predominant species: *Rubus chaemaemorus, Eriophorum vaginatum, Oxycoccus microcarpus, Sphagnum fuscum* and *Polytrichum juniperum* var. *gracilis*.

A striking feature of this relatively flat area is that the cavities between the tussocks are usually filled with water during floods or after heavy rains. Some boulders and bare rock are present. There are very few smaller stones which can be turned by hand. The total area covered by stones is less than 5% of the habitat. The soil has a good water holding capacity and is usually rather wet.

The sampled habitat is situated approximately 3 km from the glacier at an altitude of 1220 m a.s.l. In this area this habitat has only a coverage of 1% on both north-facing and south-facing slopes (J. Schmidt & E. Østbye in prep.).

Acknowledgements. – We wish to express our gratitude to all our colleagues who participated in the field work, especially A. Hagen, the late J. Hagen, J. Schmidt, H.-J. Skar and D. Svalastog, and to M. Espeland for critically reading the manuscript. The investigations have been supported by grants from the Norwegian IBP. This work is part of the Hardangervidda IBP/PT-UM project.

References

Hauge, E., Hågvar, S., Østbye, E. & Melåen, J. 1978. Pit-fall catches of surface-active arthropods in some high mountain habitats at Finse, south Norway. III. Araneida. *Norw. J. Ent. 25*, 207–220.

Hågvar, S. & Østbye, E. 1972. Quantitative and qualitative investigations of the invertebrate fauna under stones (the Hypolithion in some alpine habitats at Finse, south Norway, *Norsk ent. tidsskr. 19*, 1–10.

Hågvar, S., Melåen, J. & Østbye, E. 1974. Quantitative studies of the invertebrate fauna in an alpine snow-bed community at Finse, south Norway. *Norsk ent. Tidsskr. 21*, 45–51.

Hågvar, S., Østbye, E. & Melåen, J. 1978. Pit-fall catches of surface-active arthropods in some high mountain habitats at Finse, south Norway. II. General results on group level, with emphasis on Opiliones, Araneida and Coleoptera. *Norw. J. Ent. 25*, 195–205.

Lien, L., Østbye, E., Hogstad, O., Haande, K. M., Haande, P. S., Hagen, A., Skar, H.-J., Skartveit, A. & Svalastog, D. 1974. Bird surveys in high mountain habitats, Finse and Stigstuv, Hardangervidda, south Norway, 1967–72. *Norw. J. Zool. 22*, 1–14.

Østbye, E., Berg, A., Blehr, O., Espeland, M., Gaare, E., Hagen, A., Hesjedal, O., Hågvar, S., Kjelvik, S., Lien, L., Mysterud, I., Sandhaug, A., Skar, H.-J., Skartveit, A., Skre, O., Skogland, T., Solhøy, T., Stenseth, N. C. & Wielgolaski, F. E. 1975. Hardangervidda, *Ecol. Bull. 20*, 225–264.

Skartveit, A. 1976. Energy exchange at the earth's surface with emphasis on an alpine tundra ecosystem. *Rapp. Høyfjellsøkol. Forsk. Stn., Finse, Norge 1976 (1)*, 1–147.

Contribution from the Norwegian IBP/PT-UM sections.

Pit-fall catches of surface-active arthropods in some high mountain habitats at Finse, south Norway. II. General results at group level, with emphasis on Opiliones, Araneida, and Coleoptera

SIGMUND HÅGVAR, EIVIND ØSTBYE & JAN MELÅEN

Hågvar, S., Østbye, E. & Melåen, J. 1978. Pit-fall catches of surface-active arthropods in some high mountain habitats at Finse, south Norway. II. General results at group level, with emphasis on Opiliones, Araneida, and Coleoptera. *Norw. J. Ent.* Vol. 25, pp. 195–205. Oslo. ISSN 0029-1897.

Pit-fall catches covering three years in five high mountain habitats are presented, mainly on the level of family and order. The habitats, situated between 1220 and 1350 ma.s.l., were: a tussock or mesotrophic mire habitat, a snow bed, an oligotrophic dry heath, an eutrophic meadow and a pioneer ground site. Emphasis was laid on the following groups: Opiliones (one species, *Mitopus morio* Fabr.) Araneida, and the two coleopterous families Carabidae and Staphylinidae. These were the most important surface-active invertebrate predator groups in this area. Of these Opiliones gave the highest catches. The seasonal changes in catches of Opiliones showed no fixed pattern from year to year. However, each of the three other groups mentioned showed a rather fixed phenology pattern which was repeated each year, despite marked differences in climate. Araneida had their main activity periods in spring and autumn, Carabidae in spring, and Staphylinidae during summer. Thus, the predator groups tended to alternate in activity during the snow-free season. The main catches of Opiliones and Carabidae were taken in the eutrophic meadow and in the pioneer ground. A common feature of these two habitats, of importance to both groups, was the easy access to stones suitable as shelter during rest. The highest catches of Araneida were made in the two most moist habitats: the tussock habitat and the eutrophic meadow. The highest catches of Staphylinidae were from the same two habitats and the snow bed.

Sigmund Hågvar, Norwegian Forest Research Institute, 1432 Ås-NLH, Norway; Eivind Østbye & Jan Melåen, Zoological Institute, University of Oslo, Blindern, Oslo 3, Norway.

This paper presents the total arthropod material collected by pit-fall traps during three years in five alpine habitats near Finse, Hardangervidda, south Norway (60°36′N, 7°30′E) (UTM 32V MN 11). The presentation is mainly at the level of order and family. Emphasis has been laid on the following groups: Opiliones, Araneida, and the two coleopterous families Carabidae and Staphylinidae. These are the major predatory groups in the actual high mountain area. Individual species of Araneida and Coleoptera will be treated in two successive articles.

Authorship was mainly the responsibility of S. Hågvar. E. Østbye was responsible for the planning of the study.

Material and methods

The five habitats have been described in detail by Østbye et al. (1978). A short review will be given here. The pioneer ground is situated quite near a glacier, and the habitat is about 200 years old. It is rich in surface stones and does not have a continuous vegetation cover. The eutrophic meadow is rather moist and rich in vegetation. The oligotrophic dry heath, which is a dominant vegetational type in the area, is to a large degree covered by lichens. In the snow bed, the snow melts off rather late, and the vegetation is dominated by *Salix herbacea*. Finally, the tussock habitat has an extensive tussock formation and an oligotrophic dwarf mire vegetation on ombrogenous, topogenous peat bog. The five habitats are situated in the mid- and low-alpine zones, between 1220 and 1350 m a.s.l.

In each habitat, fifteen traps, 7 cm in upper diameter, were operated during most of the snow-free season. They were placed in three rows, 5 m between each trap and row, and were emptied about every two weeks. The climate during the three seasons is described in Østbye et al. (1978).

Table I. Total catches of arthropods per 15 pit-fall traps during three years in five alpine habitats. Numbers in brackets: juvenile stages (in addition).

Habitat	Pioneer ground			Eutrophic meadow			Oligotrophic dry heath			Snow bed			Tussock habitat		
Group Year	1969	1970	1971	1969	1970	1971	1969	1970	1971	1969	1970	1971	1969	1970	1971
Opiliones (Mitopus morio)	977	936	998	1323	958	951	815	332	434	936	347	492	880	362	614
Araneida	73	168	173	347	499	487	230	290	271	185	285	239	558	435	382
Acarina	137	546	840	822	1046	2405	249	587	2537	1259	1030	1262	172	261	763
Collembola	2082	3488	5965	4741	7740	15491	1906	3682	6664	5911	4397	6787	2771	3371	6675
Plecoptera							1			1				1	(1)
Thysanoptera		1		1	1			4							
Homoptera (Hem.)	1096	1066	150	16	1	4	84	52	45	21	21	1	10	1	31
Heteroptera (Hem.)							6	3	1						
SUM Hemiptera	1096	1066	150	17◀	1	4	90	55	46	21	21	1	10	1	31
Mecoptera (Boreus sp.)	7		1	5		2	1							1	
Trichoptera				1	1	4	1		1	1			6		2
Lepidoptera		1 (5)	5 (3)	2 (1)	1	18		1 (1)	4			1		1	6 (3)
Carabidae (Col.)	77 (3)	121 (11)	151 (21)	156 (3)	153 (8)	176 (4)	9	15 (2)	10 (2)	62 (6)	59 (1)	24	54 (9)	54 (7)	73
Staphylinidae (Col.)	34	15	100	378	230	499	21	20	49	116	83	296	256	36 (1)	125
Byrrhidae (Col.)	3	19	1	4	2	6	3			1	1		1	4	4
Curculionidae (Col.)	2	11	15	6	5		3		1	2	8	10		3	1
Rest Col.	(1)			1		(1)		(1)				1	5 (2)	8	4 (4)
SUM Coleoptera	116 (4)	166 (11)	267 (21)	545 (3)	390 (8)	681 (5)	36	35 (3)	60 (2)	181 (6)	151 (1)	331	316 (11)	105 (10)	207 (4)
Nematocera (Dipt.)	1191 (4)	4132 (2)	9998 (17)	217 (7)	677 (1)	2028 (5)	67	129	328	281 (6)	308 (6)	563 (7)	64 (14)	217 (15)	933 (4)
Brachycera (Dipt.)		1	1						4						4
Cyclorrhapha (Dipt.)	28	53	57	54	44	26	29	9	3	92	12	9	212	7	20
SUM Diptera	1219 (4)	4185 (2)	10056 (41)◀	271 (8)◀	721 (1)	2054 (5)	96	138	335	374 (6)	320 (6)	572 (7)	276 (14)	224 (15)	957 (14)◀
Symphyta (Hym.)	1					1	1			1		1			1
Apocrita (Hym.)	223	620	972	75	70	69	19 (2)	26 (4)	45	44	79	192	47	13	27
SUM Hymenoptera	224 (1)◀	737◀ (4)◀	972	75 (1)◀	71 (1)◀	70 (2)◀	20 (2)	26 (5)◀	45 (3)◀	45	80◀ (1)◀	193	47 (1)◀	18◀	28
TOTAL	5931 (9)	11294 (22)	19427 (65)	8150 (13)	11429 (10)	22167 (12)	3445 (2)	5150 (9)	10397 (5)	8914 (12)	6631 (8)	9878 (7)	5036 (26)	4779 (25)	9665 (22)

◀Marks numbers which are higher than the sum of subcategories above. This is due to a few individuals which were not identified to subcategory.

Results

The catches of different arthropod groups in all five habitats during three years are listed in Table I. The numbers given represent the total catches during the snow-free season in fifteen traps. If one or more traps had to be eliminated during a given period, e.g. because they were filled with water, an estimate of catches per fifteen traps was made. In Table I distinctions are made between adults and juveniles for the following groups: Plecoptera, Lepidoptera, Coleoptera, Diptera, and Hymenoptera.

In the following presentation of catches, emphasis has been laid on the following groups, for which the method may be considered useful (see first part of Discussion): Opiliones, Araneida, Hemiptera, and Coleoptera (mainly Carabidae and Staphylinidae). In Figs. 1–6, showing seasonal changes in catches, each plot has been placed in the middle of a sampling period. Furthermore, each plot indicates the total catches in fifteen traps, adjusted to a standard period of fourteen days. The symbols used for each habitat are given in Fig. 1.

The catches of Opiliones *(Mitopus morio* Fabr.) are presented in Fig. 1. In all three years, the total catches were highest in the eutrophic meadow and pioneer ground, and lowest in the oligotrophic dry heath. However, the main trend of the curves during the season was not the same for all three years. Also, different habitats may have rather different curve shapes within the same year; this was especially so in 1969 and 1970.

Fig. 2 shows the catches of Araneida. Contrary to Opiliones, the amount of Araneida trapped in the pioneer ground was always very low. The highest total catches were either taken in the tussock habitat or the eutrophic meadow. The catches were always very similar in the oligotrophic dry heath and the snow bed. In 1970 and 1971, the general picture was the same in the habitats yielding the highest catches, with a maximum in June and in September, and with low catches in mid-season. In 1969, no maximum early in the season was recorded. A maximum may have occurred before the traps were placed in the habitats, as the traps started to function later that year than in the two following years.

The Hemiptera material was wholly dominated by Homoptera. Homoptera (mainly Cicadoidea) were caught in very high numbers in the pioneer ground, but only in small amounts in other habitats (Fig. 3). Among these other habitats, the catches were highest in the oligotrophic dry heath. The catches in pioneer ground were much higher during the two first years than in 1971. The main material was taken

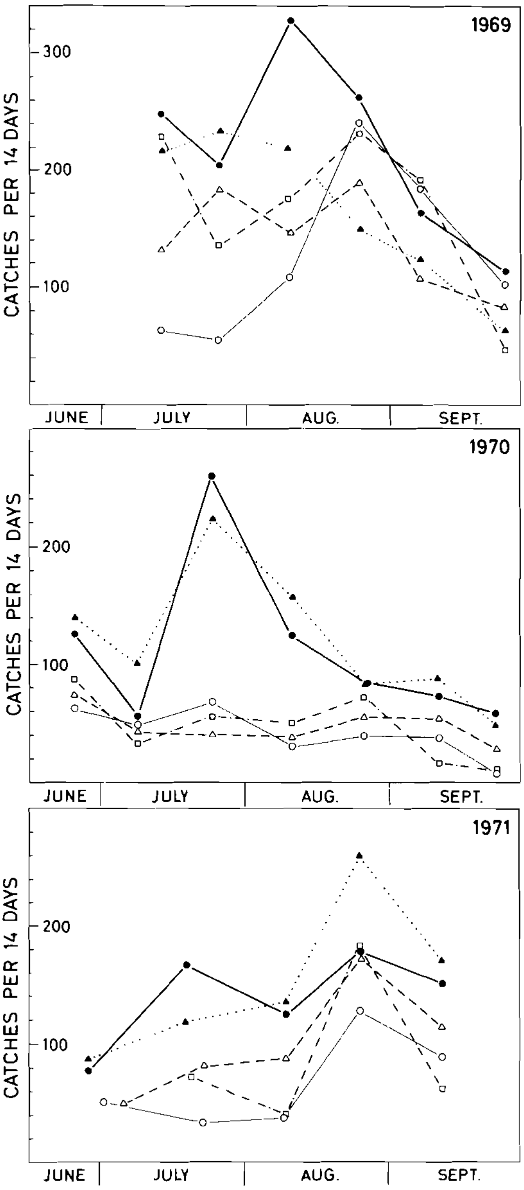


Fig. 1. Seasonal variations in pit-fall catches of Opiliones *(Mitopus morio)* during three years in five alpine habitats. Symbols: ▲ – the pioneer ground habitat, △ – the tussock or mesotrophic mire habitat, ● – the eutrophic meadow habitat, ○ – the oligotrophic dry heath habitat, □ – the snow bed habitat.

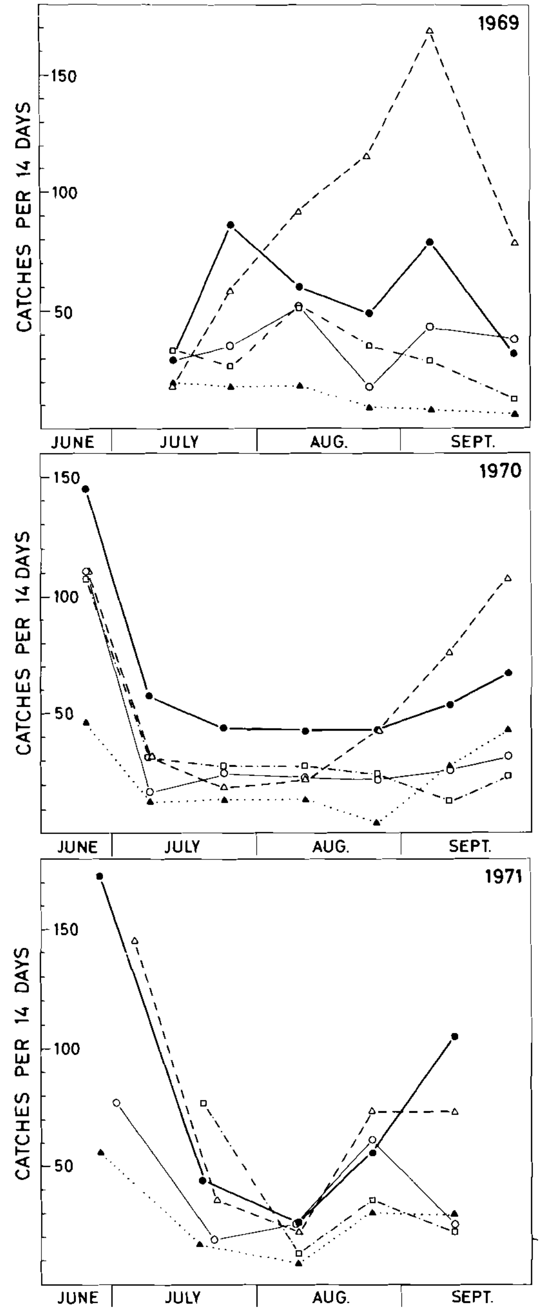


Fig. 2. Seasonal variations in pit-fall catches of Araneida during three years in five alpine habitats. Explanation of symbols is given in Fig. 1.

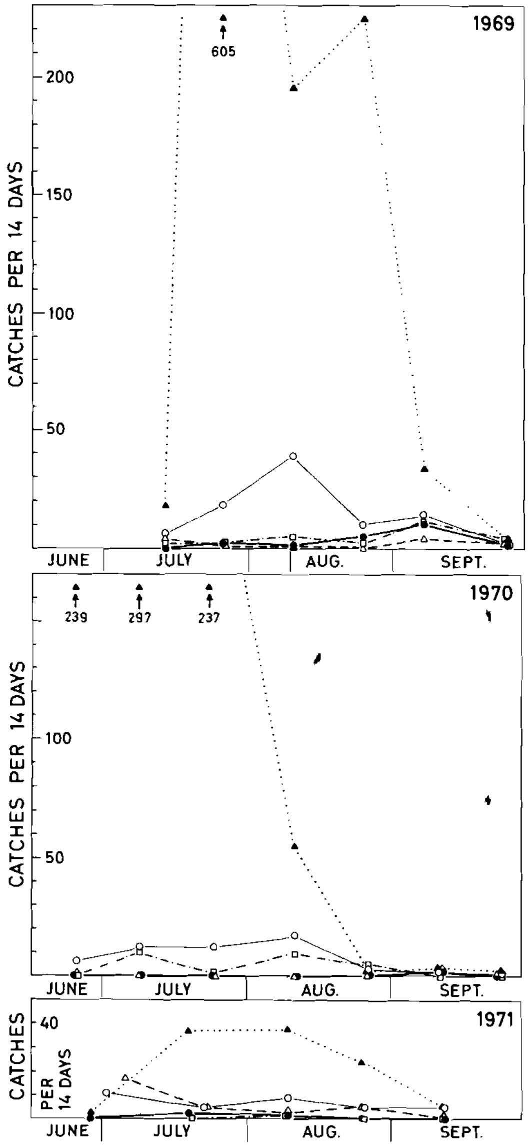


Fig. 3. Seasonal variations in pit-fall catches of Homoptera (mainly Cicadoidea) during three years in five alpine habitats. Explanation of symbols is given in Fig. 1.

in July and August, but high catches can occur even in June (1970).

Fig. 4 illustrates the catches of Carabidae. For all years the eutrophic meadow gave the highest number of animals, followed by the pioneer ground. The oligotrophic dry heath always gave very low catches of Carabidae. For all habitats, except the oligotrophic dry heath, the catches were highest shortly after snow melt, i.e. in June and part of July, becoming low throughout August and September. This picture was repeated every year.

The oligotrophic dry heath also gave very low catches of Staphylinidae (Fig. 5). Contrary to the

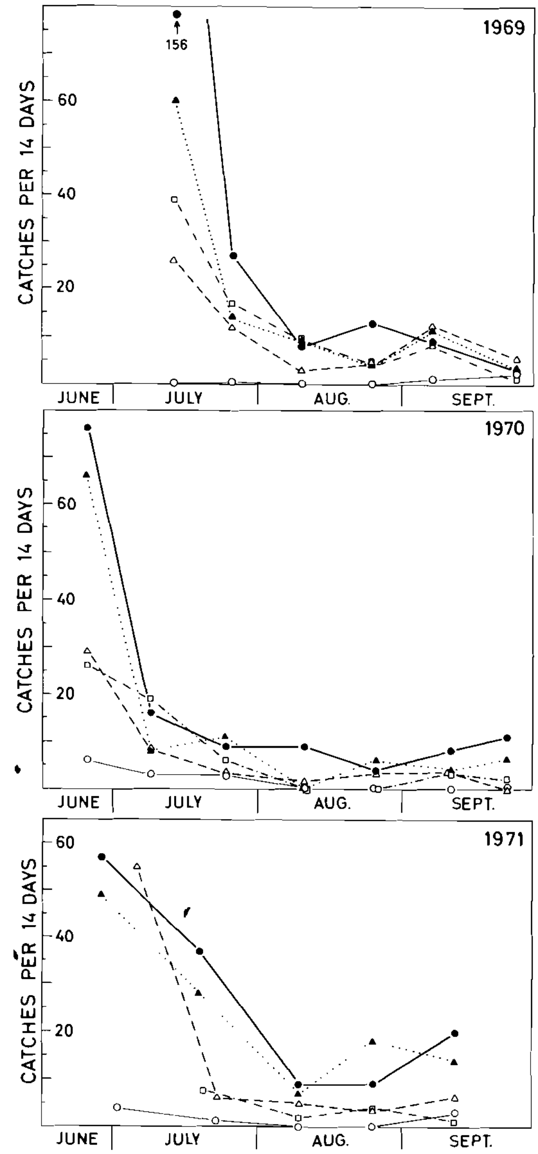


Fig. 4. Seasonal variations in pit-fall catches of Carabidae (Col.) during three years in five alpine habitats. Explanation of symbols is given in Fig. 1.

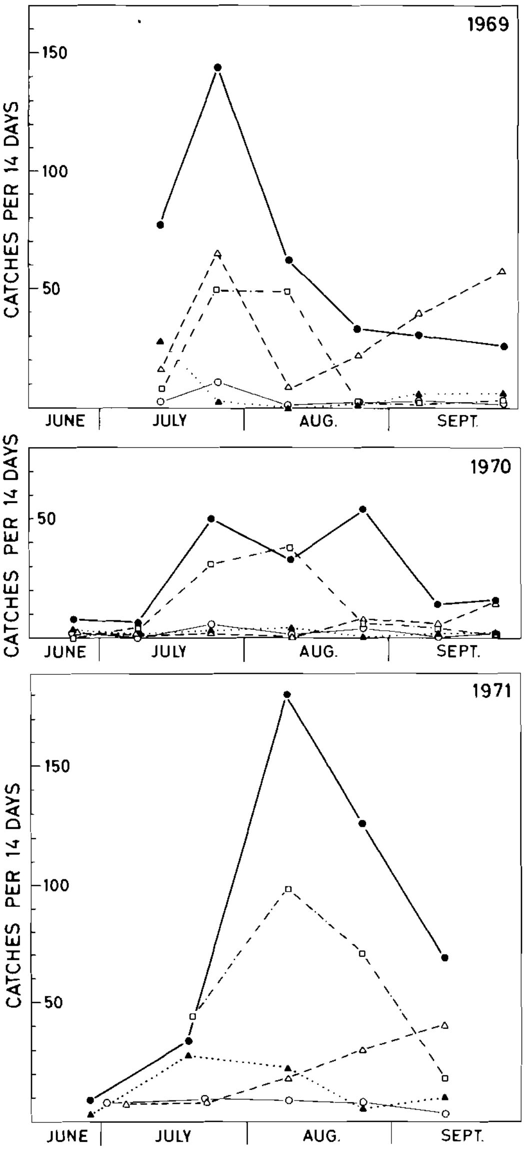


Fig. 5. Seasonal variations in pit-fall catches of Staphylinidae (Col.) during three years in five alpine habitats. Explanation of symbols is given in Fig. 1.

two former groups, however, even the pioneer ground proved to yield very little of this material. In all years, the bulk of this material was taken in the eutrophic meadow. During 1969, quite a few animals were also taken in the tussock habitat, and in 1971, the snow bed gave the second highest catches, also at a rather high level. There seems to be a general trend every year in the habitats giving the highest yields, for the main catches to be taken in the middle of the collecting season. In September each year, the catches from the tussock habitat were relatively high compared to the other habitats.

The picture of the total catches of Coleoptera (Fig. 6) is mainly a combination of Carabidae and Staphylinidae, as other families were relatively poorly represented. The eutrophic meadow always gave the highest catches, and the oligotrophic heath always the lowest catches of Coleoptera. The relative position between the

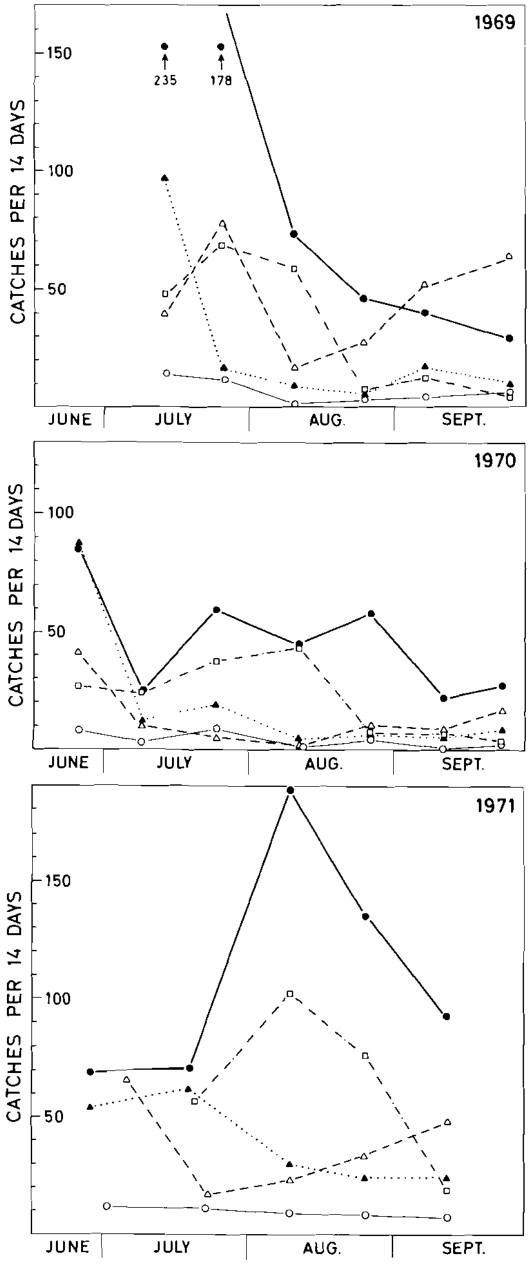


Fig. 6. Seasonal variations in pit-fall catches of Coleoptera during three years in five alpine habitats. Explanation of symbols is given in Fig. 1.

Table II. For some major arthropod groups, the habitat(s) which gave the highest pit-fall catch(es) is denoted with +, and the habitat(s) which gave the lowest pit-fall catch(es) is denoted with -.

Group	Pioneer ground	Eutrophic meadow	Oligo-trophic dry heath	Snow bed	Tussock habitat
Opiliones: *Mitopus morio*	+	+	-		
Araneida	-	+			+
Homoptera	+	-		-	-
Carabidae	+	+	-		
Staphylinidae	-	+	-		
Total Coleoptera		+	-		

other three habitats varied from year to year. As Carabidae were poorly represented in August and September, the coleopterous catches during these months were wholly dominated by Staphylinidae. Due to the high catches of Carabidae early in the season, total catches of Coleoptera might be highest in June or July (1969 and 1970).

For each of the groups presented in Figs. 1–6, the habitat (s) with the highest or lowest catch is respectively denoted as + or − in Table II. The eutrophic meadow gave high catches for all groups except Homoptera. Second is the pioneer ground, which gave catches of Opiliones and Carabidae approximately on a level with the eutrophic meadow. Moreover, high catches of Homoptera, but very low catches of Araneida and Staphylinidae, are typical for the pioneer ground. Third is the tussock habitat, which, together with the eutrophic meadow, gave high catches of Araneida. The snow bed and the oligotrophic dry heath did not yield the largest catches of any group. However, the snow bed gave medium catches of all the actual groups except Homoptera. The oligotrophic dry heath gave medium catches of Araneida and Homoptera, but very low catches of the other groups listed in Table II, apart from rather high catches of Opiliones in 1969.

We mention here a few other typical surface-active groups, which were poorly represented, but for which the method is probably suitable: Heteroptera, Mecoptera (the wingless *Boreus* sp.), Byrrhidae, and Curculionidae. Heteroptera is evidently a very rare group in this high mountain area, with only a few specimens trapped in the oligotrophic dry heath. *Boreus* sp., a well-known winter-active insect, occurred in all habitats except in the snow bed, but only during the last half of the season. Of the two coleopterous families Byrrhidae and Curculionidae, some specimens were taken in all habitats, mainly during the first half of the season. The highest catches of both were recorded in pioneer ground.

Here are a few remarks on the other groups trapped by this method (Table I). High numbers of Acarina were taken in all habitats, especially in the eutrophic meadow, the oligotrophic dry heath, and the snow bed. The main part of the material was trapped in the first half of the snow-free season. Still larger catches were made of Collembola, indicating a high activity of this group on the soil and litter surface of all habitats. The snow bed had the highest catches in 1969 and the eutrophic meadow the highest catches during the two next years, but the levels of the catches were not very different in the five habitats. In all habitats except the pioneer ground, Collembola represented more than half of the total pit-fall catches in all years. This percentage was lower in the pioneer ground mainly because of the large catches of Nematocera in this habitat. Most often the bulk of the Collembola was trapped in mid-season.

As seen from Table I, considerable amounts of Apocrita and Nematocera were trapped. For both groups, the catches were very much higher in the pioneer ground than in the other four habitats, and their peaks were in mid-season. Cyclorrhapha were represented to some degree in all habitats, mainly in the first half of the season.

The following groups were poorly represented in the material (Table I) and will not be further discussed: Plecoptera, Thysanoptera, Trichoptera, Lepidoptera, Brachycera, and Symphyta.

Discussion

The method: Its usefulness and its limitations

The usefulness of pit-fall traps has been discussed by several authors, e.g. Southwood (1966), Westerberg (1977), and Westerberg & Granstrøm (1977). The main conclusions of interest for the present material seem to be as follows:

Pit-fall catches of a given group are a measure of the 'surface-activity' of that group. This 'surface-activity' depends on three factors: 1. The density of animals, 2. The degree of activity of individuals, and 3. Restrictions to active movement necessitated by obstructions on the soil surface, mainly vegetation. The second factor varies with the developmental stage, with microclimate, and for some groups e.g. Araneida, with reproductive and non-reproductive periods. The third factor may change during the season within the same habitat, but is above all a factor which restricts the possibility of using differences in catches between habitats as a measure of relative density in these different habitats. Only if the vegetation is more or less equally dense at the soil surface, and if the microclimate is similar in the two habitats, can differences in catches during a certain period be taken as a measure of relative differences in density. If, however, the catches are larger in a habitat with denser vegetation and with a microclimate which is not more favourable than in another habitat, the density of animals is probably larger in the first habitat.

One of the main functions of pit-fall traps is to illustrate seasonal variations in activity of a species or group within one type of habitat. Such data may also reflect life cycles and reproductive periods. Very often, climatic factors cause a modification effect on the catch size

Westerberg (1977) recommended 20–30 traps (upper diam. 6.8 cm) per habitat for quantitative studies, which is somewhat higher than used in the present study. However, the periodically high catches of several groups indicate that the main trends in seasonal variations are correct.

For Cicadoidea, Westerberg & Granstrøm (1977) found that the seasonal changes in pit-fall catches were parallel to the changes in population size. Araneida did not, however, show this correlation.

Concerning the usefulness of qualitative studies, Westerberg (1977) considered 15–25 traps to be sufficient for taking the main species of the following groups: Araneida, Coleoptera (especially Carabidae), Formicidae and Proctotrupoidea among Hymenoptera, Cicadoidea, Heteroptera, Orthoptera and Opiliones.

Westerberg (1977) found that catches became, to some degree, selective after 5–7 days, e.g. Staphylinidae seemed to be attracted to the traps, and Araneida were to some degree repelled from them. As the catching periods were about two weeks in the present study, this may represent a source of error. This factor was, on the other hand, relatively constant. It was not possible, for practical reasons, to empty the traps weekly.

As the distance between traps and rows were 5 m, each trap 'covered' an area of 25 m^2 or more (those along the outer margins). In fact, only 3 traps of the 15 had neighbouring traps on all four sides. Westerberg (1977) found that if the distance between traps was 1 m or more, the traps worked independently, i.e. the catch in one trap did not reduce the potential catch in a neighbouring trap. In the present material, the traps along the outer margins of the 'trap system' did not achieve higher catches than the traps in the inner part. Still, of course, the presence of a trap will to some degree reduce the population of a species locally around the trap. At the same time, however, this reduction may be compensated for by immigration from the surroundings. We believe that with 25 m^2 or more as a potential catching area for each trap, the main trends in the seasonal changes in catches are due primarily to variations in activity. Catches will be discussed with this background.

Surface activity and habitat preference of the major predator groups

In this high mountain area, the most important surface-active invertebrate predator groups are evidently Opiliones, Araneida, Carabidae, and Staphylinidae. Of these, Opiliones yielded the highest catches and occurred rather numerously in all habitats, even in the oligotrophic dry heath.

As these predators need rather close contact to prey before discovering it, the amount of prey caught will depend on the distance covered per day by each predator specimen. Differences in pit-fall catches between habitats will express such differences in 'hunting activity', as the catches depend on the number of animals passing over a certain small area per time unit.

From Table II it is clear that the hunting activity of the dominant predators was highest in the eutrophic meadow, with high catches of all the four groups mentioned above. The pioneer ground was second, with high catches of Opiliones and Carabidae, while the tussock habitat had high catches of one predator group, Araneida.

The vegetation is very dense in the eutrophic meadow, and provides a rather high resistance to movement of surface-active invertebrates. When catches of the four groups still show such high values in this habitat, it must mean that the densities of these groups are also highest in this habitat. The high catches of Opiliones and Carabidae in the pioneer ground may partly be explained by the relatively low resistance offered by vegetation to acticity. In the tussock area, however, we may assume a rather high spider density, as high catches were made in a habitat with rather dense vegetation. The very low catches of Araneida and Staphylinidae in pioneer ground indicate very low densities of surface-hunting species of these groups, since the sparse vegetation should give a high catchability of active animals. Below, are listed some more comments on the separate groups.

Opiliones and Carabidae showed the same pattern with respect to relative catch size between habitats: Catches were highest in the pioneer ground and the eutrophic meadow, and lowest in the oligotrophic dry heath. This feature may probably be explained by similarities in the living pattern, and above all by the common habit of resting under suitable stones when not hunting.

Of the two favoured habitats, the pioneer ground had a very high coverage of stones, approximately 30% (Hågvar & Østbye 1972). This is the highest stone coverage of all the five habitats studied. A large portion of the stones was suitable as cover for Opiliones and Carabidae during rest. The habitat itself is rather dry, but the microclimate below stones may be favourable. The pioneer ground probably also offers adequate amounts of suitable prey.

The other habitat with high catches of the same two groups, the eutrophic meadow, is very different from the former, being rather moist with a rich vegetation. However, in common with the pioneer ground it allows probably good access to prey and to suitable 'resting stones'. Stones cover less than 10% of this habitat, but are often a suitable size (Hågvar & Østbye 1972). Comparing these two habitats, the moisture of the hunting ground seems to be unimportant. The snow bed too had a high stone coverage (12–20%) but the general density of surface invertebrates, which might serve as prey, is very low (Hågvar & Østbye 1974). The oligotrophic dry heath and the tussock area are very poor in suitable stones (Hågvar & Østbye 1972), and their pit-fall catches indicated rather low densities of suitable prey.

Opiliones hunt smaller invertebrates by touch (Phillipson 1960), and the single species present in the actual alpine area, *Mitopus morio*, can often be observed in the field, typically walking rather fast. As the different habitats in the Finse area are often small in extension and thus make up a rather complicated mosaic (J. Schmidt & E. Østbye, in prep.), one animal may come into contact with several types of habitat during one day's hunt. The fairly high catches of *M. morio* compared to other groups in all the five habitats indicate that it has a great tolerance for passing through different habitats.

The catches of Staphylinidae and Araneida, on the other hand, showed another distribution pattern between habitats. For both groups the catches were high in the eutrophic meadow and very low in the pioneer ground. Because of the sparse vegetation and the high catchability in the latter habitat, the density of both groups must have been much higher in the eutrophic meadow, at least where surface-active species are concerned. Even the tussock habitat gave rather high catches of both groups. A rich vegetation and correspondingly low catchability in this habitat indicate high densities of both groups. The eutrophic meadow and the tussock habitat were the habitats with the highest soil moisture.

The stone coverage seems to be of minor importance for pit-fall catches of Staphylinidae and Araneida, as the eutrophic meadow is rich and tussock area poor in stones. However, as shown by Hågvar & Østbye (1972), the fauna of larger arthropods occurring under stones is dominated by Araneida in all five habitats. Although some species of Araneida are obviously favoured by the presence of stones, many may occur numerously even in almost stone-free habitats like the tussock one.

Catches of other groups

Of the other groups listed in Table I, the method can probably be considered useful for Heteroptera and Homoptera (mainly Cicadoidea) (Westerberg & Granstrøm 1977, Westerberg 1977), and even for the actual wingless Mecoptera and the coleopterous families Byrrhidae and Curculionidae.

Homoptera was the only group among these where the catches differed greatly between habitats. The very high catches of Homoptera in the pioneer ground strongly indicate a preference for this habitat. This may be attributed to the presence of a favoured host plant. Very small numbers of Heteroptera, all specimens being trapped in the oligotrophic dry heath, were caught each year. This group is typically very poorly represented at high altitudes, the species number and density being strongly reduced from lowland to alpine habitats (Lindberg 1945, Hågvar 1976). General low catches of Byrrhidae and Curculionidae give a misleading picture of their relative density compared to other groups. Both groups are slow-moving, phytophagous animals which often rest below stones (Hågvar & Østbye 1972). However, the method confirms their presence in all five habitats, with little variation in total catches. Mecoptera is typically an autumn- and winter-active form, which lives off mosses (Strübing 1950, 1958, Svensson 1966, Fjellberg & Greve 1968, Østbye & Sømme 1969). The species seems to be eurytopic, as it was trapped in all habitats except the snow bed.

A few comments are given below on some of the other groups trapped, although the method is strictly designed for typical surface-active groups.

Acarina and Collembola seem to exhibit an intense surface activity in all habitats. It is a well known fact that these two groups play an important role among invertebrates in alpine and arctic habitats.

A striking feature each year are the very high catches of Nematocera and Hymenoptera Apocrita in some habitats. The highest catches of both groups occurred in the pioneer ground. We believe that these groups seek shelter under the roof above the jars and in this connection are trapped. Large concentrations of e.g. Nematocera have been observed sitting on the under side of the lids, perhaps seeking shelter from winds. The pioneer ground habitat especially may periodically be subject to strong winds. On the other hand, the very large catches of these groups in the pioneer ground are possible only if the general density in this actual habitat is very high. From a purely methodological point of view, it is interesting to note that pit-fall traps in alpine habitats can give valuable material on these two groups, often difficult to achieve by other methods.

Faunal differences between habitats

The method allows only a few reflections on this feature. However, the high catches of all four predator groups (and also of several other groups) in the densely vegetated eutrophic meadow, strongly indicated that this habitat of all five, has the most varied and dense fauna of surface-active invertebrates. Near the other end of both the moisture and soil fertility scales lies the oligotrophic dry heath, with generally low catches. Although in this habitat vegetation will obviously slow down the movability of surface-active animals, the very low catches indicate a relatively poor fauna. The other three habitats probably lie between these two extremes in regard to density of surface-active invertebrates.

As to relative composition of the surface-active fauna, the pioneer ground is separated from the eutrophic meadow by the small amounts of Araneida and Staphylinidae. Catches of these groups are so low that they must reflect very low real densities compared to Opiliones and Carabidae. However, the pioneer ground probably had the highest density of Homoptera. Looking at Table I, it is evident that the catches of many other groups were also high in this habitat. It is interesting to note that this, the youngest habitat, only about 200 years old, was one of the ones which gave the highest pit-fall catches.

Differences in catches between years

For each of the groups presented in Figs. 1–6, the habitats giving high, medium or low catches were mainly the same for all three years. Looking at the habitats which gave the highest catches of a given group, the total catches were not very different in all three years for Araneida and Carabidae. However, the catches of Araneida, and perhaps also Carabidae, would probably have been larger in 1969 if the traps had been put out earlier. Homoptera gave much lower catches in 1971 than in the two first years, catches of Opiliones were lower during the second and third years compared to the first, and the catches of Staphylinida were lowest in the second year. Thus the material does not indicate any common trend in variation of catch sizes between years for these groups.

1970 was a peak small rodent year, while the small rodent density was medium high in 1969 and low in 1971. It is difficult to relate the referred data to phases in the small rodent cycle because climatic differences between years are also important. However, the minima in recorded catches of the groups mentioned above, occurred either in the peak or the succeeding year.

Seasonal changes in catches

It is interesting to note that three of the four typical predator groups, i.e. Araneida, Carabidae, and Staphylinidae, showed rather fixed patterns regarding seasonal changes in catches. For each group, the same pattern was repeated in different habitats and also from year to year. This fact justifies the presentation of catches at the family and order level. Furthermore, the different shapes of the curves for seasonal catches in the three groups indicate that the groups tend to alternate in predation activity, so that seasonal changes in the total activity of larger invertebrate predators tend to be reduced. In spring, Carabidae and Araneida show peaks in activity; during summer Staphylinidae have their main hunting period, and in the autumn Araneida are again very active.

The fourth group, Opiliones, consisting of a single species, shows, however, no fixed pattern in catches, either in different habitats during the same season, or in the same habitat from year to year. The changes observed are discussed below in relation to climate.

Climate and activity of predators

The activity of all the actual predator species will, of course, be modified by climate. However, for Araneida, Carabidae, and Staphylinidae, the total phenology pattern of each group seems to be so fixed that even rather different climatic conditions from year to year do not disturb the main trend during the season.

Concerning the single species of Opiliones, however, no clear pattern of seasonal changes is evident from catches.

According to H. Kauri (pers. comm.), the eggs are laid in spring. After hatching, the population of the species will gradually be reduced during summer and autumn. In all years, there was a general reduction in catches during September. However, every year there were one or two marked peaks in catches in some habitats. Such peaks might occur in different months, for instance in July (1970), or in late August (1971). Of course the catchability of the specimens may vary with age, but if so this factor should not differ from year to year. Differences in the pattern of catches during the season must probably be attributed to different climatic factors. The peak recorded in all habitats during late August of 1971 is correlated with a dry warm period. Most of August in 1969 was also dry and very warm. In this period catches were rather high in all the five habitats. As, however, the catches were also high before and after this warm and dry period, this weather combination does not seem to be necessary for a high level of activity. Slagsvold (1976) found a correlation between mean air temperature and pit-fall catches of this species. Other factors, such as low wind speeds, may also be important for the species in this high mountain area.

Variation in curve shapes between habitats within the same year may partly be caused by different microclimatic conditions in the habitats, and perhaps too by different habitat preferences during different weather conditions. One may also assume that during very active periods, the animals become more evenly distributed in the terrain, with increasing densities in suboptimal habitats. The marked increase in catches in the oligotrophic dry heath during the warm and dry August of 1969 might be an example of this. At the end of August and at the beginning of September, the oligotrophic dry heath was among the habitats with highest catches. Earlier in the season, the catches in this habitat were clearly lower than in any of the others.

The marked peak recorded in two habitats in late July 1970 did not, however, coincide with a warm and dry period. On the contrary, it was rainy and relatively cold. This peak may be a result of the hatching of a new generation. In some habitats, there was also a tendency for a small peak in July even in the two other years.

Acknowledgements. – We wish to express our gratitude to all our colleagues who participated in the field work, especially A. Hagen, the late J. Hagen, J. Schmidt, H. J. Skar and D. Svalastog, and to M. Espeland for critically reading the manuscript. The investigations have been supported by grants from the Norwegian IBP. This work is part of the Hardangervidda IBP/PT-UM project.

References

Fjellberg, A. & Greve, L. 1968. Notes on the genus *Boreus* in Norway. *Norsk ent. Tidsskr. 15*, 33–34.

Hågvar, S. & Østbye, E. 1972. Quantitative and qualitative investigations of the invertebrate fauna under stones (the hypolithion) in some alpine habitats at Finse, south Norway. *Norsk ent. Tidsskr. 19*, 1–10.

Hågvar, S., Melåen, J. & Østbye, E. 1974. Quantitative studies of the invertebrate fauna in an alpine snow-bed community at Finse, south Norway. *Norsk ent. Tidsskr. 21*, 45–51.

Hågvar, S. 1976. Altitudinal zonation of the invertebrate fauna on branches of birch (*Betula pubescens* Ehrh.). *Norw. J. Ent. 23*, 61–74.

Lindberg, H. 1945. Zur Frage der vertikalen und horisontalen Verbreitung der europäischen Heteropteren. Ergebnisse von Einsammlungen im Rila-Gebirge in Bulgarien. *Notul. ent. 25*, 118–129.

Phillipson, J. 1960. A contribution to the feeding biology of *Mitopus morio* (F.) (Phalangida). *J. Anim. Ecol. 29*, 35–44.

Østbye, E., Haande, K. M., Haande, P. S., Hågvar, S., Melåen, J. & Skartveit, A. 1978. Pit-fall catches of surface-active arthropods in some high mountain habitats at Finse, south Norway. I. Introduction, methods, material, climate and habitat descriptions. *Norw. J. Ent. 25*, 189–193.

Slagsvold, T. 1976. The phenology of *Mitopus morio* (Fabr.) (Opiliones) in Norway. *Norw. J. Ent. 23*, 7–16.

Sømme, L. & Østbye, E. 1969. Cold-hardiness in some winter-active insects. *Norsk ent. Tidsskr. 16*, 45–48.

Southwood, T. R. E. 1966. *Ecological methods*. 391 pp., Chapman and Hall, London.

Strübing, H. 1950. Beiträge zur Biologie von *Boreus hiemalis* L. *Zool. Beitr. N. F. 1.*, 51–110.

Strübing, H. 1958. Schnee-insekten. *Neue Brehm Büch. Heft 220*, 1–47.

Svensson, S. A. 1966. Studier över nogra vinteraktiva insekters biologi. *Norsk ent. Tidsskr. 13*, 335–338.

Westerberg, D. 1977. Utvärdering av fallfällemetoden vid inventering av fält- och markskiktets lägre fauna. *Statens Naturvårdsverk PM 844, VINA Rapp. 5*, 1–72.

Westerberg, D. & Granström, U. 1977. Jämförelse av fångster från fallfellor, fönsterfellor och dammsugningsprovtagning av spindlar (Araneida) och stritar (Cicadoidea). *Statens Naturvårdsverk PM 845, VINA Rapp. 6*, 1–40.

Received 10 May 1978

Contribution from the Norwegian IBP/PT-UM sections.

Pit-fall catches of surface-active arthropods in some high mountain habitats at Finse, south Norway. III. The species of Araneida

ERLING HAUGE, SIGMUND HÅGVAR & EIVIND ØSTBYE

Hauge, E., Hågvar, S. & Østbye, E. 1978. Pit-fall catches of surface-active arthropods in some high mountain habitats at Finse, south Norway. III. The species of Araneida. *Norw. J. Ent.* Vol. 25, pp. 207–220. Oslo. ISSN 0029-1897.

Altogether 4251 spiders were taken by pit-fall trapping, and 522 hand-collected from under stones, in five alpine habitats during 3 snow-free seasons. Situated between 1220 and 1350 m a.s.l., these were: A tussock habitat (mire), snow bed, an oligotrophic dry heath, an eutrophic meadow, and pioneer ground. Forty species from four families were recorded, among which were several typical alpine species. Linyphiidae was the dominant family, followed by Lycosidae. Gnaphosidae and Thomisidae were less abundant. The number of species varied from 16 in the tussock habitat to 22 in the oligotrophic dry heath. The oligotrophic dry heath contained the largest number of species (six) not shared by the other habitats. Only five species were common to all habitats. Shannon-Weaver diversity indexes were low, varying from 1.69 to 2.34. Lists are given showing relative dominance between species for all habitats. Species composition and remarks on the ecology of the species involved are included in the discussion. Figures give the phenological data for nineteen species. Seventeen species periodically took advantage of the microhabitat under stones.

Erling Hauge, Zoological Museum, N-5014 Bergen-Univ. Norway. Sigmund Hågvar, Norwegian Forest Research Institute, N-1432 Ås-NLH, Norway. Eivind Østbye, Zoological Institute, Box 1050, University of Oslo, Blindern, Oslo 3, Norway.

As is the case for most invertebrate groups, our knowledge of the spider fauna in Norwegian high mountain habitats is scant. The present paper deals with spider material collected by pit-fall traps during three years (1969–71) in five alpine habitats near Finse, Hardangervidda, south Norway (60°36'N, 7°30'E) (UTM 32V MN 11). The main purposes were to study the species composition in different habitats and to reveal the phenology pattern of the actual species. In addition, a smaller sample of spiders was collected by hand under stones in all habitats (Hågvar & Østbye 1972). The total catches of Araneida have been presented in a previous paper (Hågvar, Østbye & Melåen 1978).

The main task of writing together with the identifications was the responsibility of E. Hauge, while S. Hågvar performed the calculations and presentations of the data. E. Østbye was responsible for the planning of the study.

Material and methods

The five habitats have been described in detail by Østbye et al. (1978). A short review will be given here. The pioneer ground is situated quite near a glacier, and the habitat is about 200 years old. It is rich in surface stones and does not have a continuous vegetation cover. The eutrophic meadow is rather moist and rich in vegetation. The oligotrophic dry heath, which is a dominant vegetational type in the area, is to a large extent covered by lichens. In the snow bed, the snow melts rather late, and the vegetation is dominated by *Salix herbacea*. Finally, the tussock habitat has an extensive tussock formation and an oligotrophic dwarf mire vegetation on ombrogenous, topogenous peat bog. The five habitats are situated in the mid- and the low-alpine zones, between 1220 and 1350 m a.s.l.

In each habitat, fifteen traps, 7 cm in upper diameter, were operated during most of the snow-free season. They were placed in three rows, 5 m between each trap and row, and were emptied about every two weeks. In total, 4251 spiders were trapped, and in addition, 522 specimens were collected under stones.

For a more detailed discussion on the usefulness of the pit-fall trap method, see Hågvar et al. (1978). The climate during the three seasons is described in Østbye et al. (1978).

Table I. Per cent distribution of the different spider families among adults and juveniles in catches from each of the five habitats. Total catches are also given. Data from three years.

	Habitat Family	Pioneer ground	Eutrophic meadow	Oligotrophic dry heath	Snow bed	Tussock habitat
Adults	Linyphiidae	83.7	98.6	52.5	92.4	87.8
	Lycosidae	13.4	1.4	42.0	7.2	11.7
	Gnaphosidae	2.9	-	3.6	0.4	0.5
	Thomisidae	-	-	1.9	-	-
	Total number	246	941	635	473	1060
Juveniles	Linyphiidae	67.0	99.7	36.2	96.7	94.7
	Lycosidae	33.0	0.3	59.7	3.3	4.5
	Gnaphosidae	-	-	3.4	-	0.8
	Thomisidae	-	-	0.7	-	-
	Total number	106	314	149	61	266
	% juveniles	30.1	25.0	19.0	11.4	20.1

The material is preserved in 80% alcohol and deposited at the Zoological Museum, Bergen.

Results and discussion

As pointed out in a previous article in this series (Hågvar, Østbye & Melåen 1978), the pit-fall method is selective and expresses the activity level of the animals rather than their density. In spite of this, as the same method was used in all habitats, the catches in different habitats give valuable information on phenology, species composition and, to some degree, on density variation.

The families represented

The spider material collected under these extreme high mountain conditions is limited to only four families (Table I). Linyphiidae was the dominant one, followed by Lycosidae. Gnaphosidae and Thomisidae were only taken in very small quantities.

The highest percentage of Linyphiidae was found in the eutrophic meadow (almost 100%). Even in the pioneer ground, tussock habitat, and snow bed, the Linyphiidae percentage was quite high. However, in the oligotrophic dry meadow (the only really dry locality), the percentage of Linyphiidae dropped to 52.2% for adults and 36.2% for juveniles.

The proportion of juveniles in the total catches was generally quite low, varying from 11.9% in the snow bed to 30.1% in the pioneer ground (Table I). This is an obvious underestimation of the juvenile content of the populations, due to the higher activity level and thus catchability of adult animals.

The species composition in the catches

Only adults were identified to species. Altogether 40 species were trapped, varying from 16 to 22 in the respective habitats. The total number of adult spiders caught within each species in different habitats is presented in Table II. Obviously, great differences exist in the composition of the spider material collected in the various habitats. The differences can be indicated by the Sörensen index of similarity (Sörensen 1948) (Table III). The index values are all low and vary between 35 and 65. This implies that even under the extreme conditions of this high mountain area, very different ecological conditions exist. These differences, which are reflected by the different plant associations, have a profound effect on the species composition of spiders. Only five of the total of 40 species recorded were taken in all five habitats.

If we calculate the Shannon/Weaver index of general diversity (Shannon & Weaver 1963) from the data in Table II, the following values are achieved: Pioneer ground 2.34, snow bed 2.34, eutrophic meadow 2.31, oligotrophic dry heath 1.92, and tussock habitat 1.69, respectively. The first three habitats have similar values, which are also clearly higher than those for the two last ones. Compared to indexes calculated from various forest habitats in Western Europe (Jocque 1973), the values from the actual alpine habitats are all quite low, as could be expected.

A common feature of the spider fauna of all five habitats is a predominance of typical alpine and northern species. Below, the species composition of each habitat is discussed.

The pioneer ground

The species list from this habitat contains many exclusive alpine species, at least as far as southern Norway is concerned. Among these should be mentioned the five most dominant species in that locality: *Hilaira frigida, Cale-*

Table II. Total numbers(♂/♀) of adult spiders and their dominances (%) in pit-fall trap material from five habitats during three years. Species recorded under stones are also denoted (+).

SPECIES / HABITAT	PIONEER GROUND			EUTROPHIC MEADOW			OLIGOTROPHIC DRY HEATH			SNOW BED			TUSSOCK HABITAT		
	♂/♀	dominance (%)	u.stones	♂/♀	dominance (%)	u.stones	♂/♀	dominance (%)	u.stones	♂/♀	dominance (%)	u.stones	♂/♀	dominance (%)	u.stones
Ceratinella brevipes (Westr.)				3/7	1.1					0/1	0.2	+			
Walckenaera cuspidata Blw.										1/2	0.6		5/6	1.0	
W. karpinskii (O.P.-Cbr.)							5/6	1.7		1/0	0.2	+			
Gonatium rubens (Blw.)	1/1	0.8		0/4	0.4		28/127	24.4		22/58	16.9				
Oedothorax retusus (Westr.)							0/1	0.2		1/0	0.2				
Trichopterna mengei (Simon)	0/1	0.4		228/85	33.3	+	1/0	0.2		29/28	12.1		520/41	52.9	
Metopobactrus prominulus (O.P.-Cbr.)							1/0	0.2							
Tiso aestivus (C.L. Koch)	27/13	16.3		1/0	0.1							+			
Erigone atra (Blw.)				0/1	0.1					3/0	0.6		7/3	0.9	
E. arctica (White)	1/1	0.8		0/1	0.1										
E. tirolensis C.L. Koch	7/8	6.1	+	63/58	12.9	+				42/24	14.0	+			
E. psychrophila Thorell	1/2	1.2		17/63	8.5	+							5/25	2.8	+
Collinsia holmgreni (Thorell)	5/3	3.3	+	54/130	19.6	+	0/1	0.2		31/59	19.0	+	3/15	1.7	+
Latithorax faustus (O.P.-Cbr.)				1/1	0.2		11/7	2.8							
Caledonia evansi O.P.-Cbr.	28/2	12.2		12/0	1.3	+						+			
Rhaebothorax sphagnicola Holm													65/58	11.6	+
R. morulus (O.P.-Cbr.)				3/1	0.4		0/1	0.2		10/10	4.2	+	0/1	0.1	
R. monticola Holm							3/8	1.7					0/3	0.3	
Diplocentria replicata Holm													1/1	0.2	
Hilaira frigida (Thorell)	28/23	20.7	+	111/26	14.6	+	41/31	11.3	+	29/6	7.4	+	8/11	1.8	+
H. nubigena Hull							38/4	6.6					71/20	8.6	
Oreonetides vaginatus (Thorell)	9/5	6.5	+	30/10	4.3	+	4/9	2.0	+	10/20	6.3	+	12/14	2.5	
Porrhomma campbelli F.O.P.-Cbr.				0/1	0.1										
Agyneta decora (O.P.-Cbr.)													20/8	2.6	
Meioneta nigripes (Simon)	2/20	8.9	+												
Bathyphantes gracilis (Blw.)	0/2	0.8		12/4	1.7		0/1	0.2		1/3	0.6				
Lepthyphantes alacris (Blw.)										1/1	0.4	+			
L. tenebricola (Wider)	5/3	3.2	+	2/1	0.3							+			
L. complicatus (Emerton)	2/0	0.8					1/2	0.5	+						
L. mengei Kulcz.							0/3	0.5							
L. pallidus (O.P.-Cbr.)							1/0	0.2							
Tricca alpigena (Doleschal)				2/2	0.4		5/11	2.5		1/0	0.2		10/18	2.6	
Pardosa palustris (L.)	1/0	0.4		5/2	0.5		120/122	38.1	+	43/33	16.1	+	68/38	10.0	
P. traillii (O.P.-Cbr.)	17/16	13.4													
P. septentrionalis Westr.	2/1	1.2													
P. riparia C.L. Koch				0/1	0.1										
Micaria alpina C.L. Koch	7/2	3.7													
Gnaphosa leporina (C.L. Koch)							2/0	0.3							
G. lapponum (C.L. Koch)							16/6	3.5		3/0	0.6		2/1	0.3	
Oxyptila rauda arctica Kulcz.							5/3	2.8							
O. atomaria (Panzer)							0/1	0.2							
TOTAL NUMBER OF SPECIMENS	246			941			635			473			1060		
NUMBERS OF SPECIES	18		6	20		7	22		4	17		12	16		4
NUMBERS OF SPECIES UNDER STONES ONLY			0			0			0			3			0
NUMBERS OF SPECIES NOT SHARED BY THE OTHER HABITATS	4			2			6			1			3		
SHANNON-WEAVERS INDEX	2.34			2.31			1.92			2.34			1.69		

donia evansi, Tiso aestivus, Pardosa traillii and *Meioneta nigripes*. In addition should be mentioned *Erigone psychrophila, Collinsia holmgreni,* and *Lepthyphantes complicatus*. All these eight species were not found below the timber line by Holm (1950) in the Torneträsk area, northern Sweden (although *H. frigida, T. aestivus* and *L. complicatus* were found in Holm's regio subalpina).

The remaining species from the pioneer ground may (at least in northern Scandinavia) also be quite frequent in the regio silvatica, but even here species such as *Oreonetides vaginatus* and *Trichopterna mengei* have their highest frequencies above the timber line. Both of these, and perhaps also *Micaria alpina* (only taken in the pioneer ground), ought to be classified among the characteristic alpine species of southern Norway. *O. vaginatus* was caught in all five

Table III. A comparison of the spider fauna in the five habitats using Sörensen's index of similarity (S x 100) (Sörensen 1948), based on data from Table II.

	Pioneer ground	Eutrophic meadow	Oligotrophic dry heath	Snow bed	Tussock habitat
Pioneer ground		63	40	46	35
Eutrophic meadow	63		48	65	50
Oligotrophic dry heath	40	48		63	53
Snow bed	46	65	63		62
Tussock habitat	35	50	53	62	

localities at Finse (Table II), indicating a eurytopic species in the mountain areas. With the reservation that previous records of *Pardosa eiseni* in Norway are correct, the finding of *P. traillii* here should be regarded as the first record from Norway, or even Scandinavia (the material has been checked by Dr. Torbjörn Kronestedt, Stockholm). The species is, as far as we know, previously known only from Great Britain, where it has been taken only in mountain areas in northern England and Scotland, especially in screes (Locket & Millidge 1951). It was trapped only in the pioneer ground at Finse.

The tussock habitat

Here the lowest number of species was recorded (16). However, the tussock habitat gave the highest catches of spider specimens. This combination explains the low diversity index. The habitat is humid, and the species list (Table II) contains a relatively high number of hygrophilus species. The dominant one, *Trichopterna mengei* (52.9%), belongs to these, as does the second dominant, *Rhaebothorax sphagnicola* (11.6%). *T. mengei* has been characterized as a hygrophilous species by Locket & Millidge (1951), Wiehle (1960), and Palmgren (1965, 1972, 1976). Palmgren (1965) thus found this species in great quantities on the beaches of lakes in the Kilpisjärvi area (northern Finland). This is also in accordance with the fact that the species in our material is the dominant one on the eutrophic meadow (33.3%), and also very common in the snow bed (12.1%), while it is hardly present on the oligotrophic dry meadow (0.2%), and in the pioneer ground (0.4%).

Rhaebothorax sphagnicola is reckoned by both Holm (1950) and Palmgren (1965) to be a pronounced hygrophilous species. According to the latter, it is stenotopic but frequent on moors. At Finse, the tussock area is the only locality where this species is found. Holm (1950) found the species from regio subalpina up to about 1100 m a.s.l. in regio alpina, and Palmgren (1965) from regio silvatica up to about 1200 m a.s.l. In southern Norway it should probably be reckoned as a typical alpine species.

Other species in the tussock habitat which are limited to humid conditions are *Erigone psychrophila, E. atra, Walckenaeira cuspidata,* and probably *Agyneta decora*. The last is reckoned to be rare and stenotopic. It was found only in this habitat, while the more eurytopic *Erigone atra* has been found also in the two other humid habitats, the snow bed, and the eutrophic meadow. According to Palmgren (1965), *Hilaira nubigena* has its highest frequencies in relatively humid habitats; and most of the habitats listed by Holm (1950) are humid. However, the fact that the species was quite common on the dry meadow as well reflects a larger flexibility than indicated by literature. It is, however, more stenotopic than *H. frigida*.

The eutrophic meadow

As for the tussock habitat, the list from the eutrophic meadow is topped by *Trichopterna mengei* (33.3%), The high percentage of *Collinsia holmgreni* (19.6%) here, and even in the snow bed (19.0%), is consistent with the characterization given by Brændegård (1958): '... a humid species'. In the other habitats it is present in smaller quantities, especially on the oligotrophic dry heath (Table II). The humid conditions of the eutrophic meadow may also be connected with a high percentage of *Erigone psychrophila* (otherwise 2.8% on the tussock habitat and a few specimens on the pioneer ground). It is absent on the dry meadow and the snow bed. Most specimens of *Bathyphantes gracilis* have been found on the eutrophic meadow. According to Palmgren (1965), Dahl (1912), Tretzel (1952) and Knülle (1953), the species is hygrophilous; while Braun & Rabeler (1969), referring to several authors, indicate that the species is more flexible where humidity is concerned. In our material, it is absent from the wet tussock area, while it is present (1 specimen!) at the dry meadow. Obviously, humidity is not the main factor regulating its habitat choice. Other xerophilous elements occurring in low numbers on the wet meadow are *Rhaebothorax morulus* and *Tiso aestivus*.

The snow bed

Hygrophilous elements on the snow bed are *Collinsia holmgreni* (19.0%), *Trichopterna mengei* (12.1%), *Erigone atra* (0.6%), and *Oedothorax retusus* (0.2%). However, the hygrophilous elements are not so pronounced here as they are on the eutrophic meadow and on the tussock habitat. The total for the whole season shows strong elements of both hygrophilous and less hygrophilous species in catches from this habitat. This mixture explains the high diversity index. Characteristic for the habitat is rather moist conditions during the first period after snow melt, while conditions may become more dry late in the season.

The oligotrophic dry heath

The highest number of species was found in this habitat (22 species). This is the only really dry locality of the five. Typical is the absence of, or a very low percentage of, several 'hygrophilous' species which may be more or less common on the other localities. On the other hand these localities lack some xerophilous species which occur in the dry heath list: *Oxyptila rauda arctica, Rhaebothorax monticola* (also 3 specimens on the tussock area), and *Metopobactrus prominulus*. The dry meadow is the only locality which has a member of Lycosidae as the dominating species *(Pardosa palustris)*. In this connection it is noteworthy that the relatively large forms – Lycosidae, Thomisidae, and Gnaphosidae – dominate the picture here more than in the other localities (Table I). Gnaphosidae are also relatively frequent on the pioneer ground. One possible explanation of this might be that the thermic conditions on the oligotrophic dry heath and the partly dry, rocky pioneer ground favour such large, heat-demanding species.

Phenological and ecological remarks on the species

The seasonal variations in the catches of the most common species are shown in Figs. 1–19. Each plot has been placed in the middle of a sampling period and represents the total catch of adults in fifteen traps, adjusted to a standard period of fourteen days. In 1969, data from the second sampling period in the snow bed are lacking. The percentage of males in the catches is only included in the columns when the total number of adults trapped in a given sampling period exceeded ten.

A high number of *Pardosa palustris* immediately after snow melt coincides with a relatively high percentage of males in the catches (Fig. 1). This percentage falls steeply over a short period of time. Females occur throughout the whole season. This picture is typical for the data from 1970 and 1971. In 1969 we probably lost the spring peak, as the traps were set out later after snow melt that year. This yearly pattern agrees with Palmgren (1965) from northern Finland, and also with several other authors e.g. Dahl & Dahl (1927), Tretzel (1954), Pearson & White (1964), Merrett (1968), and Palmgren (1972). It seems therefore that the actual alpine populations do not deviate much from lowland populations as concerns phenology. However, Steigen (1976) has demonstrated a 3 year life cycle in the Norwegian high mountains for this species. It is obvious that it is the adult part of the population in any actual year which predominates in the catches.

In the first collecting period of the season, the remaining *Pardosa* species in our material are represented by males only. *P. traillii* (Fig. 2): 1 ♂ 9–17 July 1969, 13 ♂♂ 16 June–3 July 1970. Eight out of the 15 females were caught as late in the season as August/September in 1969 and 1971. The very few specimens of *P. septentrionalis* (2 ♂♂ +1 ♀) were caught 16 June – 3 July 1970.

A characteristic feature of the *Trichopterna mengei* material from Finse (Fig. 3) seems to be that the species is relatively inactive early in the season. This concerns especially the males, whose absolute numbers and relative abundance in the catches increase strongly towards the end of each season. In literature there is a general tendency for the largest numbers of males to be found in spring and autumn (Wiehle 1960, Palmgren 1965, 1976). Palmgren (1976, Fig. 3) indicates several adult specimens in winter (January–March) in northern Finland. It is reasonable to suppose that this species is eurychron, with a maximum number of adults from early autumn to early spring, and with a relatively low number of active adults (especially males) in early spring-midsummer. The last statement agrees well with results from quantitative samples from northern Norway (Hauge 1977).

As with *Pardosa palustris,* we probably lost an early spring peak in 1969 for *Hilaira frigida* (Fig. 4) due to a late start of sampling that season. Both sexes are trapped throughout the whole season, but it seems clear that male activity shows a marked peak in early spring and late autumn. There was a less marked minimum in midsummer 1969 than in the following year. In contrast to our data, Palmgren (1975) found that males were sparse in spring, and that a maximum number of adults were found in late summer/autumn.

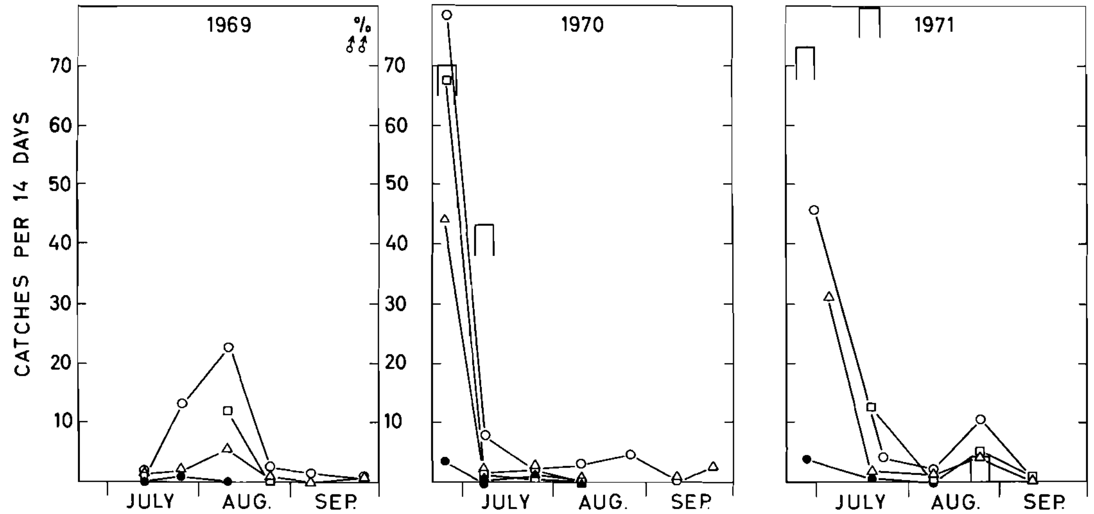


Fig. 1. Seasonal variations in pit-fall catches of adult *Pardosa palustris* during three years. Columns indicate the percentage of males during a given sampling period, when the total number of adults was ten or more. Symbols: ▲ – the pioneer ground habitat, △ – the tussock or mesotrophic mire habitat, ● – the eutrophic meadow habitat, ○ –the oligotrophic dry heath habitat, □ – the snow-bed habitat.

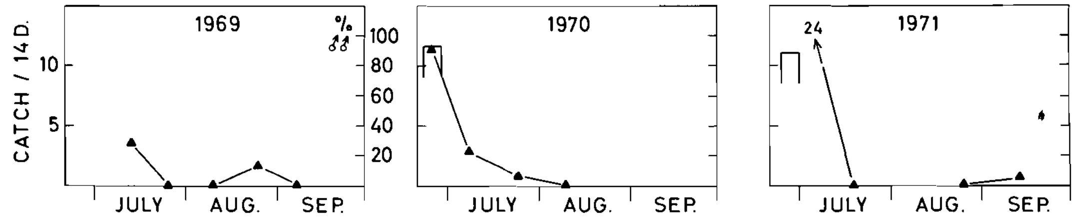


Fig. 2. Seasonal variations in pit-fall catches of adult *Pardosa traillii* during three years. Explanation of symbols is given in Fig. 1.

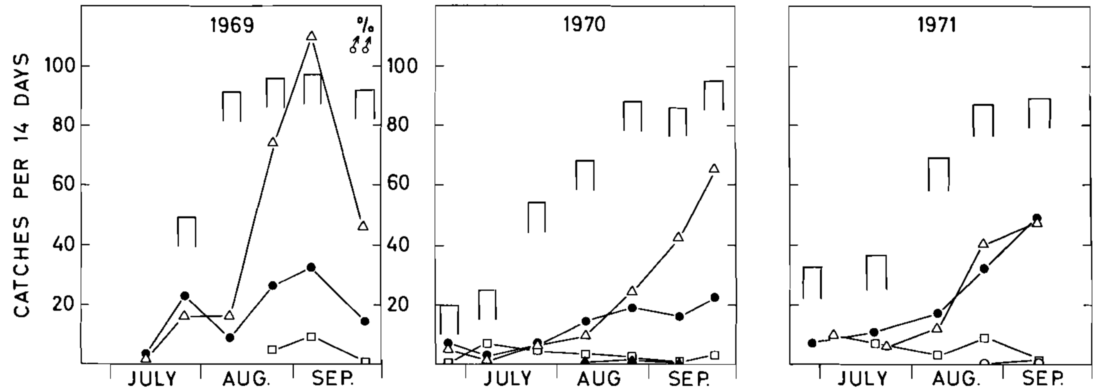


Fig. 3. Seasonal variations in pit-fall catches of adult *Trichopterna mengei* during three years. Explanation of symbols is given in Fig. 1.

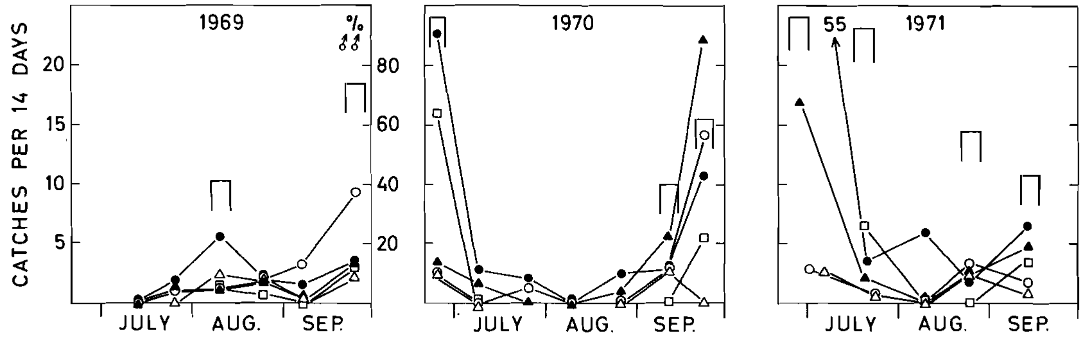


Fig. 4. Seasonal variations in pit-fall catches of adult *Hilaira frigida* during three years. Explanation of symbols is given in Fig. 1.

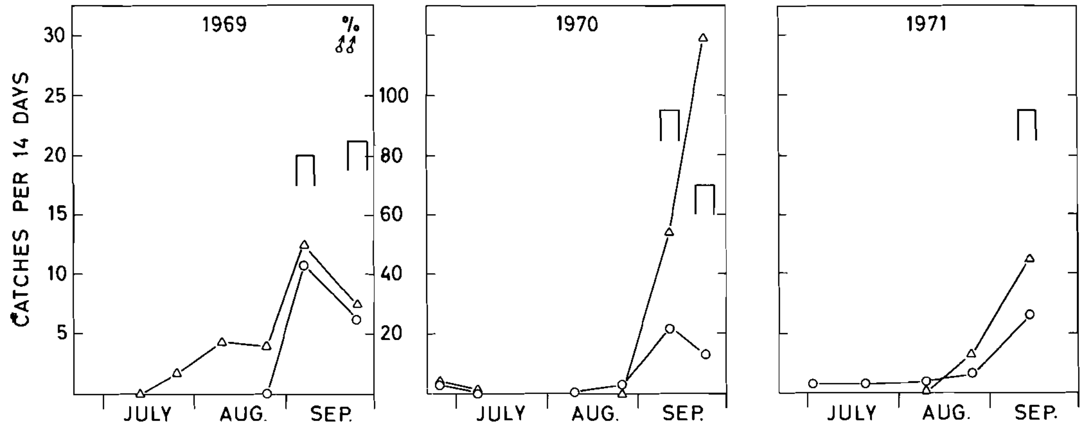


Fig. 5. Seasonal variations in pit-fall catches of adult *Hilaira nubigena* during three years. Explanation of symbols is given in Fig. 1.

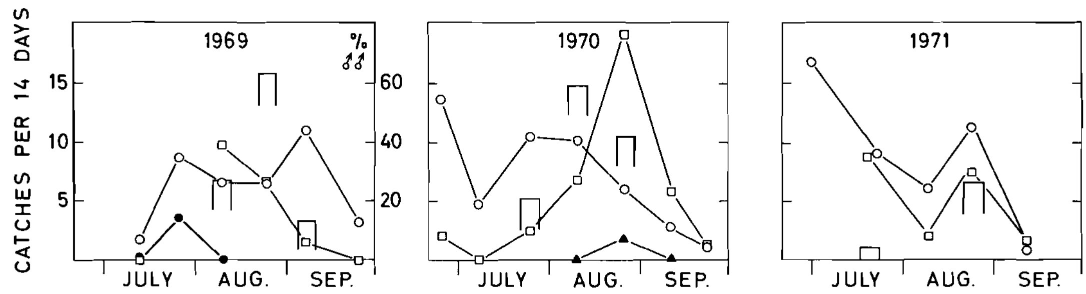


Fig. 6. Seasonal variations in pit-fall catches of adult *Gonatium rubens* during three years. Explanation of symbols is given in Fig. 1.

H. nubigena (Fig. 5) is phenologically more in accordance with Palmgren (1975): The majority of our catches are concentrated at the end of each season (August–September/October), while only a few specimens were taken in the first sampling period of the season. However, the remnants of an adult population of both sexes in spring indicate that this species in the Finse area, like *H. frigida*, maintains an adult population during the winter months towards spring. The difference between the actual *Hilaira* species seems to be that adults of *H. frigida* are active during a longer period in spring and summer.

Gonatium rubens is absent from the tussock area only, and the largest catches were taken in the dry meadow (24.6%) and in the snow bed (16.9%) (Table II). The numbers of females are quite large from about June/primo July and during the rest of the snow-free period. However, the first males are caught not earlier than ca. medio July and reach a sort of maximum about medio August/beginning of September (Fig. 6). After that time very few males are taken in the traps. This maximum period agrees fairly well with Wiehle (1960) (most ♂♂ in August/September). Thus in this Finse population there is no significant delay as concerns the time for adults compared to the lowland populations in Middle-Europe. Merrett (1969) indicates a still later autumn period ('male activity from September to mid- December') and females active throughout the whole year. Palmgren (1965, 1975) found both sexes from spring to autumn, and relatively high numbers of males in summer. Tretzel (1954) indicates a spring aspect (most ♂♂ in April), and some males also in January and August. A spring and autumn maximum is also indicated by Vilbaste (1964, Tab. 10), while she otherwise (Vilbaste 1969) gives only an autumn aspect.

The catches of *Caledonia evansi* (Fig. 7) are strongly concentrated to the very end of the season, quite in accordance with Palmgren (1972): 'Seasonal type XIII'.

Collinsia holmgreni is also a mountain species (see Palmgren 1976), but, in contrast to *C. evansi,* it has been found in all five localities. Phenologically it is in accordance with Palmgren (1976), both sexes being active throughout the whole snow-free season. Fig. 8 may indicate a certain minimum in the males' relative abundance around August/beginning of September, with a maximum in activity before and after that period. Probably a new adult population is built up in the autumn (high activity in September). These adults hibernate and cause another maximum in activity during July.

All four *Erigone* species are absent from the dry meadow (Table II), and all are present at the wet meadow. The maximum male activity of *E. tirolensis* (Fig. 9) is close to the beginning of the season. A certain minimum occurs in the middle of the season, while the activity increases further towards the end of the season. Thus, this species should also be included in eurychron species with relatively high numbers of overwintering adults. This is in contrast to Palmgren (1976), who suggests that the species owerwinters as juveniles. The same conclusions can be drawn for *E. psychrophila* (Fig. 10). Males are lacking in the pit-fall catches during the middle of each season (ca. July–August).

None of the three *Rhaebothorax* species have been found in the pioneer ground, but all were taken at the tussock habitat (Table II). *R. sphagnicola* is obviously the most stenotopic species; a specialist which accounts for 11.6% of all adult specimens in the tussock area. These ecological data should fit well with data and statements presented by Holm (1939, 1950) and Palmgren (1965). The greatest concentrations of adult specimens (especially males) of this species were trapped in the earliest sampling periods of the season (Fig. 11, we missed the first period in 1969). Both sexes are found until about the middle of August. From that time for one month onwards (except for one male), only females were found. From the middle of September again, a few males were caught in the traps, which seems to confirm Palmgren's (1976) assumption that the species overwinters as adult. However, contrary to the present material, he did not find males in spring. Holm (1943) found males in July, which were probably overwintered animals.

R. morulus (Fig. 12) was taken at four localities, and is probably the most eurytopic of these three *Rhaebothorax* species. The material is small and spread throughout the whole season for both sexes, and thus lies within the range of Palmgren's data (Palmgren 1976, Fig. 37).

R. monticola, here reported for the first time in Norway, was found at two localities (Table II). It is by Holm (1943) reckoned to be a rather xerophilous species, and it seems to be restricted to regio subalpina and regio alpina (Holm 1950). The few females in our material were evenly distributed over the season, while the three males were all caught in the period 15 August – 15 September.

Oreonetides vaginatus (Fig. 13) has a peak of activity early in the season, but a few males were found as late as in August. Later in the season, the number of males in the catches increased again. It is obvious that adult animals overwinter. Palmgren (1965) also found in northern Finland mainly adult males during early spring and late autumn, and only relatively few females and no males during summer. Lockett & Millidge

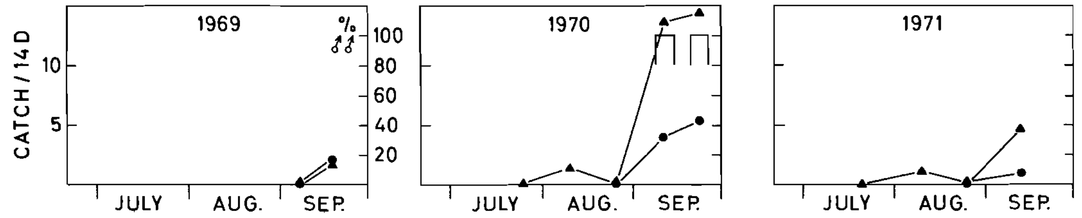


Fig. 7. Seasonal variations in pit-fall catches of adult *Caledonia evansi* during three years. Explanation of symbols is given in Fig. 1.

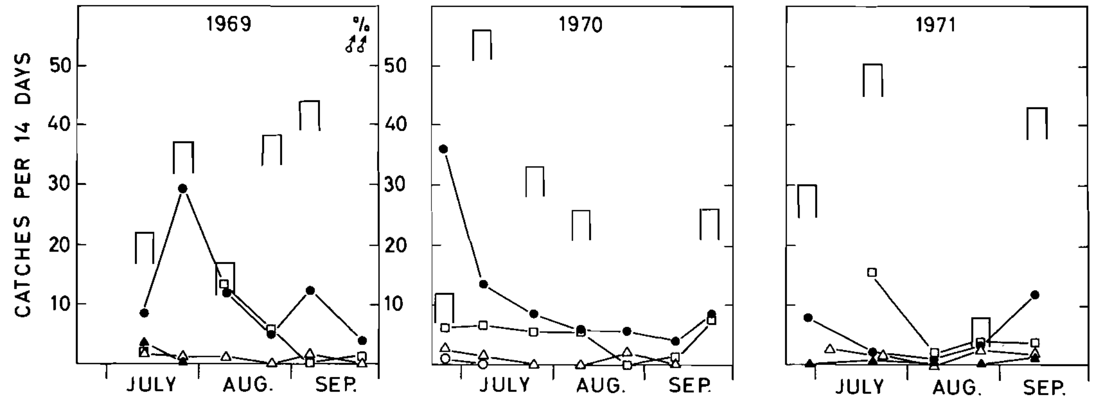


Fig. 8. Seasonal variations in pit-fall catches of adult *Collinsia holmgreni* during three years. Explanation of symbols is given in Fig. 1.

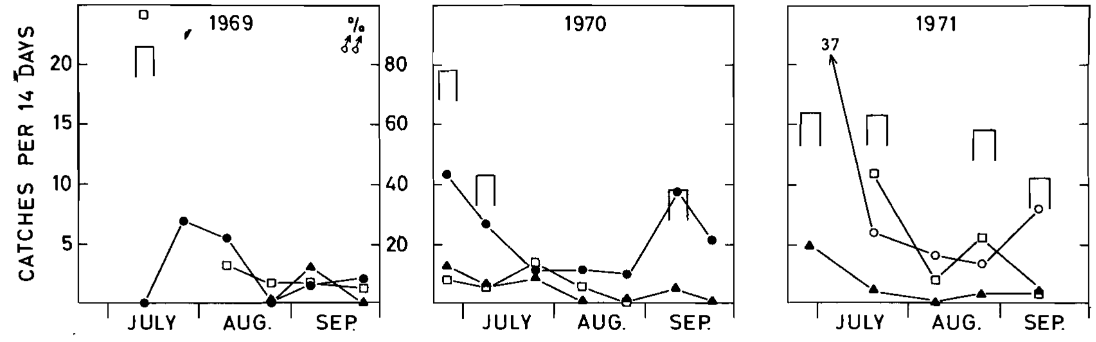


Fig. 9. Seasonal variations in pit-fall catches of adult *Erigone tirolensis* during three years. Explanation of symbols is given in Fig. 1.

(1951), however, report adults in late summer and autumn only.

Only relatively few specimens of *Tiso aestivus* were caught (Fig. 14), but adult animals seem to occur throughout the whole season. There is probably a tendency for most males to be trapped during the first half of the season. At least in 1969 and 1970, males were absent from about the beginning of August, but in 1971 we found a certain number of males also in August/September.

Meioneta nigripes was found only in the pioneer ground (Fig. 15), and was relatively sparse throughout the whole season. The only

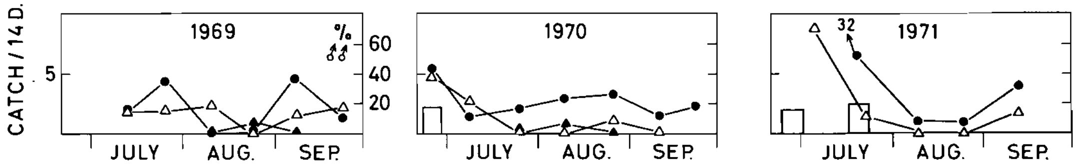


Fig. 10. Seasonal variations in pit-fall catches of adult *Erigone psychrophila* during three years. Explanation of symbols is given in Fig. 1.

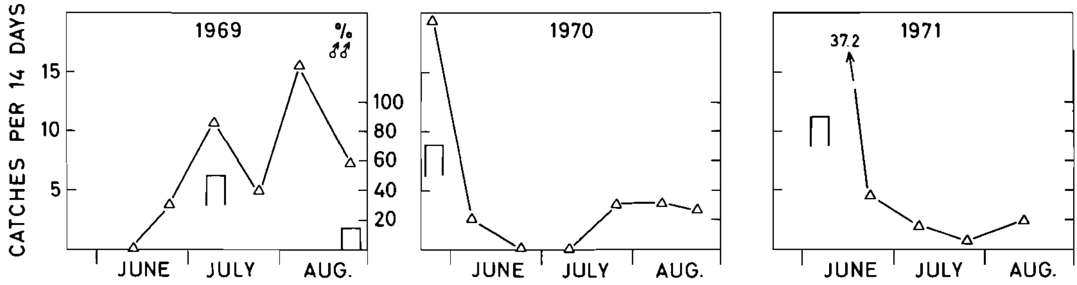


Fig. 11. Seasonal variations in pit-fall catches of adult *Rhaebothorax sphagnicola* during three years. Explanation of symbols is given in Fig. 1.

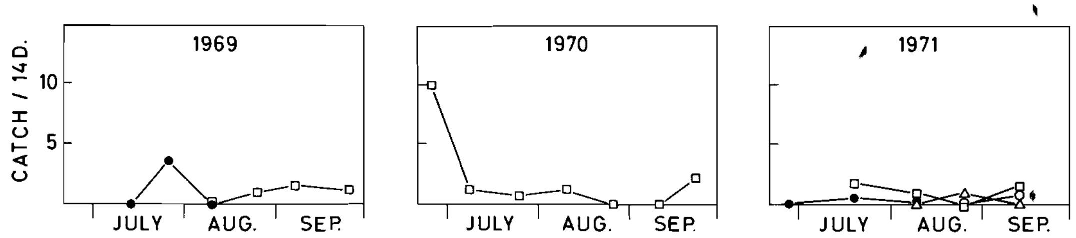


Fig. 12. Seasonal variations in pit-fall catches of adult *Rhaebothorax morulus* during three years. Explanation of symbols is given in Fig. 1.

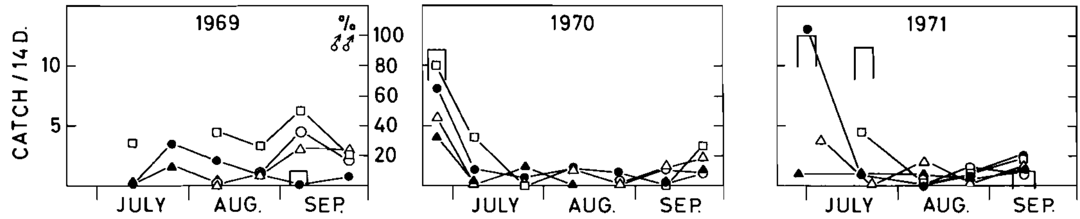


Fig. 13. Seasonal variations in pit-fall catches of adult *Oreonetides vaginatus* during three years. Explanation of symbols is given in Fig. 1.

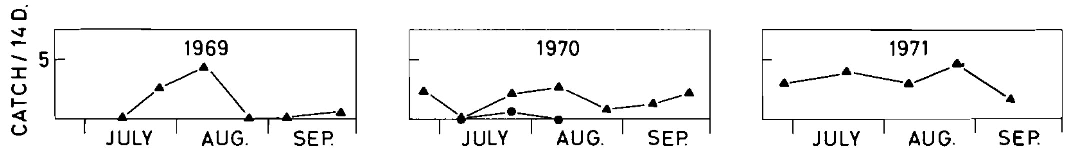


Fig. 14. Seasonal variations in pit-fall catches of adult *Tiso aestivus* during three years. Explanation of symbols is given in Fig. 1.

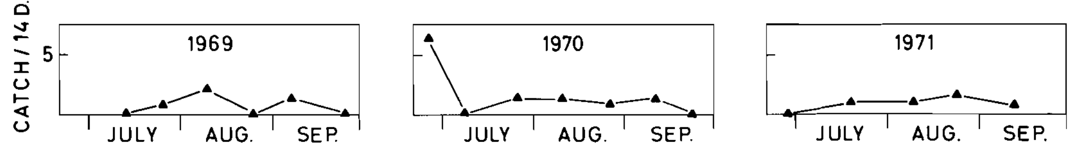


Fig. 15. Seasonal variations in pit-fall catches of adult *Meioneta nigripes* during three years. Explanation of symbols is given in Fig. 1.

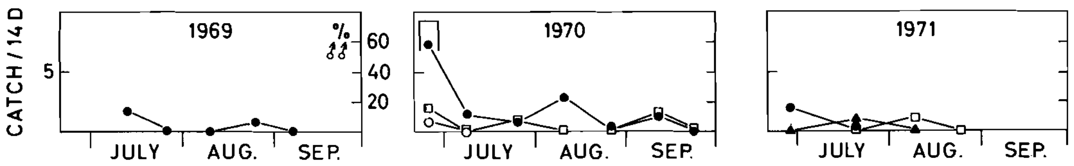


Fig. 16. Seasonal variations in pit-fall catches of adult *Bathyphantes gracilis* during three years. Explanation of symbols is given in Fig. 1.

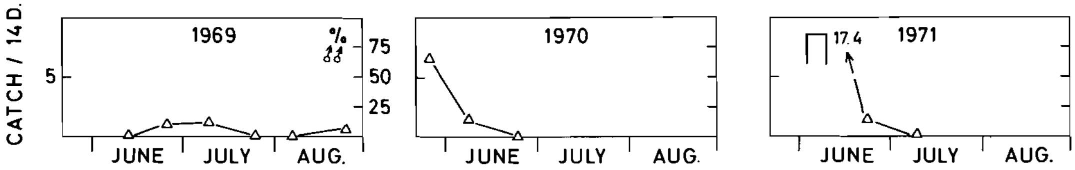


Fig. 17. Seasonal variations in pit-fall catches of adult *Agyneta decora* during three years. Explanation of symbols is given in Fig. 1.

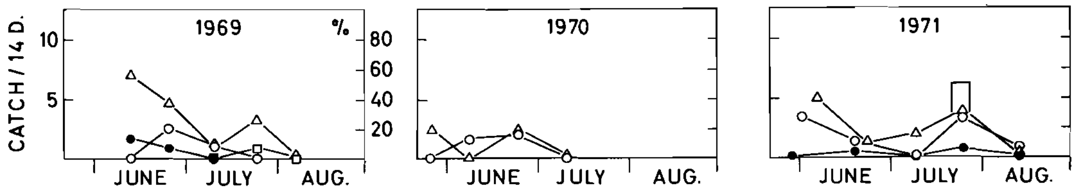


Fig. 18. Seasonal variations in pit-fall catches of adult *Tricca alpigena* during three years. Explanation of symbols is given in Fig. 1.

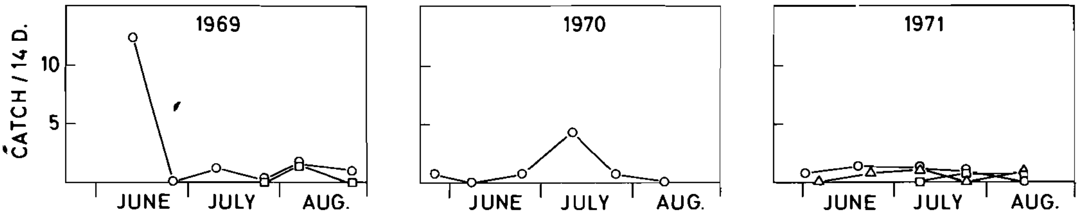


Fig. 19. Seasonal variations in pit-fall catches of adult *Gnaphosa lapponum* during three years. Explanation of symbols is given in Fig. 1.

two males were caught in the period of 16 June – 3 July 1970. Palmgren (1965, 1975) indicates adult specimens only in the midsummer.

Most males of *Bathyphantes gracilis* (Fig. 16) were concentrated at the beginning of the season. None were found later than in August.

All of the 20 males and 6 of the 8 females of *Agyneta decora* were limited to June/July (Fig. 17), which confirms that this species can also in these high-mountain areas be reckoned as a typical summer species.

Tricca alpigena (Fig. 18) was absent from the pioneer ground. In other localities, mature animals were found spread over the whole season. Females were taken as late as 20 September (1971), and males up to the beginning of September.

Most specimens of *Gnaphosa lapponum* were found in the oligotrophic dry heath. Both males and females were trapped from July to September/October (Fig. 19).

The remaining species were less common in the pit-fall catches than the species mentioned above, but will be briefly mentioned.

Ceratinella brevipes.A total of 3 ♂♂ + 11 ♀♀ were found in the snow bed and the eutrophic meadow from about medio June to about medio September. This is a palearctic species, which in northern Fennoscandia seems to be more common in the lowland areas. In regio alpina it has not earlier been found higher than 850–950 m a.s.l. (Holm 1950, Palmgren 1965).

Walckenaera cuspidata. Very few specimens: 6 ♂♂ from the middle of July to the middle of September and 8 ♀♀ taken from the middle of July to the middle of September. Habitats: the tussock habitat and the snow bed.

W. karpinskii. A total of 6 males (middle of July to the beginning of October) and 6 females (middle of July to the middle of September). Habitats: the snow bed and the oligotrophic dry heath.

Metopobactrus prominulus. A single male at the oligotrophic dry meadow (15–29 September 1970).

Oedothorax retusus. One male (16 August–2 September 1969) in the snow bed and one female (9–17 July 1969) in the oligotrophic dry meadow.

Latithorax faustus. Twelve males and eight females were taken spread over the whole season (June–September). The relatively high dominance (2.5%) at the oligotrophic dry heath (Table II) does not agree with the common view on humidity preference of the species, referred to by Palmgren (1965): 'Eine Characterart der Moore und in Siebproben von Ufern'. Humid habitats are also most given by Holm (1950), Palmgren (1972), and Braun (1961). The last author characterizes the species as hygrophilous. It is a northern (Huhta 1965) or a subarctic-boreal species (Holm 1950), which in northern areas is not pronounced alpine. In the Torneträsk area, it was found only up to 'regio subalpina inferior' (600 m a.s.l.) (Holm 1950). In southern Norway, it has previously been found up to about 1100–1300 m a.s.l. in Sogn (Kauri 1966).

Diplocentria replicata. One male and one female on the tussock area 11 July–3 August 1971. This is probably the most southern record in Scandinavia. In Norway it is previously known from Saltfjellet, Nordland (Hauge 1974).

Erigone arctica maritima. One female 17 July–3 August 1970, one female 15 August–6 September 1970, and one female and one male 3–9 September 1971. Habitat: the eutrophic meadow.

E. atra. All males (except 3) were from about medio August–October (3 ♂♂ 5 July–2 August 1971). Females occurred from the middle of June to the end of the season. Habitats: the tussock habitat, the snow bed and the eutrophic meadow.

Porrhomma campbelli. One female from the eutrophic meadow 17 July–3 August 1969. Previously known in Norway only from Svartisen, Nordland (Waaler 1966).

Lepthyphantes alacris. Rare: One male 5 July–2 August 1971, and one female 13 July–5 August 1970). Habitat: the snow bed. It is a northern forest species, which in northern Scandinavia has been taken in the alpine area up to about 850–880 m a.s.l. (Holm 1950, Palmgren 1965). The species is more common in mountain areas in southern Europe (Wiehle 1960, Braun 1961).

L. tenebricola. Seven males and four females were trapped in the pioneer ground and in the eutrophic meadow. All specimens occurred in the first half of the season (none later than about medio August). It is not a typical mountain species. In northern Norway, it occurs commonly in forested areas.

L. mengei. Neither can this species be reckoned as belonging to the alpine species. According to Palmgren (1965) it is sparse in the lower mountain heaths (about 6–700 m a.s.l.) in northern Finland. Holm (1950) found very few specimens up to regio sub-alpina. It occurs in Iceland, but not in the central highlands (Brændegård 1958). The three females from our oligotrophic dry heath were caught late in the season: 11 September–8 October 1969. This agrees with the usual late activity period of this species.

L. pallidus. A single male on the oligotrophic dry meadow (15 August – 5 September 1970).

L. complicatus. Found only on the pioneer ground and on the oligotrophic dry heath. This is the most pronounced alpine species of all the actual *Lepthyphantes* species. Two males and two females were taken about medio June-medio July and one male and one female about medio August-medio September.

Pardosa riparia. A single female in the eutrophic meadow (4 July–3 August 1971).

Micaria alpina. Seven males and two females, only from the pioneer ground. All specimens (except 1♂ 3–17 August 1971) were caught in June/July.

Gnaphosa leporina. Only two females on the oligotrophic dry meadow (9 July–3 August 1969).

Oxyptila rauda arctica. Both sexes were taken in the second half of the season in the oligotrophic dry heath.

O. atomaria. A single female in the oligotrophic dry heath (11 September–8 October 1969).

Spiders collected under stones

In addition to the pit-fall catches, 522 spiders were collected from under stones in the five habitats. The adults (314 specimens) have been identified to species. Spiders were always dominant among the larger arthropods found under stones (Hågvar & Østbye 1972). The species recorded in the various habitats are indicated by crosses in Table II. Altogether, seventeen species were observed under stones.

All species taken under stones were also caught in pit-fall traps in corresponding habitats, with the exception of three species in the snow bed. The habitat with the highest fraction of spider species occurring under stones was the snow bed (twelve of twenty species). For many species, this microhabitat is obviously valuable during certain phases of the life cycle or during certain periods of the day. There are, however, several species which do not seem to use this microhabitat at all.

Of the adult specimens collected under stones, four species make up 79.2%: *Collinsia holmgreni* 30.0%, *Hilaira frigida* 20.8%, *Erigone tirolensis* 16.1% and *Oreonetides vaginatus* 12.3%. Next comes *Lepthyphantes tenebricola* (6.6%) which is rather seldom represented in the pit-fall traps (Table II). The latter was, according to Holm (1950) found under stones only in the regio alpina. *O. vaginatus* was found by Holm *only* under stones in regio alpina, and most specimens of *C. holmgreni* and *H. frigida* were collected from under stones by him.

Of the remaining species, very few individuals were taken under stones. Two species, *Trichopterna mengei* and *Pardosa palustris,* were taken in large numbers in the pit-fall traps, while only a few individuals were observed under stones. For these very active species, the hand-collecting method may have been selective, resulting in an underestimation of their occurrence under stones.

Acknowledgements. – We wish to express our gratitude to all our colleagues who participated in the field work, especially A. Hagen, the late J. Hagen, J. Schmidt, H.-J. Skar and D. Svalastog, and to M. Espeland for critically reading the manuscript. The investigations have been supported by grants from the Norwegian IBP. This work is part of the Hardangervidda IBP/PT-UM project.

References

Braun, R. 1961. Zur Kenntnis der Spinnenfauna in Fichtenwälder höherer Lagen des Harzes. *Senck. biol 42,* 375–395.

Braun, R. & Rabeler, W. 1969. Zur Autökologie und Phänologie der Spinnenfauna des Nordwestdeutchen Altmoränen-Gebietes. *Abh. senckenberg. naturforsch. Ges. 522,* 1–89.

Brændegård, J. 1958. *The Zoology of Iceland Vol. III.* 113 pp, Munksgaard, KBH. og Reykjavik.

Dahl, F. 1912. Über die Fauna des Plagefenngebietes. pp. 575–622 in Cowentz, H. (ed.) *Beiträge z. Naturderkmalpfläge 3,* Berlin.

Dahl, F. & Dahl, M. 1927. Spinnentiere oder Arachnoidea II: Lycosidae s.lat. (Wolfspinnen in weiteren Sinne). *Tierw. Dtl. 5,* 1–80.

Hauge, E. 1974. Notes on little known spiders in Norway. *Norsk ent. Tidsskr. 21,* 159–160.

Hauge, E. 1977. The spider fauna of two forest habitats in northern Norway. *Astarte 10,* 91–99.

Holm, Å. 1939. Neue Spinnen aus Schweden. *Ark. Zool. 31 A (8),* 1–38.

Holm, Å. 1943. Zur Kenntnis der Taxonomie, Ökologie und Verbreitung der schwedischen Arten der Spinnengattungen Rhaebothorax Sim., Typhochraestus Sim. und Latithorax n.gen. *Ark. Zool. 34A,* 1–32.

Holm, Å. 1950. Studien über die Spinnenfauna des Torneträskgebietes. *Zool. Bidr. Uppsala 29,* 103–213.

Holm, Å. 1960. Notes on arctic spiders. *Ark. Zool. 12,* 511–514.

Huhta, V. 1965. Ecology of spiders in the soil and litter of Finnish forests. *Ann. Zool. Fenn. 2,* 260–308.

Hågvar, S. & Østbye, E. 1972. Quantitative and qualitative investigations on the invertebrate fauna under stones (the Hypolithion) in some alpine habitats at Finse, South Norway. *Norsk ent. Tidsskr. 19,* 1–10.

Hågvar, S., Østbye, E. & Melåen, J. 1978. Pit-fall catches of surface active arthropods in some high mountain habitats at Finse, south Norway. II. General results on group level, with emphasize on Opiliones, Araneida and Coleoptera. *Norw. J. Ent. 25,* 195–205.

Jocque, R. 1973. The spider fauna of adjacent woodland areas with different humus types. *Biol. Jb. Dodonaea 41,* 153–178.

Kauri, H. 1966. En kolleksjon av Araneae og Opiliones fra Sogn. *Norsk ent. Tidsskr. 13,* 394–395.

Knülle, W. 1953. Zur Taxonomie und Ökologie der norddeutschen Arten der Gattung Erigone Aud.. *Zool. Jahrb. 83,* 63–110.

Lockett, G. H. & Millidge, A. F. 1951. *British spiders I.* 310 pp., Ray Society, London.

Merrett, P. 1968. The phenology of spiders on heathland in Dorset. Families Lycosidae, Pisauridae, Agelenidae, Mimetidae, Theridiidae, Tetragnathidae, Argiopidae. *J. Zool. 156,* 239–256.

Merrett, P. 1969. The phenology of the Linyphiid spiders on heathland in Dorset. *J. Zool. 157,* 389–307.

Østbye, E., Haande, K. M., Haande, P. S., Hågvar, S., Melåen, J. & Skartveit, A. 1978. Pit-fall catches of surface-active arthropods in some high mountain habitats at Finse, south Norway. I. Introduction, methods, material, climate and habitat descriptions. *Norw. J. Ent. 25,* 189–193.

Palmgren, P. 1965. Die Spinnenfauna von Kilpisjärvi in Lappland. *Acta Zool. Fenn. 110,* 1–70.

Palmgren, P. 1972. Studies on the spider populations of the surroundings of Tvärminne Zoological Station, Finnland. *Commentat. Biol. Soc. Sci. Fenn. 52,* 1–133.

Palmgren, P. 1975. Die Spinnenfauna Finnlands und Ostfennoscandiens VI. Linyphiidae I. *Fauna Fennica 28,* 1–102.

Palmgren, P. 1976. Die Spinnenfauna Finnlands und Ostfennoskandiens. VII. Linyphiidae II. *Fauna Fennica 29,* 1–126.

Pearson, R. G. & White, E. 1964. The pheonology of some surface-active arthropods of moorland country in North Wales. *J. Anim. Ecol. 33,* 245–258.

Shannon, C. E. & Weaver, W. 1963. *The Mathematical Theory of Communication.* 117 pp., University of Illinois press, Urbana.

Sørensen, T. 1948. A method of establishing groups of equal amplitude in plant society based on similarity of species content. *K. Danske Vidensk. Selsk. 5,* 1–34.

Steigen, A. L. 1975. Energetics in a population of *Pardosa palustris* (L.) (Araneae, Lycosidae) on Hardangervidda. pp. 129–144 in Wielgolaski, F. E. (ed.) *Ecological studies. Analysis and synthesis. Vol. 17. Fennoscandian Tundra Ecosystems, Part 2.* Springer Verlag, Berlin, Heidelberg, New York.

Tretzel, E. 1952. Zur Ökologie der Spinnen. Autökologie der Arten im Raum von Erlangen. *Sitz.-ber. Phys.-med. Soc. Erlangen 75,* 36–131.

Tretzel, E. 1954. Reife- und Fortplanzungszeit bei Spinnen. *Z. Morph u. Ökol. Tiere 42,* 634–691.

Vilbaste, A. 1964. Über die Fauna und Dynamik der Spinnen auf den Auwiesen Estlands. *Eesti NSV Teaduste Akad. Toimetised (Biol.) 13,* 284–301.

Vilbaste, A. 1969. Über die Struktur und jahreszeitliche Dynamik der Spinnenfauna der Niedermoore Estlands. *Eesti NSV Teaduste Akad. Toimetised (Biol.) 18,* 390–407.

Waaler, P. F. 1966. Porrhomma campbelli F. O. P.-Cambridge (Araneae, Linyphiidae) in Norway. *Norsk ent. Tidsskr. 13,* 407.

Wiehle, H. 1960. Spinnentiere oder Arachnoidea, XI: Micryphantidae-Zwergspinnen. *Tierw. Dtl. 47,* 1–620.

Received 10 May 1978

Generic switch-over in *Isotoma nivea* Schäffer, 1896. A new case of cyclomorphosis in Collembola (Isotomidae)

ARNE FJELLBERG

Fjellberg, A. 1978. Generic switch-over in *Isotoma nivea* Schäffer, 1896. A new case of cyclomorphosis in Collembola (Isotomidae). *Norw. J. Ent.* Vol. 25, pp. 221–222. Oslo. ISSN 0029-1897.

Populations of *Isotoma nivea* Schäffer were studied in Skjåk in Oppland County, Norway. During the period October–April, an apparently undescribed species of *Vertagopus* was present together with *I. nivea*. Careful examination of specimens in ecdysis at the end of April proved that this '*Vertagopus*' was a winter form of *I. nivea*. During a single moult the typical clavated spur hairs of *Vertagopus* were transformed to the shorter, pointed spur hairs of *Isotoma*. At the same time the subapical sensilla of Ant. IV changed in shape from rod to globule, the eye size was reduced, and the apical tooth of mucro became larger. The possibility that the genus *Vertagopus* developed through retainment of the winter form of cyclomorphic *Isotoma*, is briefly discussed.

Arne Fjellberg, Marlo, N-2690 Skjåk, Norway.

During the autumn of 1977 an apparently undescribed species of *Vertagopus* was discovered in Skjåk, Oppland County in Norway. The species occurred under bark on felled trees in company with *Vertagopus cinereus* (Nicolet) and *Isotoma nivea* Schäffer (=*Isotoma albella* in Gisin (1960) nec Packard, 1873). The unknown *Vertagopus* showed a great overall similarity to *I. nivea*, differing of course by its long, clavated spur hairs on tibiotarsi, characteristic of the genus *Vertagopus*. Also the eyes were larger, the apical tooth of mucro was smaller, and the subapical sensilla of Ant. IV was shaped like a small rod, not like a globule as in *nivea*.

The following spring the species was studied in more detail. On 23 April 1978, a population was found in which many of the specimens were in ecdysis. The old and the new cuticle could be examined on the same individual. In some specimens the old skin could even be peeled off, and both the old and the new one could be studied in detail. It then turned out that the *Vertagopus* sp. was just transforming into typical *I. nivea*. The long, clavated spur hairs were changing to shorter, pointed hairs (Fig. 1A). The subapical sensilla of Ant. IV was changing from a small rod to a small globule (Fig. 1B), the apical tooth of mucro became larger (Fig. 1D) and the distinct eye lenses (Fig. 1C) became hardly visible at all. Both males and females were affected. All the individuals were unreproductive. Apparently the *Vertagopus* sp. is just a winter form of *I. nivea*.

The winter form was first discovered on 16 October. It was recollected in spring on 9 April. Both times the population was a mixture of the winter form and the normal *nivea* form. As I have no samples from the intervening winter period, I do not know whether all individuals change or not. Probably the phenomenon is regulated by temperature, and thus depends on the conditions in the actual locality. The species has a wide distribution in Europe, so it is possible that the *Vertagopus* form will not be found in places with much warmer winters than Skjåk.

The regular occurrence of summer and winter forms was first described from *Isotoma hiemalis* Schött (Fjellberg 1976). In this species only mucro shape was influenced. The phenomenon was later seen in *I. blufusata* Fjellberg and *I. neglecta* Schäffer (Fjellberg 1978). Also here the mucro was involved, but in addition the shape of the Ant. IV subapical sensilla was changed. The cyclomorphosis in *I. nivea*, also involving eye size and tibiotarsal spur hairs, is thus the most extensive known so far.

If the kind of 'generic switch-over' here observed in *I. nivea* is widespread in Collembola, this might have serious consequences for taxonomy or even have phylogenetic implications. Theoretically the morphological characteristics of the genus *Vertagopus* could have been derived from a cyclomorphic *Isotoma* of the *nivea* type when climate turned cooler or the species moved to colder environments. Perhaps

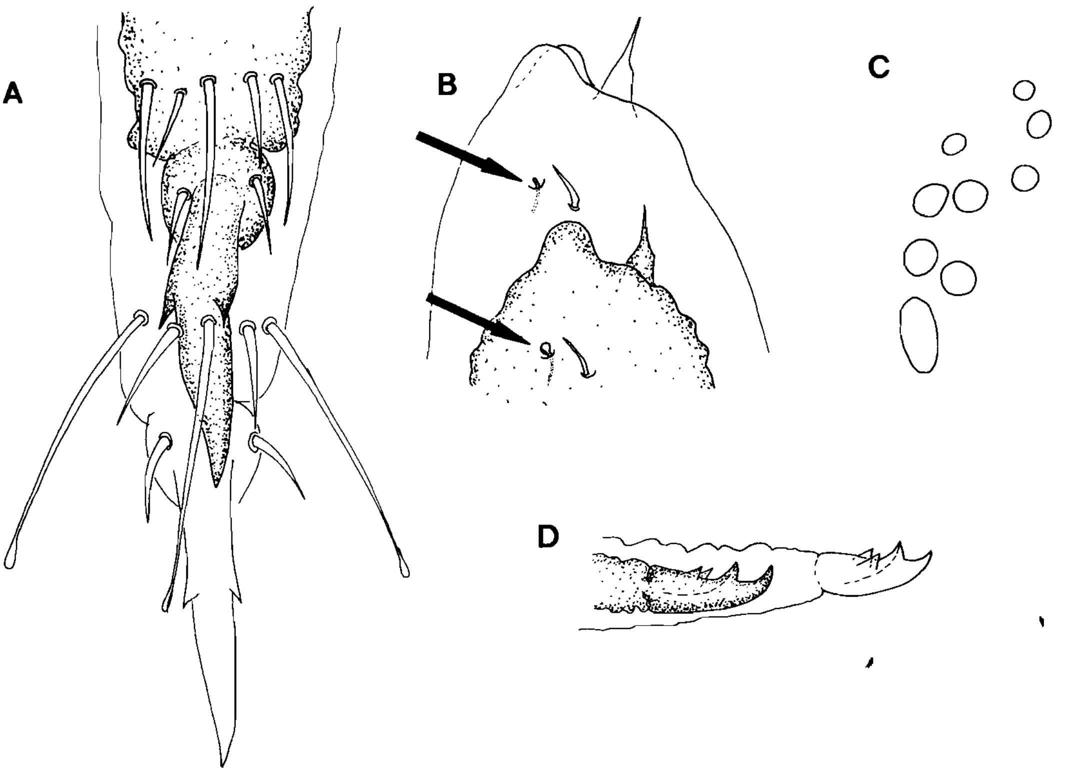


Fig. 1. Isotoma nivea. A: Tibiotarsus II of a specimen in ecdysis, showing transformation from the *Vertagopus* form (clavated spur hairs) to the normal form (dotted). B: Tip of Ant. IV of a specimen in ecdysis with transformation of the subapical sensilla from rod to globule (arrows). C: PAO and eyes of the *Vertagopus* form. D: Tip of dens with mucro of a specimen in ecdysis showing transformation of mucro shape.

some of the many northern species of *Vertagopus* are just forms of *Isotoma* visitors from the south which keep their winter wear all the year! The evidence at present is not quite convincing, but at least it is a tempting speculation that might move someone to do the necessary research. The field seems open for experimental work.

References

Fjellberg, A. 1976. Cyclomorphosis in *Isotoma hiemalis* Schött, 1893 (*mucronata* Axelson, 1900) syn. nov. (Collembola, Isotomidae). *Rev. Écol. Biol. Sol. 13:* 381–384.

Fjellberg, A. 1978. New species of the genus *Isotoma* from North America (Collembola, Isotomidae). *Ent. scand. 9,* 93–110.

Gisin, H. 1960. *Collembolenfauna Europas.* 312 pp. Geneva.

Received 8 May 1978

Short Communications

Norw. J. Ent. Vol. 25, No. 2, 1978

Notes on *Wesmaelius ravus* (Withycombe, 1923) and *Wesmaelius mortoni* (McL., 1899) (Neuroptera, Planipennia) in Norway

LITA GREVE

Wesmaelius ravus (Withycombe) is reported from inner Telemark county. One female was caught in a light-trap at Sauherad on 16 Sept. 1974. This is the first certain record for Scandinavia. *Wesmaelius mortoni* (McL.) is reported from inner Telemark and inner Hordaland counties. One female was taken together with the female of *W. ravus*, another was taken in a light-trap at Teigen, near Odda between 17–22 Aug. 1977.

Lita Greve, Zoological Museum, University of Bergen, N-5014/Bergen-Univ., Norway.

One female of each of the species of *Wesmaelius ravus* and *Wesmaelius mortoni* were collected together in a light-trap at Sauherad, Sauherad, inner Telemark, south eastern Norway on 16 Sept. 1974. The light-trap was fitted with actinic tube lights (Phillips Actinic TL/03). Another female of *Wesmaelius mortoni* was collected in a light-trap at Teigen, near Odda, inner Hordaland county, western Norway at UTM 32 VLM 655716. This light-trap was a Robinson trap fitted with mercury vapour bulbs (Phillips HPL 125 W).

W. ravus has once earlier been reported from Scandinavia, from the western part of the Hardangervidda mountain plateau. Three males and one female were found as a part of a large wind-drifted material consisting of 323 Neuroptera. The individuals of *W. ravus* amounted to about 1% of the total material found. *W. mortoni* was also found in the same material, seven males and three females, about 3.5% of the total material (Greve 1969). Both species are confined to conifers and the locality at the Hardangervidda at 1150–1200 m a.s.l. could not be the original biotope for the specimens. They must have drifted with wind from some area not too far away. Some Neuroptera in the material were alive when caught, and most specimens were undamaged, if dead. The most likely original biotope was suggested to be along some inner part of the Hardangerfjord.

The record of *W. ravus* is the first certain one from Scandinavia. In northern Europe the species is known from a few places in England (Killington 1936/37) and has been taken a few times in southern Finland (Meinander 1962, 1963). *W. mortoni* was reported for the first time in Norway from Dombås by Kimmins (1963). *W. mortoni* has been found scattered in Finland and in Sweden, but is considered rare (Meinander 1962).

The new material gives no certain clue to the origin of the wind-drifted material at Hardangervidda, since both of these two species are found to east and west of the Hardangervidda plateau.

W. ravus is believed by authors to prefer the upper parts of trees and thus avoids conventional netting. Light-traps, on the other hand, are known to successfully collect other species of the genus *Westmaelius* (Andersen & Greve 1975, Nielsen 1977), and might yield more material of these two species in the future. Compared with material of other Neuroptera species from light-traps, however, *W. ravus* and *W. mortoni* must be considered rare species in the Norwegian fauna.

Acknowledgements – I wish to express my gratitude to Dr. Torgeir Edland, The Agricultural University of Norway, 1432 Ås-NLH and Cand. real. Trond Andersen, Zoological Museum, Univ. of Bergen, for collecting the material.

References

Andersen, T. & Greve, L. 1975. Neuroptera in light-traps at Osterøy, Hordaland. *Norsk. ent. Tidsskr. 22,* 123–128.

Greve, L., 1969. An aerial-drift of Neuroptera from Hardangervidda, western Norway. *Årb. Univ. Bergen. Mat. Naturv. ser. 2,* 1–15.

Killington, F.J. 1936, 1937. *A Monograph of the British Neuroptera I–II.* Ray Society Vol. 122–123. 270 pp. London.

Kimmins, D.E., 1963. Notes on two British species of Neuroptera *Boriomyia mortoni* (McL.), and *B. killingtoni (Morton), with description of a new specis of the mortoni* group *Boriomyia. Ent. Gazette 14,* 140–149.

Meinander, M., 1962. The *Neuroptera* and the *Mecoptera* of eastern Fennoscandia. *Fauna Fenn. 13,* 1–96.

Meinander, M., 1963. Notes on Finnish Neuroptera and Mecoptera. *Not. Ent. 18,* 160–164.

Nielsen, E.S., 1977. Studies on lacewings (N.s.t.) in a Danish beech stand. *Ent. Meddr. 45,* 45–64.

Received 26 January 1978

Piophila vulgaris Fall. (Dipt., Piophilidae) new to Spitsbergen, Svalbard

ULRIK LOHM

Some Diptera Brachycera species are reported from the inner part of the Isfjorden area, of which *Piophila vulgaris* Fall. (Piophilidae) is new for Spitsbergen.

U. Lohm, Department of Entomology, University of Uppsala, Box 561, S-751 22 Uppsala, Sweden.

In spite of several investigations, both old and recent, on the composition of the insect fauna of Spitsbergen, small collections made during visits to the inner part of the Isfjorden area turned out to contain a species previously not recorded: *Piophila vulgaris* Fall. (Dipt., Piophilidae). The records are as follows: Templet Bjonahamn 21 July 1954 4 specimens, Sassenfjord Templet 24 July 1954 10 specimens, Gipshuken Anservika 29 July 1966 2 specimens, Gipshuksodden 30 July 1966 1 specimen. In 1966 two of the specimens were caught crawling in the fur of a dead arctic fox on a talus slope exposed to the southwest and one flying in the vicinity of a cottage. Other Diptera species caught on the same arctic fox were *Boreëllus atriceps* Zett. (Calliphoridae) and *Neoleria prominens* Beck. (Heleomyzidae). *P. vulgaris,* sometimes regarded as synanthropic, has a wide distribution in Europe and is also known from, for example, Greenland and Iceland (Hennig 1943).

Other Diptera Brachycera observed in the Gipshuken-Templet area were: *Rhamphomyia caudata* Zett. (Empididae), *Mesosyrphus dryadis* Holmgr. (Syrphidae), *Coelopa frigida* Fabr. (Coelopidae), *Copromyza fumipennis* Stenh. (Sphaeroceridae), *Phormia terrae-novae* R.D. (Calliphoridae), *Spilogona dorsata* Zett., *S. megastoma* Boh., *Acroptena frontata* Zett. (Muscidae), *Lasiomma? octoguttatum* Zett. (Anthomyidae), *Scatophaga furcata* Say., and *S. litorea* Fall. (Scatophagidae).

The material was collected by the Swedish Spitsbergen Expedition 1954 and the present author (for reports see Rapp 1955 and Ehrenroth & Lohm 1967). It is kept at the Department of Entomology, University of Uppsala.

Acknowledgements – I wish to express my gratitude to Drs M. Ackland, H. Andersson and L. Hedström for identifying or checking the species.

References

Ehrenroth, B. & Lohm, U. 1967. Faunistiska och floristiska iakttagelser vid mellersta Västspetsbergen sommaren 1966. *Fauna och Flora 62,* 263–278.

Hennig, W. 1943. Piophilidae. pp. 1–38 in Lindner, E. (ed.) *Die Fliegen der Palaearktischen Region 40.*

Rapp, A. 1955. En sommarmånad på Spetsbergen. *Ymer 75,* 121–137.

Received 23 January 1978

Norw. J. Ent. Vol. 25, No. 2, 1978 225

The food selection of *Pytho depressus* L. (Col., Pythidae)

JOHAN ANDERSEN & ARNE C. NILSSEN

Studies in the laboratory clearly show that the larva of *Pytho depressus* L. is phytophagous, living on those parts of the cambium-phloem that remain after other insects have left the layer.

Johan Andersen & Arne C. Nilssen, Institute of biology and geology, University of Tromsö, N-9001 Tromsö, Norway.

The larva of *Pytho depressus* L. lives under the bark of conifers, especially pine (*Pinus* spp.). In Denmark the life-cycle is two years at least, and in northern Fennoscandia no doubt even longer. Because of this the larvae live during several stages in the decomposition of the dead pine. In Troms county (TRi) in northern Norway large larvae, pupae, and adults are frequently found together at the same stages of *Rhagium inquisitor* L. In Germany the generation time of the latter species is two years (Hellrigl 1974), in northern Fennoscandia the time is supposed to be longer. In habitat selection as well as in life-cycle *P. depressus* and *Rhagium inquisitor* thus seem to have much in common. However, whereas it is very well known that *R. inquisitor* feeds on the cambial layer, the available information about the food selection of *P. depressus* seems to be contradictory. According to Kaszab (1969) and Palm (1951) all the members of the family Pythidae are carnivorous. However, Saalas (1917) suggests and Larsson (1945) states that *P. depressus* is a species feeding on those parts of the cambial layer remaining after other phytophagous bark insects have left.

To get more information about the food selection of *P. depressus*, larvae were studied in more detail in the laboratory. The material was collected in Holt, Øverbygd (TRi) 5 October 1977. One larva was dissected and the gut contents examined. No traces of animal remnants could be discovered, whereas meristematic tissues and other plant material were plentiful. The rest of the larvae were placed in 1 ltr glass jars with moistened absorbant cellulose paper in the bottom and pieces of bark (formerly attacked by *Tomicus piniperda* L.) above. All the loose material was taken away from the bark pieces before they were put into the glass jars. One of the glass jars also contained alive larvae of

Fig. 1. A piece of bark (inside) with a larva of *P. depressus*. The larva has removed the soft layer of the inner bark, and the loosened fibres can be seen in the left corner of the picture.

Diptera (collected together with *P. depressus*) and dead and alive specimens of *Tribolium castaneum* Hbst.

None of these animals were touched by the *Pytho* larvae. The larvae dwelled on the inside of the bark pieces and already after one day bark fibres were frequent on the cellulose paper underneath. (Fig. 1). One of the larvae was observed with bark fibres between the jaws. After some days the *Pytho* larvae had destroyed all or most of the cambial-phloem material between the galleries of *Tomicus piniperda*. Thereafter the larvae began to make burrows into the cellulose paper and finally one of them made a pupal chamber of bark fibres and cellulose paper in the bottom of the glass. The imago successfully hatched about 25–30 December 1977.

In our opinion, these observations show that *P. depressus* is mainly a phytophagous species living off the cambial-phloem layer, as also supposed or stated by Saalas (1917) and Larsson (1945).

References

Hellrigl, K. 1974. Cerambycidae, Bockkäfer. pp. 130–202 in Schwenke, W. (ed.) *Die Forstschädlinge Europas. Käfer.* P. Parey, Hamburg und Berlin.

Kaszab, Z. 1969. Pythidae. pp. 92–99 in Freude, H., Harde, K.W. & Lohse, G.A. (ed.) *Die Käfer Mitteleuropas. 8. Teredilia, Heteromera, Lamellicornia.* Goecke & Evers, Krefeld.

Larsson, S. G. 1945. Larver. pp. 152–280 in Hansen, V. (ed.). *Biller 12. Heteromerer. Danm. Fauna 50.*

Palm, T. 1951. Die Holz- und Rindenkäfer der nordschwedischen Laubbäume. *Medd. från Statens Skogsforskn.-inst. 40,* 1–242.

Saalas, V. 1917. Die Fichtenkäfer Finnlands I. *Ann. Ac. Sci. Fenn. (A) 8,* 1–547.

Received 2 March 1978

Apatania muliebris McLachlan (Trichoptera) in Norway

JOHN O. SOLEM

A record of a female of *Apatania muliebris* McLachlan subspecies *jemtlandica* Nielsen is reported. This is the second find of *A. muliebris* in Norway.

J.O. Solem, University of Trondheim, Royal Norwegian Society of Sciences and Letters, the Museum, Erling Skakkes gt. 47 B, N-7000 Trondheim, Norway.

The caddisfly *Apatania muliebris* is little known in Norway, and only one record (Forsslund 1951) seem to have been published. Males of *A. muliebris* have never been found and a parthenogenetic reproduction is very likely. Nielsen (1969) made morphological studies of *A. muliebris* and established six subspecies, in spite of the difficulties in defining subspecies of a species that reproduce parthenogenetically. Schmid (1954) gave the subspecies defined at that time the rank of species. Whether or not the various populations should have the rank of subspecies or species is not a general question for this paper. However, in their 'Check-List of the Trichoptera of North-Western Europe', Svensson & Tjeder (1975) follow Nielsen (1969) and give the rank of subspecies for the different populations of *A. muliebris*. To follow Nielsen's (1969) and Svensson & Tjeder's (1975) terminology and use the term subspecies, it has not earlier been verified which of the subspecies we have in Norway.

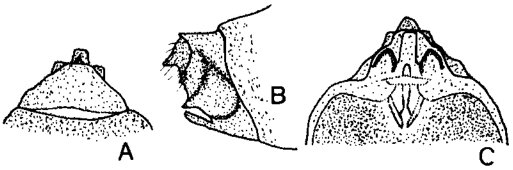


Fig. 1. Female of *Apatania muliebris jemtlandica* from Trondheim area. Dorsal (A), lateral (B), and ventral (C) view.

In 1966, Kaare Aagaard collected one single female at a small brook just outside Trondheim (UTM 32V NR 30-32 73-74) on the date 6 July; it belongs to the *Apatania muliebris* species complex, and the subspecies is *A. m. jemtlandica* (Nielsen 1969) (Fig. 1). The species is new to the Tröndelag area and the second record in Norway. According to Svensson & Tjeder (1975) two subspecies have been collected in Sweden and three in Denmark.

References

Forsslund, K.-H. 1951. Insektfund på fjället Härjehågna. *Norsk ent. Tidsskr. 8,* 196–202.

Nielsen, A. 1969. On the subspecies of *Apatania muliebris* McL. (Trichoptera). *Ent. Meddr. 37,* 313–318.

Schmid, F. 1954. Contribution à l'étude de la sous-famille des Apataniinae (Tric., Limnophilidae) II. *Tijdskr. v. Ent. 97,* 1–74.

Svensson, B.W. & Tjeder, B. 1975. Check-List of the Trichoptera of North-Western Europe. *Ent. scand. 6,* 261–274.

Received 14 April 1978

Stenolophus mixtus Hbst., an expanding Carabid beetle new to Norway

TORSTEIN KVAMME

Stenolophus mixtus Hbst. is reported new to Norway. Two specimens were collected in a light-trap on Tromøy in Aust-Agder county, South Norway. The trap was situated inside a borderline of a forest about 100 m from the coastline. The record is interesting seen in relation to the expansion of this species in Sweden, Finland, and Russia during the last hundred years.

Torstein Kvamme, Norwegian Forest Research Institute, N-1432 Ås – NLH, Norway.

Two specimens of *Stenolophus mixtus* Hbst., which is new to Norway (Lindroth 1960, Strand 1960, 1970), were collected 8 July 1977 on Tromøy, Aust-Agder county in South Norway. The locality is situated in AAy 12 according to Strand (1943), and in square no. 6 according to the UTM-EIS system proposed by Økland (1977). Both specimens were taken by Sigurd A. Bakke in a light-trap. The trap was placed just inside the borderline of a forest, about 100 m from the coast-line.

According to Lindroth (1945 a), *S. mixtus* prefers humid habitats, especially nearby ponds, rivers, and lakes with swampy and muddy soil. The species is also known from border zones of mires (Lindroth 1945 a) and from wet meadows (Lindroth 1961).

The nearest localities of *S. mixtus* are in Skåne, South Sweden and at the coast west of Ålborg, North Denmark (Fig. 1). In Sweden the species has increased its range during the last hundred years. The same phenomenon is also known from Finland and Russia (Lindroth 1945b, 1973). Two immigration routes are possible (Fig. 1): A, from Denmark across Skagerrak, carried by wind. B, along the west-coast of Sweden, from Skåne. Baranowski & Gärdenfors (1974) showed that *S. mixtus* and other Carabid beetles are often carried by wind to Sweden across the Baltic Sea from the European Continent. *S. mixtus* always has fully developed flying wings, and uses them often (Lindroth 1945a). If the climatic conditions are favourable, the species could very well have immigrated by this route. However, it is also possible that the species has followed the coast from Skåne. Further research might reveal the total range in Norway, and other aspects in relation to zoogeographical problems.

References

Baranowski, R. & Gärdenfors, U. 1974. Vinddrift av jordløpare i Sydøstra Skåne (Col., Carabidae). *Entomologen 3,* 35–52.

Lindroth, C. H. 1945 a. Die Fennoskandischen Carabidae. *Gøteb. K. Vetensk. – o. Vitterh. Samh. Handl. Ser. B IV:1,* 709 pp.

Lindroth, C. H. 1945 b. Die Fennoskandischen Carabidae. *Gøteb. K. Vetensk. – o. Vitterh. Samh. Handl. Ser. B IV:2,* 277 pp.

Lindroth, C. H. (Red. Cur.) 1960. *Catalogus Coleopterorum Fennoscandia et Dania.* 476 pp. Entomologiska Sällskapet i Lund.

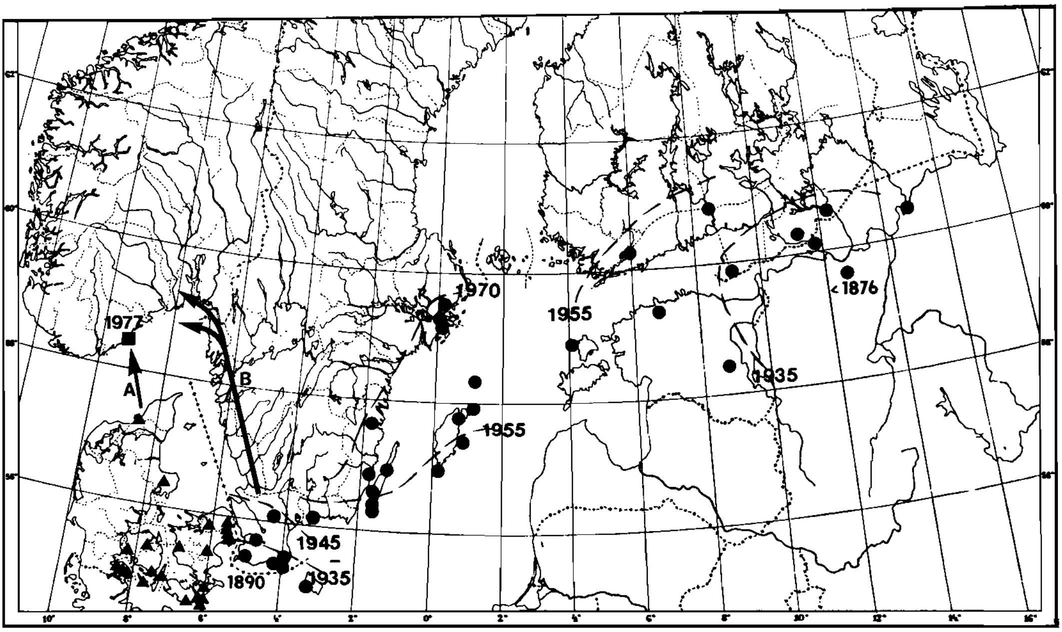


Fig. 1. The present range of *S. mixtus,* and how the range has increased during the last hundred years (modified after Lindroth 1945 b, 1973).

A and B are the possible immigration routes.
▲ =Danish records before 1950.
● =The present known range in Sweden, etc.
■ =The first Norwegian record.

Broken lines indicate the border of range at various years.

Lindroth, C. H. 1961. Skalbaggar (Col.): Sandjägare och Jordlöpare. *Sv. Insektfauna 9,* 1–209.

Lindroth, C. H. 1973. Sentida förendringar i den Nordiska insektfaunan. Exempel från Carabiderna. *Entomologen 2,* 1–8.

Strand, A. 1943. Inndeling av Norge til bruk ved faunistiske oppgaver. *Norsk Ent. Tidsskr. 6,* 208–224.

Strand, A. 1970. Additions and corrections to the Norwegian part of Catalogus Coleopterorum Fennoscandia et Dania. *Norsk Ent. Tidsskr. 17,* 125–145.

Strand, A. 1977. Additions and corrections to the Norwegian part of Catalogus Coleopterorum Fennoscandia et Dania. Second series. *Norw. J. Ent. 24,* 159–165.

Økland, J. 1977. Litt om bio-geografiske metoder, og noen nye data om utbredelse av stavtege, *Ranatra linearis,* og vannskorpion, *Nepa cinerea,* i Norge. *Fauna 30,* 145–167.

Received 12 April 1978

Norw. J. Ent. Vol. 25, No. 2, 1978 229

Contribution from the Norwegian IBP/PT-UM sections

Density of Collembola and Acarina in an alpine pioneer community near a glacier at Finse, south Norway

SIGMUND HÅGVAR, EIVIND ØSTBYE & JAN MELÅEN

The density of Collembola and Acarina was studied in a 'pioneer community', situated 1350 m a.s.l. near a glacier at Finse, Hardangervidda, south Norway. It is concluded that a time lapse of less than 200 years is sufficient for the establishment of a community of Collembola and Acarina, which, regarding density, vertical zonation, and degree of aggregation, is very similar to communities in older and fairly stable types of alpine habitat. This occurs so early in the succession that the vegetation cover was still not continuous.

Sigmund Hågvar, Norwegian Forest Research Institute, N-1432 Ås-NLH, Norway. Eivind Østbye & Jan Melåen, Zoological Institute, University of Oslo, Blindern, Oslo 3, Norway.

The densities of Collembola and Acarina have previously been studied in various alpine habitats at Finse (60°36'N – 7°30'E) (UTM 32V MN 11) and Stigstuv (60°18'N – 7°40'E) (UTM 32V MN 28), on the Hardangervidda mountain plateau, south Norway (Solhøy 1972, Hågvar, Melåen & Østbye 1974). Hardangerjøkulen, a large glacier on this mountain plateau, is retreating, leaving areas exposed for colonization of plants and animals. On 7 August 1971, twelve soil samples, each covering 16.6 cm², were taken in a 'pioneer community', situated 1350 m a.s.l., approximately 800 m from a glacier outlet, which has been exposed for not more than 200 years. The soil was morainic and quite rich in stones. The vegetation cover was not continuous. Dominant plants in the bottom layer were *Stereocaulon alpinum* and *Racomitrium canescens.* More habitat details, including chemical soil data, are given in Østbye et al. (1978). Each sample was divided into two vertical strata; 0–3 cm and 3–6 cm depth. Collembola and Acarina were extracted immediately in a high gradient apparatus modified from Macfadyen (1961, 1962).

The results are shown in Table I. Both groups have obviously a rather clumped distribution. However, it is interesting that the distribution is not more clumped in this habitat than in other types of alpine habitat which have developed a continuous vegetation cover (Solhøy 1972, Hågvar, Melåen & Østbye 1974). Regarding the vertical distribution, the concentration of the major part of the fauna in the upper 3 cm of the soil is a feature typical also of other alpine communities studied at Hardangervidda. Compared to most of these earlier studies, referred to above, the density of Collembola and Acarina measured in the 'pioneer community' is not low.

In conclusion, less than 200 years has been sufficient for the establishment of a community of Collembola and Acarina, which, regarding density, vertical zonation, and degree of aggregation, is very similar to communities in older and rather stable types of alpine habitat. Moreover, this occurs so early in the succession that the vegetation cover has still not closed.

References

Hågvar, S., Melåen, J. & Østbye, E. 1974. Quantitative studies of the invertebrate fauna in an alpine snow-bed community at Finse, south Norway. *Norsk. ent. Tidsskr. 21,* 45–51.

Table I. Density of Collembola and Acarina in an alpine "Pioneer community" near a glacier at Finse, south Norway. The habitat has been exposed for less than 200 years. Numbers are given per soil sample of 16.6 cm^2 in the 0-3 cm, 3-6 cm and 0-6 cm layer, together with mean density per m^2. The material is based upon twelve soil cores, taken 7 August 1971.

		$\bar{x}$	SD	Min.	Max.
Collembola	0-3 cm	43.5	28.0	6	88
	3-6 cm	3.0	5.5	0	20
	0-6 cm	46.5	29.7	6	89
Number/m^2	27900				
Acarina	0-3 cm	80.2	44.0	22	189
	3-6 cm	2.6	4.3	0	14
	0-6 cm	82.8	46.0	23	192
Number/m^2	49650				

Macfadyen, A. 1961. Improved funnel-type extractors for soil arthropods. *J. Anim. Ecol. 30,* 171–184.
Macfadyen, A. 1962. Soil arthropod sampling. *Adv. Ecol. Res. 1,* 1–34.
Østbye, E., Hågvar, S., Haande, K.M., Haande, P.S., Melåen, J. & Skartveit, A. 1978. Pit-fall catches of surface-active arthropods in some high mountain habitats at Finse, south Norway. I. Aim, methods and habitat descriptions. *Norw. J. Ent. 25,* 189–193.
Solhøy, T. 1972. Quantitative invertebrate studies in mountain communities at Hardangervidda, south Norway. I. *Norsk ent. Tidsskr. 19,* 99–108.

Received 22 May 1978

Bokanmeldelser

Thomas Eisner & Edward O. Wilson (eds.) 1978. *The Insects, Readings from Scientific American.* 334 pp, 325 Figs. W. H. Freeman, Reading. Pris $ 8.80 uinnb., $ 18.00 innb.

De fleste entomologer vil være enige med redaktørene av boken "The Insects" i at det er på tide å bli klar over at insekter er av intresse for alle biologer. Ikke bare på den måten de griper inn i planters og andre dyrs liv, men også fordi insekter ofte er velegnete objekter for studier av fundamentale biologiske problemer. Dette er også det essentielle innhold i denne boken, som er redigert av Thomas Eisner ved Cornell og Edward O. Wilson ved Harvard University.

Scientific American er populærvitenskap på sitt beste, og artiklene om insekter er ingen unntakelse i så måte. Boken er et utvalg av artikler som har stått i magasinet gjennom de siste 25 år, og som her er samlet uten omarbeidelser. I boken knyttes de sammen gjennom en oppdeling i temaer, og gjennom en generell introduksjon om insektenes suksess og mangfoldighet som landdyr.

Artiklene er delt i fem temaer eller hovedavsnitt. Det første tar for seg anatomi og fysiologi. Her behandles bl.a. eggskallets mikrostruktur (H. E. Hinton), flygemusklenes funksjon (D. S. Smith), metamorfose (V. B. Wigglesworth) og juvenilt hormon (C. M. Williams). I det følgende avsnitt er det samlet en gruppe artikler om adferd og neurobiologi. De omfatter bl.a. luktreseptorer (D. Schneider), feromoner (E. O. Wilson), nervesystemet og sirissenes sang (D. Bentley og R. R. Hoy), adferdsmønstrenes genetikk (S. Benzer) og navigering med polarisert lys (R. Wehner). Det tredje hovedavsnittet omhandler evolusjon og økologi. Hit hører bl.a. artikler om melanisme hos bjørkemåler (J. A. Bishop og L. M. Cook), forsvar med farger (N. Tinbergen), bananfluenes kjærlighetssang (H. C. Bennet-Clark og A. W. Ewing), evolusjon hos sommerfugl og planter (P. R. Ehrlich og P. H. Raven) og om sopphager hos insekter (S. W. T. Batra og L. R. Batra). I et avsnitt som er kalt "variasjoner i livsstil", bringes en rekke artikler om spesielle tilpasninger hos insekter. Her kan man bl.a. lese om lopper (M. Rothschild), bienes sprog (K. von Frisch), hærmaur (H. R. Topoff), slaver hos maur (E. O. Wilson) og termitter (M. Lüscher). Det siste avsnittet i boken tar for seg insektenes forhold til menneskene, bl.a. med artikler om malaria (C. A. Alvarado og L. J. Bruce-Chwatt), radioaktiv sterilisering av "screw-worm" (E. F. Knipling), integrert bekjempelse (R. F. Smith og W. W. Allen) og om betydningen av biller som nedbryter gjødsel (D. F. Waterhouse).

Det vil føre for langt å gå i detalj om de enkelte artiklene – ialt 35 – som er samlet i denne boken. Felles for dem er at det er lagt stor vekt på den pedagogiske siden ved fremstillingen. Teksten er rikelig illustrert både med fotografier og tegninger. Skjematiske oversiktstegninger og diagrammer har fått bred plass, og bidrar til å gjøre stoffet interessant og lettleselig.

Tilsammen gir boken et tverrsnitt av moderne, entomologisk forskning. Å lese den er som å foreta en vandring gjennom de viktigste oppdagelser og resultater fra de siste årtier. Allikevel er det en ting man kanskje vil savne, og det er en videreføring av stoffet. Artiklene er av forskjellig alder, og noen av dem er skrevet for mer enn tyve år siden. På de fleste områder har utviklingen gått videre, og man sitter stadig med et spørsmål om det har skjedd noe viktig siden disse artiklene ble skrevet. Det har neppe vært praktisk gjennomførlig å skrive et tillegg til hver artikkel, men en mulig løsning hadde vært å inkludere nye referanser i listen bakerst i boken. Slik hadde iallfall de lesere som ville fordype seg i stoffet hatt en henvisning til videre lesning.

Slik den er lagt opp gir denne boken selvsagt ingen fullstendig oversikt over fagområdet, og det er heller ikke meningen at den skal fungere som en lærebok i entomologi. Men som et supplement ved siden av lærebøker er den aldeles ypperlig. For alle som studerer insekter, eller underviser i entomologi ved skoler, høyskoler og universiteter, vil denne boken være en kilde til inspirasjon.

Lauritz Sømme

Bernhard Klausnitzer 1978. *Ordnung Coleoptera (Larven).* 378 pp., 1098 Textfiguren und 35 Tafeln. Dr. W. Junk b.v. Publishers, Hague. Pris 150 Gulden.

Det hollandske forlaget W. Junk har i de senare år gitt ut flere bøker med bestemmelsesnøkler over deler av den europeiske jordbunnsfaunaen. Det siste tilskuddet er Klausnitzers bok om billelarver. Denne boken bygger dels på Ghilarov's arbeide fra 1964, dels på andre. Ikke minst fordi Ghilarov's bok er skrevet på russisk, og derfor vanskelig tilgjengelig for vesteuropeere, bør utgivelsen være av interesse. Også fordi omfanget av Klausnitzers bok er vesentlig utvidet i forhold til Ghilarovs er den meget velkommen.

I alt 653 slekter fordelt på 93 familier er representert, og behandlet til slektsnivå. Fordi intensjonen er å dekke jordbunnsfaunaen, er det forståelig at viktige familier, deriblant Scolytidae, er utelatt.

Klausnitzer følger i det vesentlige samme storsystematikk som brukes av Freude, Harde & Lohse i "Die Käfer Mitteleuropas". Forfatteren grunngir avvikelsene i innledningskapitlet. I forhold til "Catalogus Coleopterorum Fennoscandia et Dania" er det derfor flere forandringer.

Innledningskapitlet omfatter også en grei kortfattet del om generell morfologi hos billelarver. Endel spesielle termer defineres, og ikke minst viktig er det at de oftest anvendte hovedkarakterene fremheves.

Oppbyggingen av boken går ut ifra en underordensnøkkel, hvoretter underordnene behandles separat og fører frem til overfamilie eller familie. Fordi forfatteren har delt stoffet opp i så mange små enheter som mulig før selve slektsbehandlingen, virker bestemmelsestabellene greie og oversiktlige.

Et vell av tekstfigurer danner et godt og instruktivt supplement til selve teksten. Dessverre er kvaliteten varierende. Noen av figurene er unødig små. Flere er også for lite omfattende, f.eks. figurene av stemmataenes innbyrdes plassering. De ville ha vært mere instruktive hvis omliggende partier av hodet hadde vært tatt med, og ikke bare markert som prikker. At trykken ikke alltid er god, slik at flere figurer har mye groing, kan forfatteren vanskelig klandres for. Om de i alt hundre habitusfigurene kan bare sies at de er vakkert utført. Samtlige bærer preg av høy og jevn kvalitet.

Litteraturlista er svært omfattende og vil utvilsomt gjøre boken til et viktig redskap for de som vil arbeide spesielt med larvesystematikk.

Familiene Catopidae, Staphylionidae, Cerambycidae, Chrysomelidae og Curculionidae behandles i et tillegg. De tre siste er bare delvis behandlet, noe som henger sammen med deres ofte lille direkte tilknytting til jordbunnen.

Opplysninger om vertsplanter, habitatvalg m.m. er for mange slekters vedkommende gitt i stikkordsform gjennom hele boken.

Et naturlig spørsmål må være hvor anvendelig boken er for norske forhold. Hovedtyngden av norske slekter er med, og denne boken er derfor den mest komplette innen sitt felt. Mye arbeide står igjen, noe forfatteren presiserer.

Boken har minussider, men konklusjonen må være at boken gir et meget solid inntrykk. En helt rett bedømmelse vil selvfølgelig bare kunne gies etter en tids bruk. Larvesystematikken har alltid vært et forsømt felt i Norge. Forhåpentlig vil dette arbeidet inspirere noen til å øke innsatsen innenfor denne disiplinen. Det er derfor å håpe at Klausnitzer og hans medarbeidere lykkes i planene om å videreføre arbeidet med en bok til artsnivå.

Torstein Kvamme

Sven Gisle Larsson. 1978. *Baltic Amber–a Paleobiological Study. Entomonograph, Vol. 1.* 192 pp. Scandinavian Science Press, Klampenborg. Pris d.kr. 120.– (d.kr. 90.– i abonnement).

Med denne boken innleder Scandinavian Science Press en ny serie av monografier – "Entomonograph". Serien vil i første rekke omfatte systematikk, faunistikk og morfologi, og flere bind er under forberedelse, bl.a. om forskjellige grupper av Lepidoptera, Hemiptera, og om Diptera; Syrphidae.

Sven Gisle Larssons bok er en omfattende oversikt om insekter og edderkoppdyr i baltisk rav. Rav har sin opprinnelse i de store skogene som vokste i det området hvor Østersjøen ligger idag. De eldste funnene er over 100 millioner år gamle, og stammer fra siste del av Kritt-tiden, og første del av Tertiær. De fleste kommer fra den mellomste del av denne perioden. Klimaforandringer i Miocene førte til at de trærne, som har gitt opphav til rav, ble presset sydover, og de yngste fossilene er minst 20 millioner år gamle.

Forfatteren legger stor vekt på å beskrive forholdene i skogene og de omstendigheter som førte til dannelsen av rav. Et av innledningskapitlene gir også en grundig beskrivelse av de forskjellige former for rav, deres kjemiske og fysiske egenskaper. Disse generelle kapitlene er kanskje de mest intressante for en leser som ikke er spesielt intressert i detaljer om de enkelte dyregruppene.

Boken er basert på en samling som omfatter mer enn 8000 fossile insekter og edderkoppdyr funnet i rav fra Danmark og Preussen. De alle fleste er insekter. Noen av dem er dårlig bevart, og kan være vanskelig å identifisere. De fleste artene er relativt fjernt beslektet med nålevende former. Dessuten fins grupper, slik som termitter, som ikke lenger lever i dette området.

Stoffet er inndelt etter det levevis de fossile insektene har hatt. Insekter, som ble fanget mer tilfeldig i kvae på trærne mens de hvilte, har rimeligvis et stort innslag av Diptera. Blant faunaen under bark og mose fantes bl.a. Collembola, Coleoptera, og Hymenoptera, foruten Diplura, Symphyla, Arachnoidea, m.fl. Den mer skjulte fauna i trestammer, svake og syke trær omfatter i første rekke et stort antall Coleoptera.

Ialt er det ganske imponerende hvilken stor og variert fauna som har blitt bevart på denne måten. Samlingen gir et usedvanlig godt innblikk i tidligere tiders fauna. Man forstår også hvilket kollosalt og vanskelig arbeid det må ha vært å bearbeide et så omfattende materiale. Selv om boken unektelig er nokså spesiell, er den en god begynnelse for den nye monografi-serien, som vi håper vil bringe flere bind av samme kvalitet.

Lauritz Sømme

NORWEGIAN JOURNAL OF ENTOMOLOGY

EDITOR
LAURITZ SØMME

VOLUME 25, 1978

UNIVERSITETSFORLAGET

Norwegian Journal of Entomology
Norsk Entomologisk Tidsskrift

EDITOR

Dr. philos. Lauritz Sømme, Zoologisk institutt, Universitetet i Oslo, Blindern, Oslo 3, Norway.

EDITORIAL COMMITTEE

Førstelektor Eivind Østbye, Konsulent Per F. Waaler, Førstekonservator dr. philos. Albert Lillehammer.

PUBLISHER

Universitetsforlaget: P.O. Box 7508, Skillebekk, Oslo 2, Norway.
P.O. Box 142, Boston, Massachusetts 02113, U.S.A.

CONTRIBUTIONS

These should be sent to the Editor. Authors are requested to follow the instructions on page 3 of the cover.
Artikler som ønskes trykt i tidsskriftet sendes redaktøren. Bidragsytere må følge anvisningen på omslagets tredje side.

SUBSCRIPTIONS

Non-members of the Norwegian Entomological Society should send their orders to Universitetsforlaget. The subscription price per volume (two issues annually) is for 1978 U.S. $22.00 (N.kr. 110.–). U.S. $ price is subject to change without notice in case of devaluation/revaluation. Notice of change of address should be accompanied by the old address. Back volumes should also be ordered from Universitetsforlaget.

NORSK ENTOMOLOGISK FORENING

ser sin hovedoppgave i å fremme det entomologiske studium i Norge, og danne et bindeledd mellom de interesserte. Medlemskontingenten er for tiden kr. 40.– pr. år. Medlemmer får tidsskriftet fritt tilsendt. Henvendelser om medlemskap sendes sekretæren: Cand. real. Trond Hofsvang, Zoologisk institutt, NLH, 1432 Ås-NLH.

© Universitetsforlaget 1978

Berlings, Lund 1978

NORWEGIAN JOURNAL OF ENTOMOLOGY

Volume 25, 1978

INNHOLD/CONTENTS

SHORT COMMUNICATIONS

Instructions to Authors

The *Norwegian Journal of Entomology* publishes papers in English, occasionally in Norwegian and German. When preparing manuscripts for publication, authors should consult current copies of the journal and follow the style as closely as possible.

MANUSCRIPT

Manuscript must be typewritten on one side of the paper only, with double spacing throughout, and with a wide margin. Authors should submit the original manuscript (preferably with two copies) to the Editor whose address is on page 2 of the cover.

Separate sheets should be used for the following: (1) Title page, with the author's name; (2) Abstract not exceeding 11 lines (770 letters and spaces) with the name and full postal address of the author underneath; (3) References; (4) Tables with their headings; (5) Legends to Figures.

In the case of articles submitted in a language other than English, the Abstract. Table headings and Figure legends must be accompanied with an English translation.

Brief *Acknowledgements* of grants and other assistance, if any, will be printed at the end of the text.

FIGURES AND TABLES

All illustrations will be considered as Figures. Each graph, drawing or photograph should be numbered in sequence with arabic numerals, and should be identfied lightly on the back with the name of the journal, the author's name, and the Figure number. The top should be indicated. The Figures should be the original drawings and should be constructed in proportion to either the entire width of the type area (14 cm) or to the column width (6.7 cm). Lines must be thick enough to allow for reduction. Letters and numbereds must not be less than 2 mm in the printed illustration. Photographs should be submitted as unmounted glossy enlargements showing good detail.

Tables should be numbered in Roman numerals, each having a descriptive heading and typed on a separate sheet. Since Tables, as well as Figures, are reproduced photographically, they should be constructed in the same proportion as for Figures. Very large Tables should be typewritten on separate sheets to be printed on facing pages. They must be typewritten on good quality paper with all rules drawn in with a fine pen.

All Figures and Tables should be referred to in the text by their number, and their approximate position indicated in the margin of the manuscript.

All drawings and microphotographs should have a scale giving the appropriate metric unit (m, cm, mm, μm, or nm).

REFERENCES TO LITERATURE

In the text. Brown (1957), Brown & White (1961). If more than two authors, Brown et al. (1963). Multiple references: 'As several authors have reported (Brown 1957, Brown & White 1961, Green et al. 1963)', i.e. chronological order, no commas between names and year.

The list of *References* should be in alphabetical order and not numbered. The international alphabetical order of Scandinavian and German vowels should be observed: Å=AA, Æ and Ä=AE, Ø and Ö=OE, Ü=UE. Indicate 1st, 2nd, 3rd, etc. works by the same author in the same year by a, b, c, etc. e.g. (White 1966a). *Ditto marks, et al. and ibid.* should not be used. Generally, titles of journals should be abbreviated according to the *World List of Scientific Periodicals.*

Examples:

Løken, A. 1964. Social wasps in Norway (Hymenoptera, Vespidae). *Norsk ent. Tidsskr. 12,* 191–218.

Schwarts, R. J. 1955. *The Complete Dictionary of Abbreviations.* 211 pp., T. Y. Cromwell Co., New York.

Whitman, L. 1951. The arthropod vectors of yellow fewer. pp. 229–298 in Strode, K. (ed.) *Yellow Fever.* McGraw-Hill, New York and London.

PROOFS

Authors will receive two copies of the first proof (page proof). One copy should be returned duly corrected without delay. All technical sections of the article, including references, names, figures (numbers, formulae), illustrations and so on, are the responsibility of the author. Authors will be required to pay for any alterations they make against the manuscript.

OFFPRINTS

Seventy-five offprints of each article without covers will be supplied free of charge. Additional offprints may be ordered at the author's own expense.

CONTENTS

Short Communications

NO ISSN 0029-1897