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Managing Editor (Administrerende redaktør)
Dr. Kjetil Bevanger, Foundation for Nature Research and Cultural Heritage Research (NINA•NIKU),
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Pit-fall catches of surface-active arthropods in high mountain habitats at Finse, south Norway. IV. Coleoptera

Eivind Østbye & Sigmund Hågvar

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Surface-active Coleoptera were collected by pit-fall traps during three years in five alpine habitats: a "pioneer ground" close to a retreating glacier, an "oligotrophic dry heath" with abundant lichens, an "eutrophic meadow" with rich vegetation, a "snow bed" dominated by *Salix herbacea*, and a "tussock habitat" in an oligotrophic peat bog. Altogether, 38 species were collected from 8 families, with a dominance of Staphylinidae (20 species) and Carabidae (7 species). Also in the number of individuals, Staphylinidae dominated (62.5 %), followed by Carabidae (33.6 %). Eight eurytopic species occurred in all five habitats: four Staphylinidae (*Arpedium quadrum*, *Liogluta alpestris*, *Anthophagus alpinus* and *Boreaphilus henningianus*), two Carabidae (*Patrobus septentrionis* and *Notiophilus aquaticus*), one Curculionidae (*Otiorhynchus nodosus*) and one Byrrhidae (*Byrrhus fasciatus*). The eutrophic meadow had the highest species number (24), and the oligotrophic dry heath the lowest (13). Evidently, many species (15) are able to live in the pioneer ground, which is only 200 years old and has a non-continuous vegetation cover. However, a dense cover of small stones (30 %) may be favourable for many species. The activity of ground living Coleoptera in the Finse area is dominated by Carabidae during spring and by Staphylinidae during summer and autumn. A sociological ordination of animals related to plant communities is attempted.

Eivind Østbye, Department of Biology, Division of Zoology, University of Oslo, P. O. Box 1050 Blindern, N-0316 Oslo, Norway.

Sigmund Hågvar, Department of Biology and Nature Conservation, Agricultural University of Norway, P. O. Box 5014, N-1432 Ås, Norway.

INTRODUCTION

The present paper deals with Coleoptera collected by pit-fall traps in the years 1969-71 and covers five alpine habitats near Finse, Hardangervidda, in southern Norway (60°36' N, 7°30' E) (UTM 32V MN 11). The main objectives were to study species composition in different habitats and to reveal the phenology pattern of the actual species. The total catches of Coleoptera have been presented in a previous paper (Hågvar et al. 1978).

MATERIAL AND METHODS

The five habitats have been described in detail by Østbye et al. (1978), and only a short review will be given here. Pioneer ground is situated quite near a glacier, and the habitat is about 200 years old. It is rocky and lacks continuous vegetation cover. The oligotrophic dry heath, which is a dominant vegetational type in the area, is to a large extent covered by lichens. The eutrophic meadow is rather moist and rich in vegetation. In the snow bed, the snow melts rather late, and the vegetation is dominated by *Salix herbacea* L. 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 a transect in the low-alpine zone, between 1 220 m a. s. l. in a valley bottom up to a glacier snout 1 350 m a. s. l..

In each habitat, 15 traps, 7 cm in upper diameter, were operated during most of the snow-free season. These were placed in three rows with 5 m between each trap and row. The traps were emptied about every two weeks. A total of 3 416 adult coleopterans were caught.

The climate during the three seasons is described by Østbye et al. (1978).

RESULTS AND DISCUSSION

As pointed out in a previous article (Hågvar et al. 1978), the pit-fall method is selective and generally expresses the "activity density", as a result of both the activity and the density of the animals. Because the animals' activity depends on both the local microclimate and the density of the vegetation, pit-fall trapping of Carabidae are often regarded to be of little value when estimating populations in various habitats (Southwood 1966). Studies on Carabidae trapping (Grüm 1959, Briggs 1961, Mitchell 1963, Greenslade 1964) indicate that the trapping efficiency varies between species and habitats, and also depends on other factors such as weather conditions and the physiological condition of the animal. The trapping efficiency for the whole Coleoptera group, especially for the Carabidae family, is by others regarded to be fairly good (Westerberg 1977). Several papers (Boer 1971, 1977, Meijer 1974, Baars 1979) imply that pit-fall trapping could be used as an indication of relative abundance in different years and sites within the same species. Even in interspecific comparisons between sites and years pit-fall trap-

ping could be of some value if performed in the proper manner (Baars 1979).

As the same method was used in all habitats during all years of the study, the catches in different habitats are supposed to give useful information on phenology, species composition and, to some degree, on density variation.

The families represented

The 38 species of Coleoptera trapped in these 5 high mountain habitats belonged to 8 families (**Table 1**). Staphylinidae and Carabidae were the two overwhelmingly dominant families, with the former being the most dominant, both with respect to species and individuals. Members of the other six families were taken only in small quantities.

The total catches from these 5 habitats, which are the most dominant habitats in the Finse area, contain a lower number of both families and species than reported earlier using a variety of sampling procedures (Østbye 1969, Østbye & Hågvar 1972).

Fifteen coleopteran families have been recorded in the Finse area with Nitidulidae being the only family from the pit-fall trapping which has not been recorded earlier. Staphylinidae and Carabidae are the families with the highest recorded species numbers at Finse: 40 and 15, respectively. For these families, we feel that the pit-fall catches may give a relevant picture of the dominant, or most active, species in the area. In numbers, Staphylinidae dominated in all habitats except in the pioneer ground where Carabidae gave the highest catches.

The eutrophic meadow gave by far the highest yield (46.3 % of the total number of Coleoptera specimens caught in the different habitats), followed by the snow bed (19.8 %),

Table 1. Percent distribution of the different coleopteran families in catches from each of the five habitats (based on specimens). Number of species (N) and total catches are also given. Combined data from three years.

Family	Habitat										Total number	
	Pioneer ground		Oligotr. dry heath		Eutr. meadow		Snow bed		Tussock habitat			
	N	%	N	%	N	%	N	%	N	%		
Carabidae	4	58.6	2	22.0	4	30.5	3	21.9	4	34.6	7	1148
Hydrophilidae	-	-	1	0.9	1	0.1	-	-	-	-	1	2
Dytiscidae	-	-	-	-	1	0.1	-	-	2	1.2	3	8
Staphylinidae	9	33.0	7	67.0	14	67.6	12	75.8	13	59.3	20	2136
Byrrhidae	1	3.9	1	4.6	2	0.7	1	0.3	2	1.8	3	48
Nitidulidae	-	-	-	-	1	0.1	-	-	-	-	1	1
Chrysomelidae	-	-	-	-	-	-	1	0.1	1	1.8	1	10
Curculionidae	1	4.4	2	5.5	1	0.9	1	1.8	1	1.4	2	63
No of specimens	539		109		1582		675		511		-	3416
No of species	15		13		24		18		23		38	-

the pioneer ground (15.8 %), the tussock habitat (15.0 %), and the oligotrophic dry heath (only 3.2 %).

and *Boreaphilus henningianus*, the byrrhid *Byrrhus fasciatus*, and the curculionid *Otiorhynchus nodosus*.

The species composition in the catches

Altogether 38 species were trapped; varying from 24 in the eutrophic meadow, 23 in the tussock habitat, 18 in the snow bed, 15 in the pioneer ground to 13 in the oligotrophic dry heath (Table 1).

Species composition in the various habitats showed clear differences (Table 2). Only 8 species were taken in all five habitats. Three additional species were recorded in four of the habitats, and another 3 species in three habitats. Eight species occurred in two of the habitats, and 16 in only one habitat.

The 8 eurytopic species are all typical for alpine areas, including the two carabids *Patrobis septentrionis* and *Notiophilus aquaticus*, the four staphylinids *Arpedium quadrum*, *Liogluta alpestris*, *Anthophagus alpinus*

The pioneer ground

The species list from this habitat shows a rather poor beetle fauna with only 15 species recorded (Table 3). The carabid species totaled 4 with *Amara alpina* as the most dominant, both totally and within this family.

Staphylinids dominated in number of species (9), but they occurred with fewer specimens than the carabids. *Psephenus longipes* was the most common species within this family, and second in dominance totally.

Except for the carabid beetles *Amara alpina* and *Notiophilus aquaticus*, and the staphylinid *Psephenus longipes*, all the other species were trapped in low numbers. Two species, the staphylinid *Bryoporus rugipennis* and the carabid *Cymindis vaporariorum* were recorded only in this habitat (Table 2).

Table 2. The species and their relative catches (in %) within each of the five habitats. Combined data for all years. Abbreviated family names: By = Byrrhidae, Ca = Carabidae, Ch = Chrysomelidae, Cu = Curculionidae, Dy = Dytiscidae, Hy = Hydrophilidae, Ni = Nitidulidae, St = Staphylinidae. Nomenclature after Silfverberg (1992).

Fam	Species	Pioneer ground	Oligotr. dry heath	Eutr. meadow	Snow bed	Tussock habitat
Ca	<i>Patrobus septentrionis</i> Dejean	3.9	20.2	17.3	20.7	29.2
Ca	<i>Notiophilus aquaticus</i> (L.)	12.1	1.8	1.4	1.0	0.6
St	<i>Arpedium quadrum</i> (Gr.)	1.3	1.8	17.8	0.7	2.7
St	<i>Liogluta alpestris</i> Heer	0.2	0.9	15.1	3.1	38.9
St	<i>Anthophagus alpinus</i> (Payk.)	0.6	9.2	12.7	25.8	1.0
St	<i>Boreaphilus henningsianus</i> Sahlb.	3.3	16.5	0.8	1.0	2.0
By	<i>Byrrhus fasciatus</i> (Forst.)	3.9	4.6	0.2	0.3	0.4
Cu	<i>Otiorhynchus nodosus</i> (Müller)	4.4	4.6	0.9	1.8	1.4
St	<i>Psephidonus longipes</i> (Mnh.)	23.7	-	15.0	40.4	1.8
St	<i>Eucnecosum brachypterum</i> (Gr.)	-	34.9	3.0	3.6	3.7
St	<i>Cephalocousya nivicola</i> (Th.)	1.3	2.7	0.1	0.1	-
Ca	<i>Amara alpina</i> (Payk.)	42.3	-	11.7	-	4.3
St	<i>Acidota crenata</i> (Fabr.)	0.2	-	0.1	-	0.4
St	<i>Lesteva monticola</i> Kies.	-	-	0.6	0.3	0.4
Hy	<i>Helophorus glacialis</i> Villa	-	0.9	0.1	-	-
St	<i>Atheta graminicola</i> (Gr.)	-	-	1.4	0.1	-
St	<i>Omalium caesum</i> Gr.	-	-	0.2	0.3	-
St	<i>Olophrum boreale</i> (Payk.)	-	-	0.3	-	0.4
St	<i>Atheta subplana</i> J. Sahlb.	-	-	0.2	-	1.3
St	<i>Atheta arctica</i> (Thoms.)	-	-	0.2	-	0.6
St	<i>Mycetoporus nigrans</i> Mäkl.	0.2	0.9	-	-	-
Ch	<i>Chrysomela collaris</i> L.	-	-	-	0.1	1.8
St	<i>Bryoporus rugipennis</i> (Pand.)	2.2	-	-	-	-
Ca	<i>Cymindis vaporariorum</i> (L.)	0.4	-	-	-	-
Cu	<i>Apion haematodes</i> Kirby	-	0.9	-	-	-
By	<i>Simplocaria metallica</i> (Sturm)	-	-	0.5	-	-
Ca	<i>Nebria nivalis</i> (Payk.)	-	-	0.1	-	-
Dy	<i>Agabus guttatus</i> (Payk.)	-	-	0.1	-	-
Ni	<i>Epuraea placida</i> Mäkl.	-	-	0.1	-	-
Ca	<i>Nebria rufescens</i> (Ström)	-	-	-	0.1	-
St	<i>Tachinus elongatus</i> Gyll.	-	-	-	0.1	-
St	<i>Atheta depressicollis</i> (Fauv.)	-	-	-	0.1	-
St	<i>Eucnecosum tenue</i> (Le Conte)	-	-	-	-	5.7
By	<i>Byrrhus pilula</i> (L.)	-	-	-	-	1.4
Dy	<i>Agabus congener</i> (Thbg.)	-	-	-	-	1.0
Ca	<i>Pelophila borealis</i> (Payk.)	-	-	-	-	0.6
St	<i>Mycetoporus erichsonianus</i> Fagel	-	-	-	-	0.6
Dy	<i>Hydroporus morio</i> Aube	-	-	-	-	0.2

The oligotrophic dry heath habitat

This habitat had the lowest recorded number of species, only 13, as well as the lowest num-

ber of specimens (Table 4). Staphylinids dominated both in number of species (7), and in specimens. Even in the most dominant species, *Eucnecosum brachypterum*, the catches

Table 3. Total catches and dominance values (%) in the pioneer ground habitat.

Species	1969	1970	1971	No	%
<i>Amara alpina</i>	62	76	90	228	42.3
<i>Psephidonus longipes</i>	80	8	49	128	23.7
<i>Notiophilus aquaticus</i>	26	9	30	65	12.1
<i>Otiorhynchus nodosus</i>	3	16	5	24	4.4
<i>Patrobus septentrionis</i>	11	4	6	21	3.9
<i>Byrrhus fasciatus</i>	4	14	3	21	3.9
<i>Boreaphilus henningianus</i>	9	1	8	18	3.3
<i>Bryoporus rugipennis</i>	3	4	5	12	2.2
<i>Cephalocousya nivicola</i>	3	1	3	7	1.3
<i>Arpedium quadrum</i>	-	1	6	7	1.3
<i>Anthophagus alpinus</i>	-	1	2	3	0.6
<i>Cymindis vaporariorum</i>	-	2	-	2	0.4
<i>Acidota crenata</i>	-	-	1	1	0.2
<i>Liogluta alpestris</i>	-	-	1	1	0.2
<i>Mycetoporus nigricans</i>	-	-	1	1	0.2
Total no of specimens	201	137	201	539	
No of species	9	12	14	15	

Table 4. Total catches and dominance values (%) in the oligotrophic dry heath habitat.

Species	1969	1970	1971	No	%
<i>Eucnecosum brachypterum</i>	9	9	20	38	34.9
<i>Patrobus septentrionis</i>	5	11	6	22	20.2
<i>Boreaphilus henningianus</i>	11	2	5	18	16.5
<i>Anthophagus alpinus</i>	1	2	7	10	9.2
<i>Byrrhus fasciatus</i>	5	-	-	5	4.6
<i>Otiorhynchus nodosus</i>	5	-	-	5	4.6
<i>Cephalocousya nivicola</i>	2	-	1	3	2.7
<i>Notiophilus aquaticus</i>	-	1	1	2	1.8
<i>Arpedium quadrum</i>	-	-	2	2	1.8
<i>Helophorus glacialis</i>	1	-	-	1	0.9
<i>Liogluta alpestris</i>	1	-	-	1	0.9
<i>Mycetoporus nigrans</i>	-	-	1	1	0.9
<i>Apion haematodes</i>	-	-	1	1	0.9
Total no of specimens	40	25	44	109	
No of species	9	5	9	13	

were small. Only 2 carabid species were recorded, with *Patrobus septentrionis* being the most common, ranking second on the list. Most species were trapped in very low numbers, and often in only one or two years.

One species, *Apion haematodes*, was recorded only in this habitat, with only one specimen.

The eutrophic meadow

This habitat gave the highest catches, both of species (24), and specimens (**Table 5**). The staphylinid *Arpedium quadrum* was dominant, closely followed by the carabid *Patrobus septentrionis*. Then followed 3 staphylinids

(*Liogluta alpestris*, *Psephidonus longipes*, *Anthophagus alpinus*), and 1 carabid (*Amara alpina*). The other species occurred only in low numbers, and some were found only in one or two years. Staphylinids dominated both in species numbers (14), and in specimens, and only 4 species of carabids were recorded. Four species, *Simplocaria metallica*, *Nebria nivalis*, *Agabus guttatus*, and *Epuraea placida*, were recorded only in this habitat, but in very low numbers. The trapping locality in the eutrophic meadow was close to a small rivulet coming from the glacier. Such wet and cold riverine habitats are typical for the carabid *Nebria nivalis*.

Table 5. Total catches and dominance values (%) in the eutrophic meadow habitat.

Species	1969	1970	1971	No	%
<i>Arpedium quadrum</i>	138	35	109	282	17.8
<i>Patrobus septentrionis</i>	93	101	79	273	17.3
<i>Liogluta alpestris</i>	68	67	104	239	15.1
<i>Psephidonus longipes</i>	176	22	40	238	15.0
<i>Anthophagus alpinus</i>	26	63	112	201	12.7
<i>Amara alpina</i>	119	29	37	185	11.7
<i>Eucnecosum brachypterum</i>	18	13	17	48	3.0
<i>Notiophilus aquaticus</i>	6	3	14	23	1.4
<i>Atheta graminicola</i>	12	3	7	22	1.4
<i>Otiorhynchus nodosus</i>	6	8	-	14	0.9
<i>Boreaphilus henningianus</i>	6	5	2	13	0.8
<i>Lesteva monticola</i>	1	1	7	9	0.6
<i>Simplocaria metallica</i>	3	3	2	8	0.5
<i>Olophrum boreale</i>	1	2	2	5	0.3
<i>Atheta subplana</i>	1	1	2	4	0.2
<i>Omalium caesum</i>	2	1	-	3	0.2
<i>Atheta arctica</i>	2	-	1	3	0.2
<i>Byrrhus fasciatus</i>	1	-	2	3	0.2
<i>Nebria nivalis</i>	-	1	1	2	0.1
<i>Acidota crenata</i>	-	1	1	2	0.1
<i>Agabus guttatus</i>	-	-	2	2	0.1
<i>Helophorus glacialis</i>	1	-	-	1	0.1
<i>Cephalocousya nivicola</i>	-	-	1	1	0.1
<i>Epuraea placida</i>	1	-	-	1	0.1
Total no of specimens	681	359	542	1582	
No of species	20	18	20	24	

The snow bed

Although this site is poor in plant species, the catches revealed 18 coleopterous species and the second highest number of specimens (Table 6). While only three carabid species were found, the staphylinids dominated, both in species (12), and numbers. *Psephidonus longipes* and *Anthophagus alpinus* dominated, followed by the carabid *Patrobus septentrionis*. All the other species were taken in very low numbers, and several were represented by only one specimen in a single year. The chrysomelid *Chrysomela collaris* was among these. This was unexpected, since this species according to our experience is one of the most common beetles in *Salix herbacea* snow beds. However, it is slow-moving and uses mainly the outer parts of the habitat which melt early (Hågvar 1975). The following species were

recorded only in this habitat: *Nebria rufescens*, *Tachinus elongatus* and *Atheta (Anopleta) depressicollis*. According to our experience, *N. rufescens* is a widespread species in this area, and can be found in several different habitats if humid enough.

The tussock habitat

This habitat was second with respect to the number of species (23). The number of specimens, however, was the second lowest. Staphylinids again dominated in number of species (13), as well as specimens, with *Liogluta alpestris* as the dominant species (Table 7). The carabids numbered 4 species with *Patrobus septentrionis* the next dominant. Most other species were recorded in very low numbers. Six species were recorded

Table 6. Total catches and dominance values (%) in the snow bed habitat.

Species	1969	1970	1971	No	%
<i>Psephidonus longipes</i>	144	45	84	273	40.4
<i>Anthophagus alpinus</i>	26	44	104	174	25.8
<i>Patrobus septentrionis</i>	70	55	15	140	20.7
<i>Eucnecosum brachypterum</i>	5	7	12	24	3.6
<i>Liogluta alpestris</i>	2	1	18	21	3.1
<i>Otiorhynchus nodosus</i>	2	8	2	12	1.8
<i>Notiophilus aquaticus</i>	6	1	-	7	1.0
<i>Boreaphilus henningianus</i>	6	1	-	7	1.0
<i>Arpedium quadrum</i>	-	1	4	5	0.7
<i>Omalius caesum</i>	1	1	-	2	0.3
<i>Byrrhus fasciatus</i>	1	1	-	2	0.3
<i>Lesteva monticola</i>	-	-	2	2	0.3
<i>Nebria rufescens</i>	-	1	-	1	0.1
<i>Atheta graminicola</i>	-	-	1	1	0.1
<i>Cephalocousya nivicola</i>	-	-	1	1	0.1
<i>Tachinus elongatus</i>	-	-	1	1	0.1
<i>Atheta depressicollis</i>	-	-	1	1	0.1
<i>Chrysomela collaris</i>	-	-	1	1	0.1
Total no of specimens	263	166	246	675	
No of species	10	12	13	18	

Table 7. Total catches and dominance values (%) in the tussock habitat.

Species	1969	1970	1971	No	%
<i>Liogluta alpestris</i>	108	17	74	199	38.9
<i>Patrobus septentrionis</i>	57	37	55	149	29.2
<i>Eucnecosum tenue</i>	29	-	-	29	5.7
<i>Amara alpina</i>	4	3	15	22	4.3
<i>Eucnecosum brachypterum</i>	9	3	7	19	3.7
<i>Arpedium quadrum</i>	3	1	10	14	2.7
<i>Boreaphilus henningianus</i>	8	-	2	10	2.0
<i>Psephidonus longipes</i>	3	2	4	9	1.8
<i>Chrysomela collaris</i>	3	6	-	9	1.8
<i>Byrrhus pilula</i>	1	3	3	7	1.4
<i>Otiorynchus nodosus</i>	4	2	1	7	1.4
<i>Atheta subplana</i>	3	2	1	6	1.3
<i>Agabus congener</i>	1	1	3	5	1.0
<i>Anthophagus alpinus</i>	-	-	5	5	1.0
<i>Atheta arctica</i>	1	1	1	3	0.6
<i>Pelophila borealis</i>	-	1	2	3	0.6
<i>Notiophilus aquaticus</i>	-	-	3	3	0.6
<i>Mycetoporus erichsonianus</i>	2	-	1	3	0.6
<i>Acidota crenata</i>	1	1	-	2	0.4
<i>Byrrhus fasciatus</i>	-	1	1	2	0.4
<i>Olophrum boreale</i>	2	-	-	2	0.4
<i>Lesteva monticola</i>	2	-	-	2	0.4
<i>Hydroporus morio</i>	1	-	-	1	0.2
Total no of specimens	242	81	246	511	
No of species	19	15	17	23	

only from this habitat: *Eucnecosum tenue*, *Byrrhus pilula*, *Agabus congener*, *Pelophila borealis*, *Mycetoporus erichsonianus* and *Hydroporus morio*. The carabid *Pelophila borealis* is a dominant species on the *Caricion-canescens-nigrae* mire habitats on sedimentation flats along the glacier rivers in the area.

Species distribution between habitats

The pioneer habitat contained an astonishing high number of species (15), considering its young age (200 years) and non-continuous vegetation cover. Even the number of spider species collected in the traps (18) was com-

parable to that found in the other four habitats (16-22 species) (Hauge et al. 1978). The considerable number of beetle and spider species so close to the retreating glacier may be due to several factors: good dispersal abilities, high habitat tolerances within a number of generalists, and probably favourable microhabitats beneath stones, which cover as much as 30 % of the ground. The dominant coleopteran in the catches from this site, *Amara alpina*, is a typical alpine species (Lindroth 1945). Another characteristic species in this barren habitat is *Notiophilus aquaticus*. In other studies of pioneer habitats in this area, *Nebria nivialis* and *N. rufescens* have been found abundant along moss-covered banks of brooks and rivulets stemming from the glacier (Østbye

1963). The absence of these species in the pit-fall traps of the pioneer ground must be due to the relatively dry conditions in the actual site.

The tussock habitat, 3 km from the glacier, is assumed to represent a climax community in the Finse area, and was rich in coleopteran species (23). However, the eutrophic meadow, only 1 km from the glacier, had the highest species number (24) and also a much higher catch of individuals than any other habitat (**Table 1**). Evidently, the development of species- and specimen-rich habitats is possible rather close to the glacier, if local conditions are favourable (soil, moisture and topography). The luxuriant, species-rich vegetation of the eutrophic meadow can sustain a rich diversity of coleopterans, although the stone cover is below 10 % (cf. Østbye et al. 1978). Also the snow bed and the oligotrophic dry heath depend greatly on local conditions and are difficult to place along an imaginary succession gradient from the pioneer ground to the tussock habitat.

Even though the oligotrophic dry heath was situated as much as 2.5 km from the glacier, this site gave the lowest number of both species (13) and specimens. The low catches may be due to a combination of several factors: The low primary productivity, the dryness, and the dense lichen vegetation in certain areas, which may strongly reduce the mobility of the coleopterans.

The snow bed represents a special situation. This habitat is found scattered in the landscape in depressions with a thick snow cover in winter. Considering the short snow-free season, and a non-continuous plant cover dominated by the tiny willow species *Salix herbacea*, this habitat contains a considerable number of coleopteran species (18). The high coverage of stones (15-20 %) and good moisture conditions may be favourable for many species.

Comparison with other Fennoscandian mountain areas

The carabid fauna has been fairly well studied in a south-north gradient in Fennoscandian mountain areas. Alpine habitats have been investigated from Hardangervidda (Finse, 60°36'N) (Østbye 1963 and 1969, Østbye & Hågvær 1972, Fjellberg 1972, Ottesen 1991) in the south, to Jotunheimen (61°30'N) (Refseth 1977, 1980), Saltfjellet (67°0'N) (Thingstad 1980, 1987), Virihaure (67°10'N) (Brinck & Wingstrand 1949, 1951), Torne-träsk (68°20'N) (Brundin 1934) and Kilpisjärvi (69°01'N) (Forsskåhl 1972) in the north.

Different collecting methods have been used, with pit-fall trapping only in the three first areas. The number of investigated habitats differ from area to area, and few of the habitats have belonged to corresponding vegetation communities. All together this makes a comparison of the variety of the carabid fauna in different areas difficult.

When similar low-alpine plant communities were put together, two main types (in broad terms) might be compared: oligotrophic dry heaths and eutrophic meadows. The number of carabid species was rather similar along the north-south gradient, with approximately 10 species in oligotrophic dry heaths, and approximately 15 species in eutrophic meadows. Also the species composition showed great similarities from south to north. Some species occurring in southern areas were replaced by others in the north, but these were usually species occurring in low numbers. *P. septentrionis* and *A. alpina* were common species in both oligotrophic and eutrophic sites in all areas except at Saltfjellet where *Amara brunnea* was in dominance. This species is common in sub- and low alpine habitats at Hardangervidda, but was not recorded at Finse.

In those areas where some of the other three habitats were studied, the dominant species, and even many of the other species, were much the same.

We agree with Thingstad's (1987) conclusion that the species number of carabids in low alpine habitats is rather unchanged along a south-north gradient in Fennoscandia.

Seasonal changes in catches

The seasonal changes in catches tend to show four main patterns. First, there are species which have their highest activity immediately after the spring snow melt, i.e. mainly in July. This is typical for the carabids *A. alpina*, *P. septentrionis* and *N. aquaticus* as well as the curculionid *O. nodosus* and the byrrhid *B. fasciatus* (Figures 1-5). Earlier studies report the same pattern for the carabid *N. nivalis* (Østbye 1963).

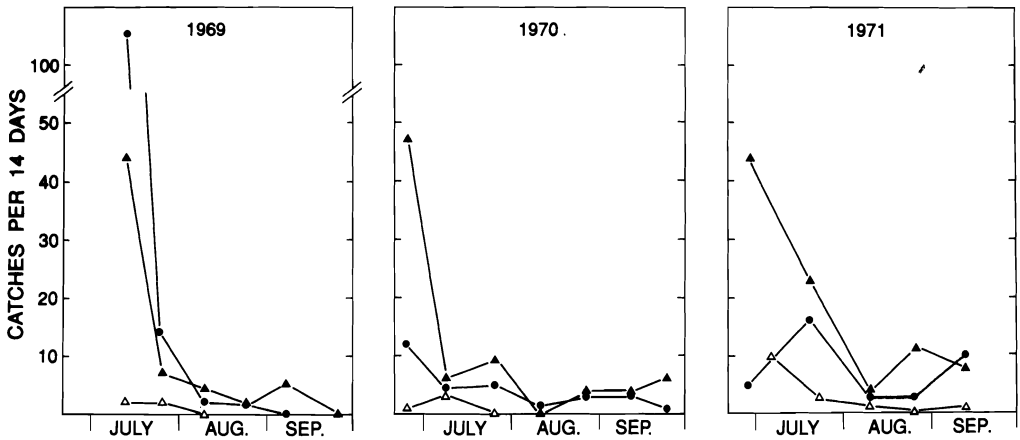


Figure 1
Seasonal variation in pit-fall catches of *Amara alpina* over three years.
Symbols:

- Filled triangle: pioneer ground habitat
- Open triangle: tussock mire habitat
- Filled circle: eutrophic meadow habitat
- Open circle: oligotrophic dry heath habitat
- Open square: snow bed habitat

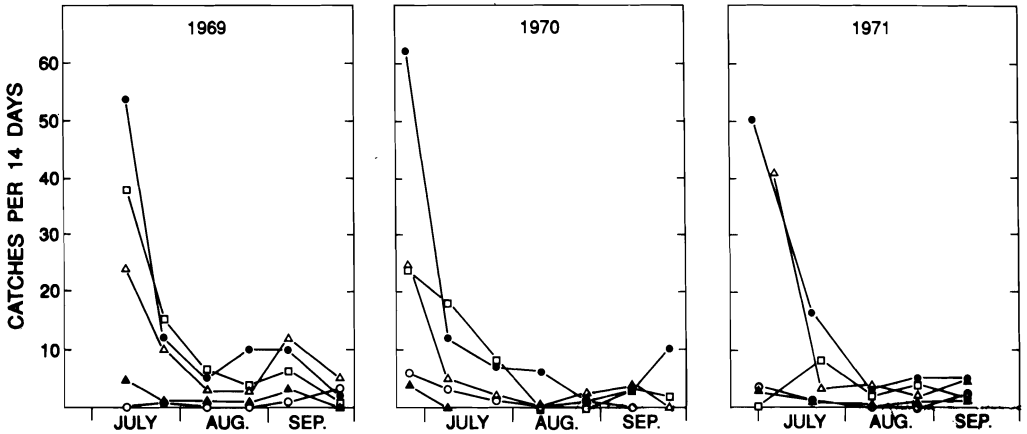


Figure 2

Seasonal variation in pit-fall catches of *Patrobis septentrionis* over three years. Explanation of symbols is given in Figure 1.

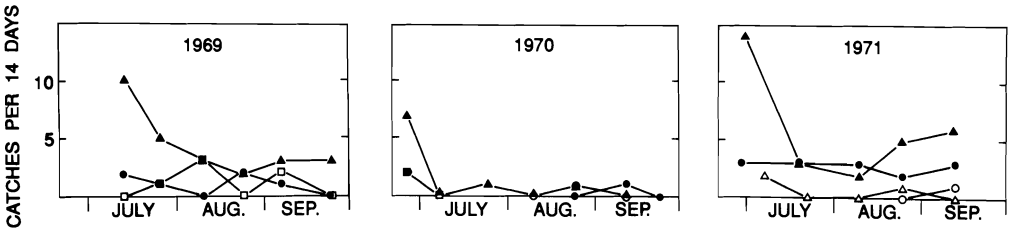


Figure 3

Seasonal variation in pit-fall catches of *Notiophilus aquaticus* over three years. Explanation of symbols is given in Figure 1.

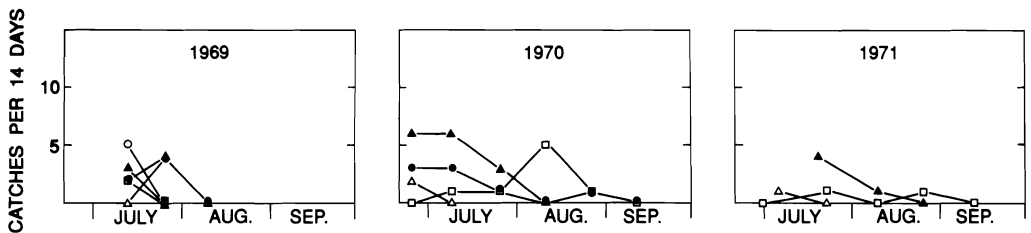


Figure 4

Seasonal variation in pit-fall catches of *Otiorynchus nodosus* over three years. Explanation of symbols is given in Figure 1.

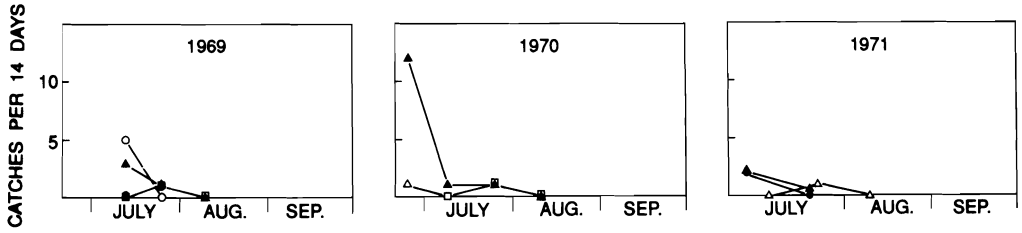


Figure 5
Seasonal variation in pit-fall catches of *Byrrhus fasciatus* over three years. Explanation of symbols is given in Figure 1.

Species of the second group start with little activity in the spring, then peak in Jul./Aug. and fall back to a low activity level again in

Sept.. This pattern is typical for many staphylinids, for instance *P. longipes*, *A. alpinus*, *A. quadrum*, and *E. brachypterum* (Figures 6-9).

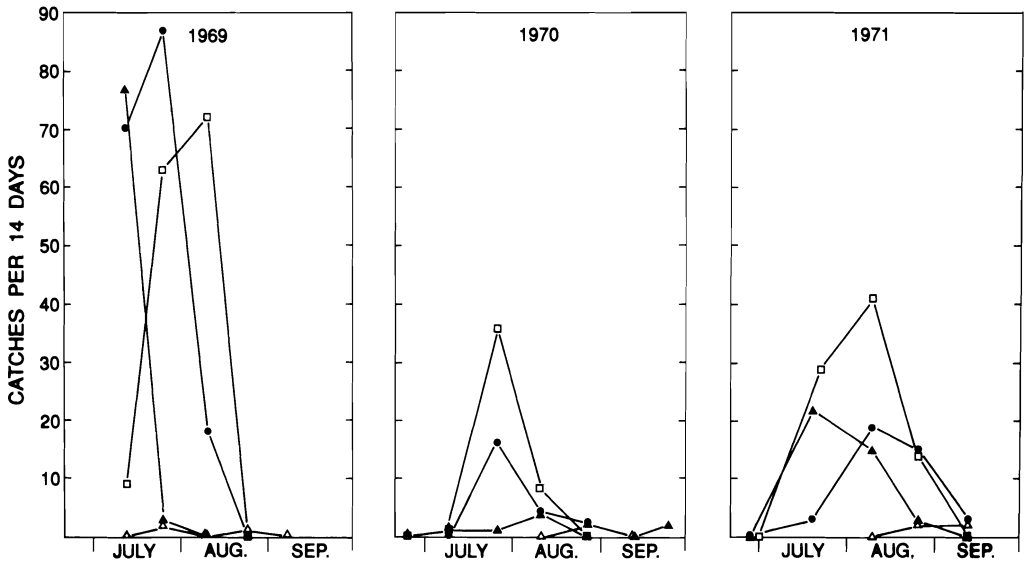


Figure 6
Seasonal variation in pit-fall catches of *Psephidonus longipes* over three years. Explanation of symbols is given in Figure 1.

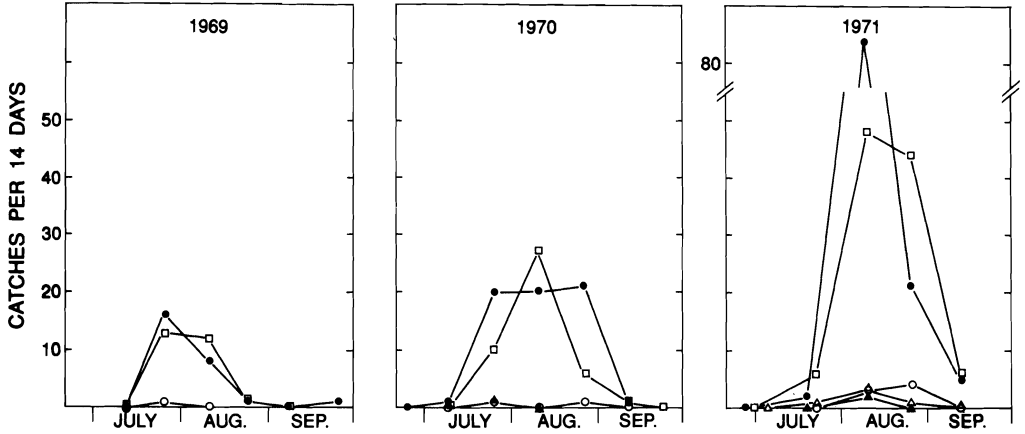


Figure 7

Seasonal variation in pit-fall catches of *Anthophagus alpinus* over three years. Explanation of symbols is given in Fig. 1.

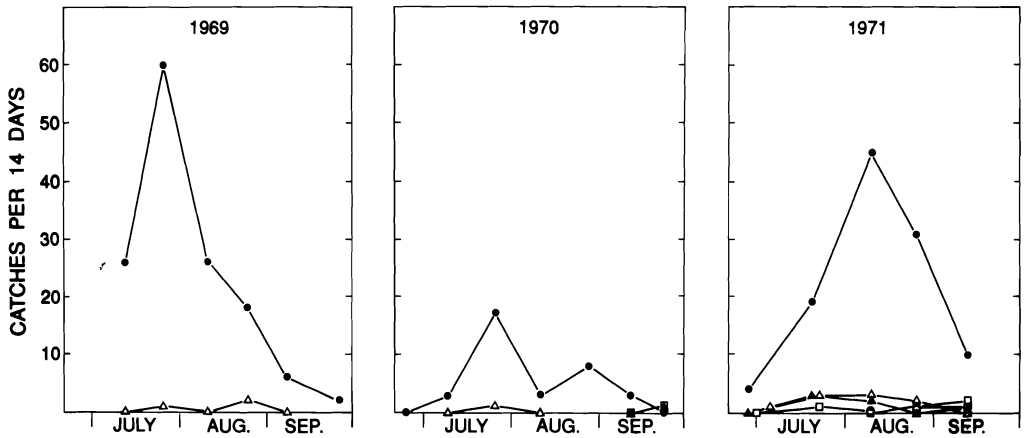


Figure 8

Seasonal variation in pit-fall catches of *Arpedium quadrum* over three years. Explanation of symbols is given in Figure 1.

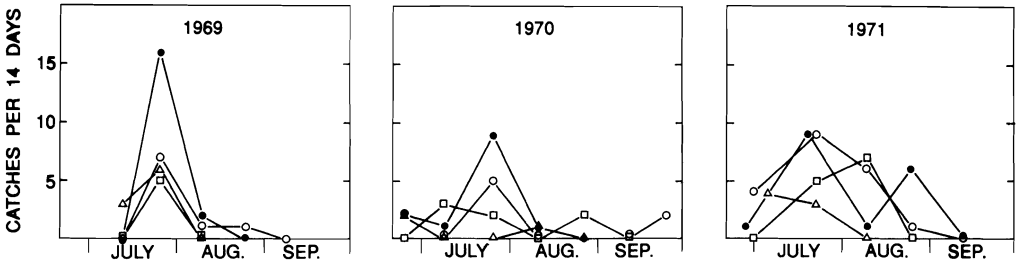


Figure 9

Seasonal variation in pit-fall catches of *Eucnecosum brachypterum* over three years. Explanation of symbols is given in Figure 1.

Low activity during spring and early summer, then with an increasing activity towards Sept. is the third pattern. This is exemplified by *L. alpestris* (Figure 10).

The fourth pattern concerns species which have no clear activity peaks during the snow-

free season. This mode is exemplified by the staphylinid *B. henningianus* (Figure 11). Very broadly, we may conclude that the activity of ground living Coleoptera in the Finse area is dominated by Carabidae during spring time, and by Staphylinidae during summer and autumn (cf. Hågvar et al. 1978).

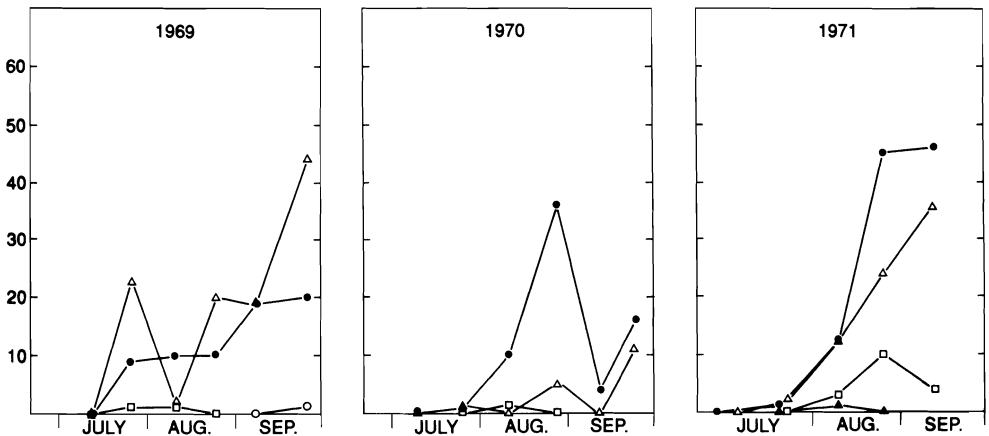


Figure 10

Seasonal variation in pit-fall catches of *Liogluta alpestris* over three years. Explanation of symbols is given in Figure 1.

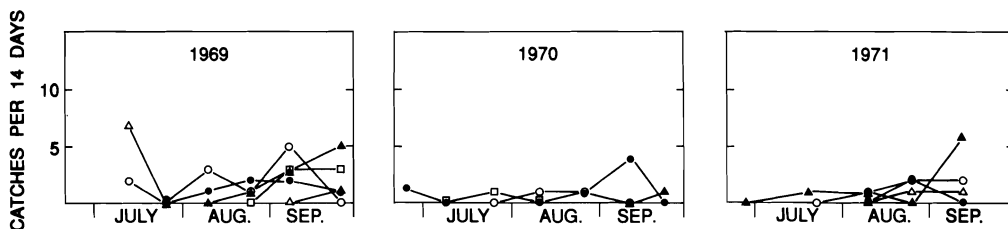


Figure 11

Seasonal variation in pit-fall catches of *Boreaphilus henningianus* over three years. Explanation of symbols is given in **Figure 1**.

Yearly changes in catches

For most species, the phenological patterns described were repeated rather clearly in different years. In some species, total catches could vary between years. However, for a given species, the highest-yielding habitats tended to be the same throughout the entire three-year period. The total catches of Carabidae gave very similar results in the different years, showing a distinct spring maximum and with highest numbers found in the eutrophic meadow and the pioneer habitat. However, total catches of Staphylinidae was lowest in 1970, mainly due to a less distinct summer peak in the eutrophic meadow (Hågvar et al. 1978). Whether this drop was due to a peak in small rodents in 1970, remains unknown. The small rodent density was moderate in 1969, and low again in 1971.

Animal sociology

A first attempt at a sociological ordination of animals typical for different plant sociological units in Norway was made for birds in high mountain areas at Finse and Hardangervidda (Østbye 1974). Bevanger (1977) tried to relate communities of birds to plant communities in alpine areas and subalpine birch forests in Mid-Norway. The method was later used on Coleoptera from alpine habitats and subalpine

birch forests on the Saltfjellet mountains in North Norway (Thingstad 1980), and on spiders from subalpine birch forests from Budal in Mid-Norway (Thingstad 1982).

An attempt at drawing a possible sociological ranking of the habitats in the Finse area with carabids and staphylinids as ecological indicators, is shown in **Figure 12**. This scheme is based on the results from this trapping experiment, supplemented with additional personal experience and published records from the area (Østbye 1963, 1969, Fjellberg 1972, Østbye & Sømme 1972, Hågvar & Østbye 1972). This sociological scheme may be valid only for a limited area, dependent as it is on the local species composition. A comparison with the sociological system Thingstad (1980) drew for the Saltfjellet area in North-Norway clearly shows this, as the carabid indicator species for corresponding plant sociological units are different from those in the Finse area.

The biological use for such a sociological system is the coupling of zoological indicators, here the carabids and staphylinids, with the more known and accepted units of plant sociology.

Niche segregation of terrestrial beetles in the Finse area has been closer studied in relation to environmental gradients and phenology by Ottesen (in press). One of his main conclu-

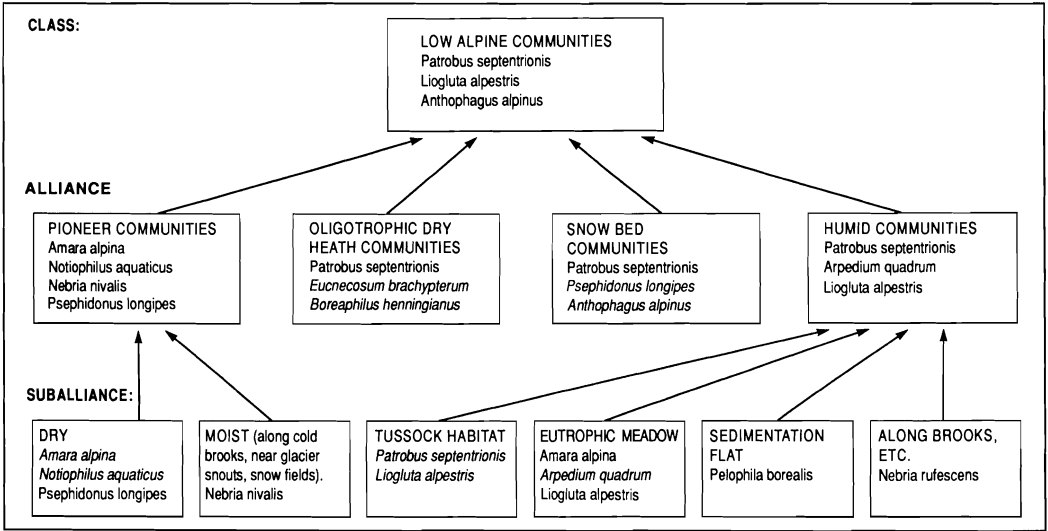


Figure 12

Classification of high mountain carabid and staphylinid communities at Hardangervidda, south Norway, with characteristic species listed. Species names are given in italics in the habitat which gave the highest catches (in percent).

sions is that soil humidity is a crucial factor regulating species composition.

ACKNOWLEDGEMENTS

We wish to express our gratitude to all our colleagues who participated in the field work, especially A. Hagen, the late J. Hagen, H.-J. Skar and D. Svalastog. The late dr.phil.h.c. Andreas Strand kindly identified most of the material and verified the rest. We are also indebted to T. Warren for correcting the English. The investigation was supported by grants from the Norwegian IBP.

SAMMENDRAG

Fallfellefangster av overflateaktive biller i fem høyfjellshabitater ved Finse, Sør-Norge

Gjennom tre år ble overflateaktive biller sam-

let med fallfeller (barberfeller) i fem ulike habitater i den lavalpine sonen, mellom 1 220 og 1 350 m o.h.: 1. Pionermark like ved en brearm. Området ble isfritt for ca. 200 år siden, er rikt på overflatestein og har ennå ikke utviklet et kontinuerlig vegetasjonsdekk. 2. Næringsfattig tørreng, som i stor grad er dekket av busklav. Dette er en dominerende vegetasjonstype i området. 3. Næringsrik fukteng, som er rik på urter. 4. Snøleie som smelter seint, dominert av musøre (*Salix herbacea*). 5. Tuemark på flat, næringsfattig myr. Tuedannelsen er utpreget, med forsenkninger som av og til er vannfylte. Lav urtevegetasjon.

Tilsammen 38 billearter fra 8 familier ble funnet. Den mest artsrike familien var Staphylinidae (20 arter), fulgt av Carabidae (7 arter). Også i individantall dominerte Staphylinidae fangstene (ca. 63 % av det totale materialet), mens Carabidae utgjorde ca. 34 %. Åtte arter forekom i alle fem habitater: fire Staphylinidae (*Arpedium quadrum*, *Liogluta alpestris*, *Anthophagus alpinus* og *Boreaphilus*

hennigianus), to Carabidae (*Patrobis septentrionis* og *Notiophilus aquaticus*), en Curculionidae (*Otiiorhynchus nodosus*) og en Byrrhidae (*Byrrhus fasciatus*). Flest arter (24) ble påvist i den næringsrike fuktenga, og færrest arter (13) i den næringsfattige tørrenga. Hele 15 arter ble tatt på pionermarka. Trolig er den høye dekningsgraden av steiner (30 %) gunstig for mange arter. Mens Carabidae har en aktivitetstopp om våren, har Staphylinidae størst aktivitet om sommer og høst. Fangstkurver gjennom sesongen er vist for de vanligste artene.

På grunnlag av karakteristiske arter er det gjort et forsøk på å definere billesamfunn knyttet til ulike habitater og habitatgrupper. Her trekkes det også inn data fra noen andre habitater som er blitt undersøkt i Finse-området.

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Life cycle strategies and seasonal distribution of mayflies (Ephemeroptera) in a small stream in Central Norway

Jo Vegar Arnekleiv

Arnekleiv, J.V. 1996. Life cycle strategies and seasonal distribution of mayflies (Ephemeroptera) in a small stream in Central Norway. - Fauna norv. Ser. B 43: 19-30.

Mayfly nymphs were sampled from a stream in Trøndelag, Central Norway, about twice monthly throughout a single year. Seasonal distribution of nymphs of 16 species are documented and nymphal growth patterns of 7 species described. Retardation in growth during winter was seen in most species except *Ameletus inopinatus* Eaton in which 51 % of growth occurred during ice cover. A univoltine life cycle dominated, 5 species belonging to the category "winter species" and 2 species to "summer species". In *Heptagenia dalecarlica* Bengtsson some individuals took one year, others two years before reaching emergence. The coexistence of closely related species in terms of temporal separation in growth and life cycles is discussed.

Jo Vegar Arnekleiv, University of Trondheim, The Museum, N-7004 Trondheim, Norway.

INTRODUCTION

Ephemeroptera are important components of the macroinvertebrate fauna of most northern rivers and streams. Marked seasonal variations in water flow and temperature characterize these habitats. Water temperature are considered to be a main factor affecting growth rates in mayfly and stonefly nymphs (Bækken 1981, Brittain 1976, 1982, 1983, Hynes 1961, Sverinsson 1977). Reduced growth during winter has been described for several species among the two groups. However, the low temperature and the extensive ice periods in northern rivers severely limit the possibility to collect material for field studies on aquatic organisms in winter. Nevertheless, studies on overwintering strategies are of vital importance for the understanding of the ecology of boreal running waters.

Previous reports on life histories of mayflies from Norway do not include the coniferous areas of Central Norway. From other parts of Scandinavia life cycle information is available for many species, cfr. Larsen (1968), Ulfstrand (1968), Bengtsson (1973), Brittain (1974, 1978, 1980), Andersen et al. (1978), Lillehammer & Brittain (1978), Bengtsson (1981), Bækken (1981), Sættem & Brittain (1985, 1993), Söderström (1988). Life cycles appear to differ markedly in various localities and with altitude (Ulfstrand 1968, Brittain 1974, 1978, Wise 1980, Clifford 1982).

The purpose of the present investigation was to examine seasonal abundance and growth patterns of mayfly nymphs in a central Norwegian stream, as part of a study of seasonal variation in benthic invertebrate communities.

STUDY AREA

The study was carried out in the stream Sagelva which drains about 82 km² of a coniferous forest area in Trøndelag, Central Norway (63°21'N, 10°38'E). The stream is ice-covered from late November until early May. The water temperature ranged from 18.1 °C (4 July 1978) to 0.1 °C (winter) (**Figure 1**). During the period of sampling (April 1978-May 1979) the discharge varied from 5 to 3330 l sec⁻¹.

The area investigated was a moderate flowing part of the stream in a mixed forest zone, about 250 m a.s.l. At the sampling site the stream is 6-8 m wide and 5-30 cm deep at mean discharge. Water velocity varied from 5 to 40 cm s⁻¹. The bottom substrate was relatively homogenous and consisted of stones, 2-10 cm diameter.

METHODS

Sampling was carried out at one locality approximately twice monthly throughout a single year. Twenty bottom samples were taken each time, using a Surber sampler covering 1500 cm² and with a mesh size of 500 µ, or 0.5 mm. The substrate was disturbed to a depth of 10 cm and specimens sorted in the field. Additional sampling for growth studies was performed using a kicking technique (Frost et al. 1971). The material was preserved in 70 % ethanol.

The analyses of growth patterns were based on total length measurements. Each nymph was measured to the nearest 0.5 mm from the anterior margin of the labrum to the posterior margin of the last abdominal segment.

The method used by Macan (1970) and Elliot (1967) was used for illustrating the life cycles.

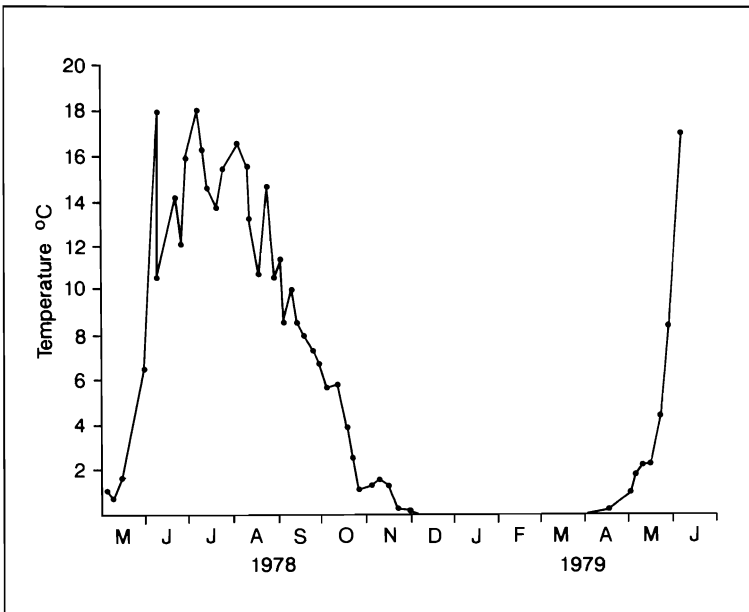


Figure 1
Water temperature in Sagelva, based on measurements between kl. 11 00 and 1500.

For species with large variations in body length, the growth was illustrated by size groups. Hatching periods were determined by the presence of small-sized nymphs (2-3 mm). Emergence periods were recognized by the presence of mature nymphs and from observations of imagines in the field.

RESULTS AND DISCUSSION

I Seasonal distribution

Mayflies were present throughout the year and constituted higher numbers than any other macroinvertebrate group. On average for the whole sampling period they constituted 44 %

of the macroinvertebrate fauna. Within this single locality a total of 11 800 mayfly nymphs were collected and 16 species recorded. Their maximum abundance was in June-July and December-January (Figure 2). High numbers of nymphs in late June - early July was due to recruitment of small nymphs of *Baetis scambus* Eaton and *Heptagenia joernensis* (Bengtsson). The increase in number of nymphs from September to January was not caused solely by recruitment, but probably also resulted from a movement to the deeper part of the stream as water flow decreased and shallow areas became frozen. Such lateral movements and concentration of nymphs has been demonstrated by Olsson (1983).

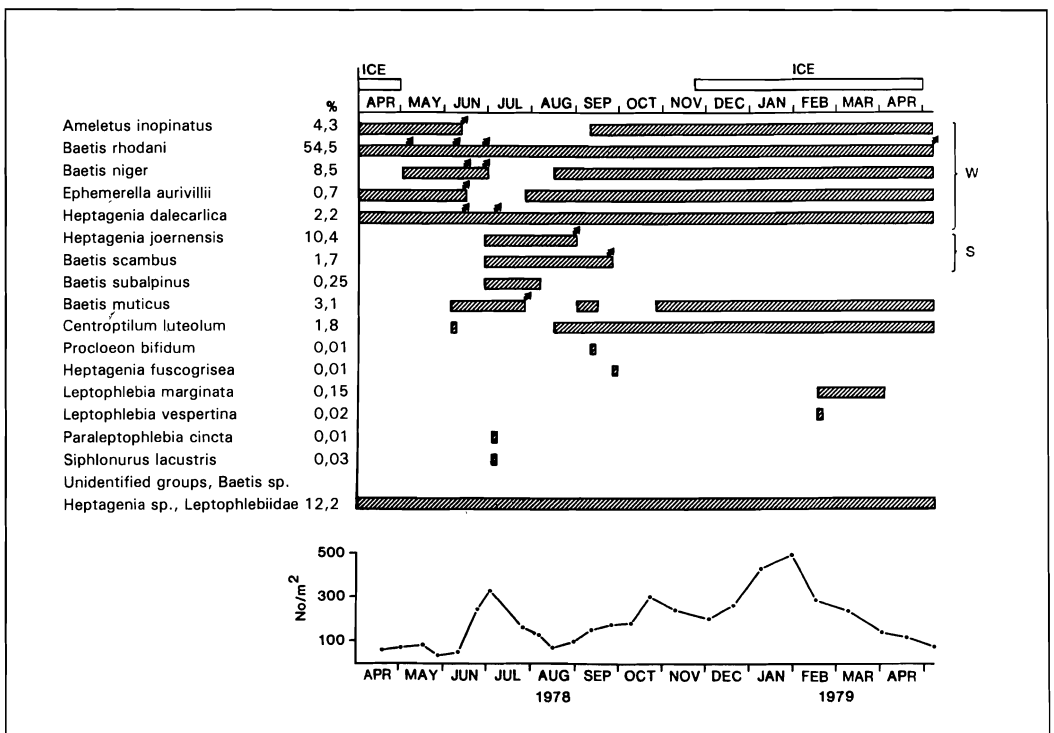


Figure 2

Seasonal distribution of mayfly nymphs in Sagelva, Central Norway, 1978-79. W shows winter species and S summer species. ↗ indicates time of emergence. Mean number of nymphs per m² is given in the lower figure.

Nymphs of *Baetis rhodani* (Pictet) and *Heptagenia dalecarlica* Bengtsson were present in benthic samples throughout the year. *Ameletus inopinatus* Eaton, *Baetis niger* (L.) and *Ephmerella aurivillii* (Bengtsson) emerged before July and nymphs of the new generation were present in the samples from August onwards. *Baetis scambus* and *Heptagenia joernensis* only occurred in the samples for a few months.

Baetis rhodani and *Heptagenia joernensis* were the dominant species, followed by *Baetis niger* and *Ameletus inopinatus*.

II Nymphal growth and life cycles

Growth patterns of the most abundant mayfly species are shown in **Figures 3-5**.

Ameletus inopinatus Eaton

A. inopinatus was univoltine with growth period from August to May (**Figure 3**). There was no decline in growth during the winter, and 51 % of growth took place under the ice. Nymphs emerged in June after a fast growing period after ice-break in May.

Although temperature are considered as the main factor affecting growth rates (Brittain 1976, 1983, Humpesch 1979) the results from Sagelva show that growth in winter is not solely temperature related but depends also on other factors, at least in some species.

Other studies (Gledhill 1959, Larssen 1968, Ulfstrand 1968 and Brittain 1974, 1978) concluded that *A. inopinatus* was univoltine, growth taking place during the winter season and the species having a long flight period (May-August).

Baetis niger (Linnaeus)

B. niger was univoltine in Sagelva (**Figure 3**). Nymphs were present throughout the whole

year except in July. There were two periods of rapid growth; one from August to November and one from late April to June. At the end of the latter period the imagines emerged. The stagnation in growth occurred when temperatures were below 2 °C. Emergence and oviposition took place in June and July, and it seems reasonable to assume a short egg incubation period since small nymphs appeared in August and the length of the nymphs were rather uniform during autumn.

Andersen et al. (1978) describes an emergence period from June to late July in the river Ekso, Western Norway. This is in agreement with the present findings from Sagelva. Elliott (1967) found an univoltine life cycle with a winter and a summer generation in England.

Baetis scambus Eaton

B. scambus (**Figure 4**) appeared as small nymphs and a few mature nymphs in July. The small nymphs grew rapidly, and emerged during September. The few mature nymphs in July may belong to a first summer generation, but lack of smaller nymphs in June makes this uncertain. It is therefore not possible to deduce whether *B. scambus* is univoltine or bivoltine in Sagelva.

Mayflies with two generations per year in Norway seem to have one winter generation and one summer generation (Brittain 1973, Larsson et al. 1978). In England, on the other hand, both *B. scambus* and *B. fuscatus* may have two fast-growing summer-generations (Elliot 1967, Wise 1980). The rapid development of the nymphs in summer makes it obvious that the timing of sampling is critical when interpreting growth patterns of this species.

Baetis rhodani (Pictet)

Nymphs of *B. rhodani* occurred throughout the year, and 3183 nymphs were measured for growth studies.

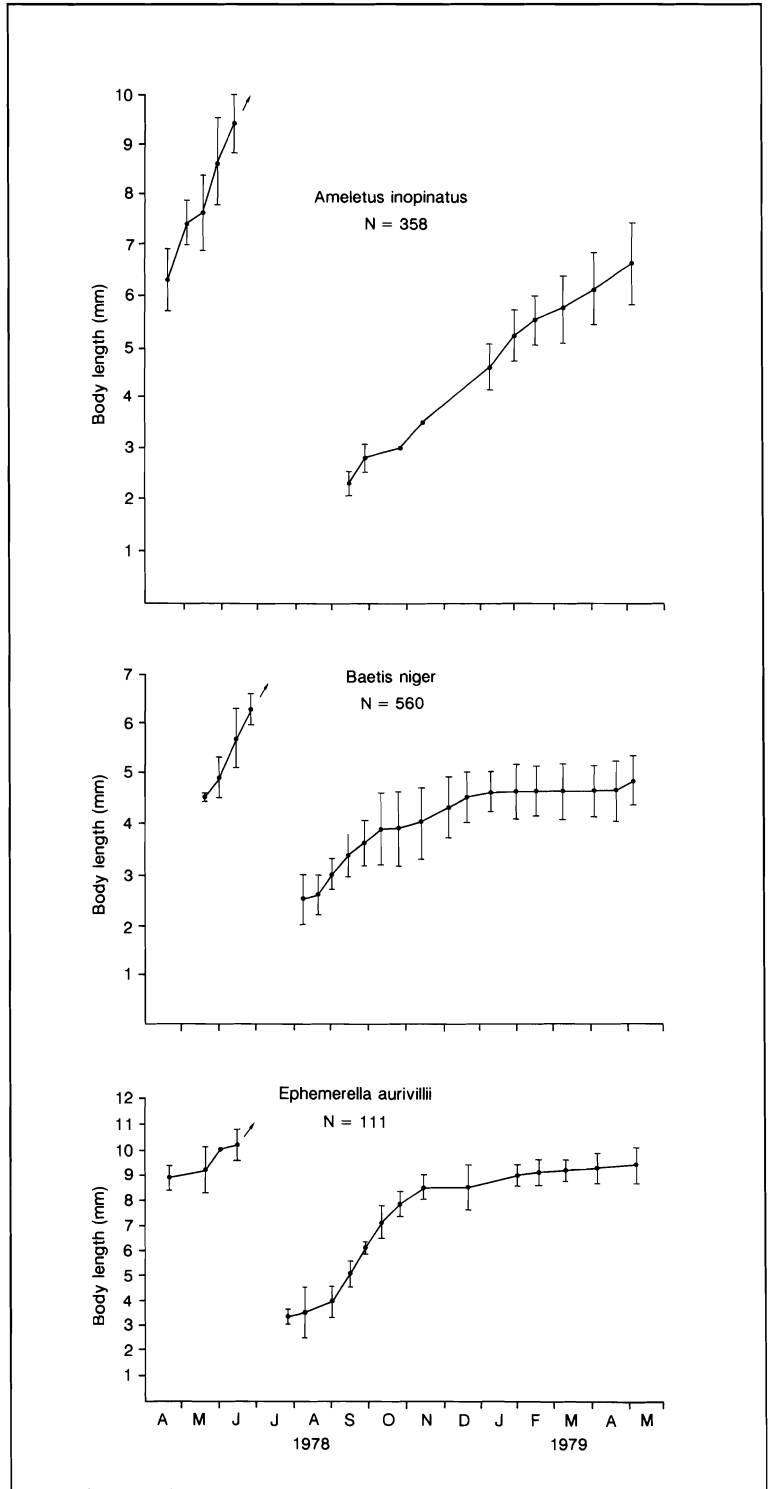


Figure 3
 Growth pattern, as mean nymphal body length (\pm S.D.), for *Ameletus inopinatus*, *Baetis niger* and *Ephemerella aurivillii* in Sagelva.

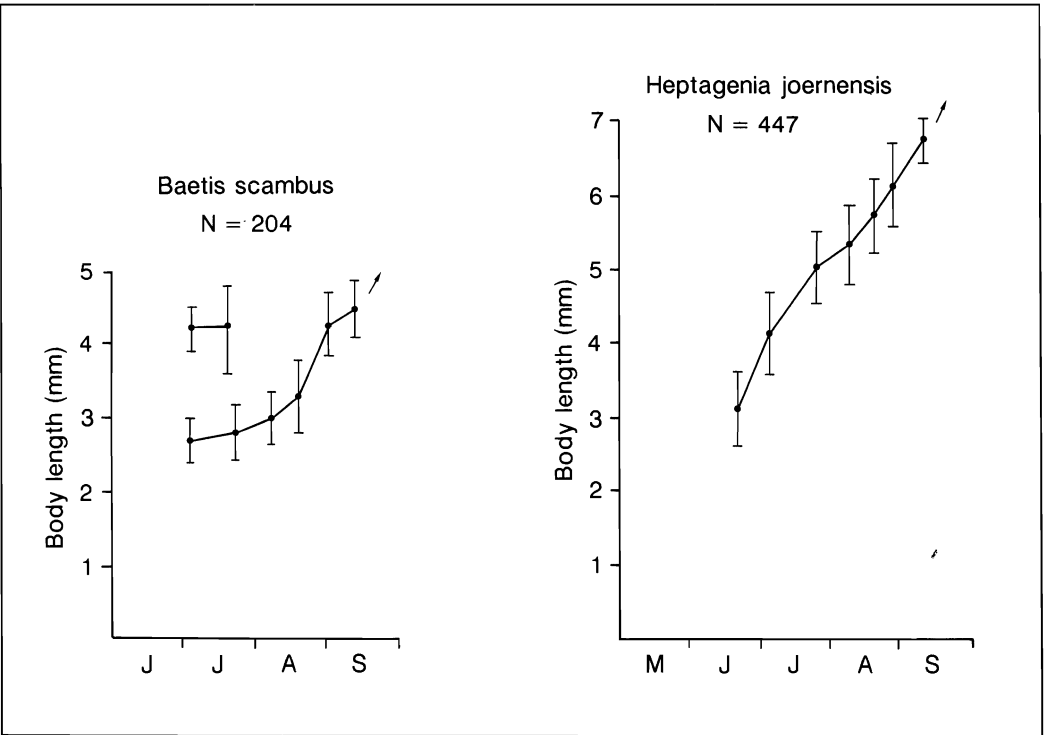


Figure 4

Growth pattern, as mean nymphal body length (\pm S.D.), for *Baetis scambus* and *Heptagenia joernensis* in Sagelva.

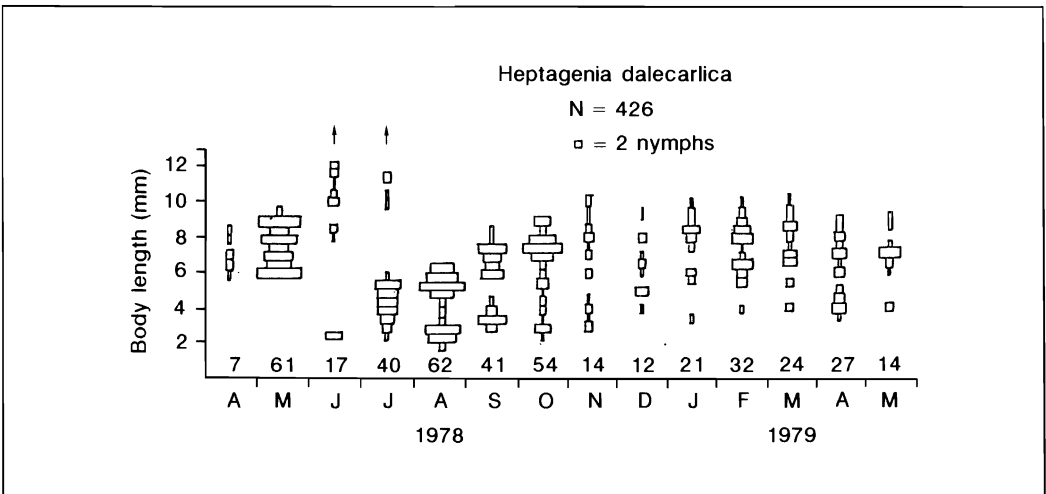


Figure 5

Frequency distribution of nymphal size classes of *Heptagenia dalearlica* in Sagelva. Sample size is given.

B. rhodani is univoltine in Sagelva (**Table 1**). The life cycle is complex and there is a continuous overlap between developmental stages during the year. Obviously, one winter generation can be distinguished. Mature nymphs emerged from May to July. No fully grown nymphs were captured in August and September. In these months and in October small nymphs (group I) dominated. These must belong to a first cohort of the new winter generation. They grew into group II and III in late autumn, but there was soon considerable variation in nymphal size from November. Nymphs appeared in group IV from October, but they were not fully grown before April.

Small nymphs (group I) were present in all months. Presumably nymphs hatched from eggs over a long period as the emergence period for *B. rhodani* is reported to be long (Ulfstrand 1968, Andersen et al. 1978). Diapausing eggs may give rise to several cohorts (Humpesch 1979), which were not detected because of too large mesh size in the Surber net. The results therefore do not permit any interpretation of several cohorts of nymphs in the winter generation as shown in the river Ekso, Western Norway (Baekken 1981).

B. rhodani has been found to have two generations per year in several localities in Scandinavia (Larsen 1968, Ulfstrand 1968, Baekken 1981) but also one generation has been recorded in mountain areas (Brittain 1978). In Sagelva, no rapid growing summer generation was detected.

Continuous overlap between developmental stages has also previously been recorded for this species (Elliot 1967, Larsen 1968, Ulfstrand 1968, Humpesch 1979, Baekken 1981). Baekken (1981) found two cohorts in the winter generation in Ekso, and the growth pattern described for the first cohort is in agreement with that found in Sagelva.

Humpesch (1979) showed a more complicated situation with ten cohorts over a period of 30 months for *B. rhodani* in Austria. This shows the flexibility of life cycle strategies in *B. rhodani* and explains its wide distribution (Illies 1978).

Heptagenia dalecarlica Bengtsson

H. dalecarlica has a complicated life cycle in Sagelva. Nymphs were present throughout the year and with a wide size distribution during most of the year (**Figure 5**).

Table 1. Percentage composition of size groups, based on body length measurements of *Baetis rhodani*. *n* is the sample size.

Month	A	M	J	J	A	S	O	N	D	J	F	M	A	M
Gr. IV (6.0-8.5 mm)	6	15	9	2	1		1	9	9	8	14	8	11	12
Gr. III (5.0-6.0 mm)	18	29	15	15		3	13	25	25	26	43	39	34	21
Gr. II (4.0-5.0 mm)	41	27	27	27		22	35	29	35	34	31	34	36	34
Gr. I (2.0-4.0 mm)	34	29	48	57	99	75	50	37	31	33	13	19	19	34
<i>n</i>	70	238	277	122	63	176	531	226	386	341	239	158	243	119

Nymphs belonging to the winter generation were fully grown in late June and July, and emerged in this period. In June and July a cohort of small nymphs appeared and grew rapidly until October. These nymphs most probably derived from eggs laid the previous year since the flight period had only just begun when they appeared. In August and September another cohort of small nymphs appeared. Evidently they derived from eggs laid during the preceding flight period. In October and November they mixed with the preceding cohort, and for the whole winter the population consisted of variable sized nymphs with no indication of a bimodal size distribution.

Hence, the results indicates that *H. dalecarlica* has two life cycle strategies. Part of the population spend a year as eggs or small quiescent nymphs, grow in summer and autumn and emerge the second summer. Another part of the population start growing soon after oviposition and complete their development in one year. These findings agrees with the results presented by Ulfstrand (1968) from Swedish Lapland.

Heptagenia joernensis (Bengtsson)

H. joernensis belongs to the category of summer species (Figure 4). No published information on the nymphal growth of this species is available from Scandinavia. In Sagelva *H. joernensis* was univoltine with a very rapid growth in summer. The first small nymphs appeared in late June and mature nymphs in mid-August. The emergence of imagines terminated in early September. The species probably overwinter in the egg stage or as small nymphs. However, interpreting the length of egg development from field data are uncertain, as pointed out by Brittain (1982). Small nymphs may be deep down in the substratum or too small to be detected by normal sampling methods. The status of *H. joernensis* in winter therefore remains unknown.

Ephemerella aurivillii (Bengtsson)

This species had an univoltine life cycle in Sagelva (Figure 3). Mature nymphs were caught from late May to 12 June, and small nymphs appeared for the first time on 25 July. Nymphs grew considerably in the period September-November, followed by a reduced growth during the whole winter period. Nymphal material showed little variation in size distribution at any time, indicating a homogenous population. The results agrees with finding from Western Norway (Larsen 1968) and Swedish Lapland (Ulfstrand 1968).

Notes on uncommon species

Some species were too rare or occurred too sporadically to allow any interpretation of life cycle.

A few large nymphs of *Baetis subalpinus* Bengtsson occurred in June and July, but were absent from samples in other months. In total 355 nymphs of *Baetis muticus* (Linnaeus) were caught during the period. Nymphs were absent in the spring of 1978, but median-sized nymphs occurred in June and mature nymphs in July. Small nymphs appeared again from late October and seemed to grow little until May.

Small nymphs of *Centroptilum luteolum* (Müller) were present in the benthos from late September and now and then through the winter. Presence of a few large nymphs with dark wing pads in late July and August 1978 suggested that emergence was imminent.

Six other mayfly species occurred only occasionally in the benthic samples (Figure 2).

III Coexistence and growth strategies

In Sagelva, six major species were univoltine and occurred together in the same habitat, but their strategies differed markedly. There was

considerable difference in growth strategy from *A. inopinatus* in which nymphs were present for about 10 months of the year and much of the growth occurs during the period of ice cover, to *H. joernensis* in which nymphal growth and occurrence are restricted to about 2 months during the summer.

The competitive exclusion principle, discussed by Illies (1952) states that no two species which occupy the same ecological niche can occur together indefinitely in the same habitat. This situation is avoided of species in the same genus by different distribution in space or in time. Occurrence of closely related mayflies in Sagelva seems mainly in agreement with this principle. Related species are separated in time both in nymphal growth and emergence periods (**Figure 2**).

Five species of the genera *Baetis* coexist in the same locality in the stream. These can be grouped in two categories according to morphology and habitat utilization. One category consists of *B. rhodani*, *B. scambus* and *B. subalpinus*. These are closely related species which are good swimmers (Müller-Liebenau 1969, Ulfstrand 1968b). In *B. scambus*, growth takes place after the emergence of *B. rhodani*, and large nymphs of *B. scambus* coexist with small nymphs of *B. rhodani* in August and September. The two species are clearly separated in the time of emergence. There is, however, a certain degree of overlap of nymphal size of the two species in September, due to the wide size distribution of *B. rhodani*. Nymphs of 4-5 mm size of both species occurs simultaneously, but they are in a different level of development. While fully grown nymphs of *B. scambus* had a body length of about 4.5-5 mm, those of *B. rhodani* reached about 7.5-8 mm. Change in diet and microdistribution with stage of development have been found in several mayfly species, among them in *B. rhodani* (Moore 1977, Baekken 1981). Even-sized nymphs of the

two species *B. rhodani* and *B. scambus* may therefore have different demands for food and shelter. It seems likely that such differences in habitat utilization enable them to coexist.

Nymphs of *B. subalpinus* were also found together with nymphs of *B. scambus* and *B. rhodani*. These nymphs occurred in low numbers and were at that time larger than nymphs of both other species.

Another category of *Baetis* spp. consists of *B. muticus* and *B. niger*. Nymphs of these species have a more cylindrical body shape and may occupy other parts of the substratum than nymphs of the first category (Müller-Liebenau 1969, Hynes 1970, Ulfstrand 1967, 1968). Mature nymphs of *B. muticus* were present in July, while *B. niger* had fully grown nymphs in late May and June. This indicates a separation in the time of emergence. In autumn and especially winter both species occurred together, but *B. niger* dominated and was present with larger nymphs than *B. muticus* at the same time.

Other investigations have also demonstrated the importance of size as a factor in ecological segregation in mayflies (Brittain 1980, 1982). Smaller specimens can inhabit smaller crevices and so do not compete with larger ones for shelter and food (Hynes 1970, Söderström 1989). Life cycle separation also was demonstrated for *B. rhodani*, *B. fuscatus* and *B. subalpinus* in Swedish Lappland (Ulfstrand 1968), but here there also was a separation in habitat.

Differences in nymphal growth periods have also demonstrated for the species *Heptagenia dalecarlica* and *Heptagenia joernensis*. Both species occurred together from June to September, with *H. joernensis* dominating. The two species have adopted different life cycle strategies, whereby *H. joernensis* is present in the nymphal stage for just 2-3 months and has a rapid growth after the emer-

gence period of *H. dalecarlica*. During the whole growing period (June-September) *H. joernensis* had larger nymphs than *H. dalecarlica*. The two species also differ in their size at maturity, average length of the fully grown nymph being 6.7 mm in *H. joernensis* and 10.7 mm in *H. dalecarlica*.

Although temporal separation in growth and life cycles is one of the most common mechanisms permitting coexistence among closely related mayflies (Brittain 1982), other differences also may be important in permitting a variety of species to coexist in the same locality. In a Norwegian mountain lake differences in nutrition, fecundity, predation pressure and size at maturity were found among the four mayfly species *Baetis macani*, *Siphonurus lacustris*, *Leptophlebia marginata* and *Leptophlebia vespertina* (Brittain 1980). Baekken (1981) found that relatively small changes in food composition could result in considerable shifts of microhabitats, enabling a different habitat choice among the different size groups of *B. rhodani*. This was considered to reduce the interaction between nymphal stages both within *B. rhodani* and between two coexisting detritivorous species. Such consideration may also be done to explain the great numbers of nymphs with a wide size distribution and the flexibility of *B. rhodani* and *H. dalecarlica* in Sagelva.

Based on the field data, the growth strategies and life cycles of lotic Ephemeroptera in Sagelva can be grouped into three categories. The first, represented by *B. scambus* and *H. joernensis*, spend the period of ice cover either as eggs or small quiescent nymphs and have a rapid growth before emergence and oviposition in late summer (summer species). The second type of strategy is also a univoltine life cycle. Nymphs hatch from eggs in the summer or in several cohorts during the autumn. Nymphal growth then continues throughout the period of ice cover. Growth is

often reduced in winter, but may be considerable as in the case of *Ameletus inopinatus*. There may be another short burst of growth after ice break before emergence occurs, as shown for *Baetis niger*. This strategy with a nymphal winter generation is the most common in Sagelva, and species belonging to this group are *Ameletus inopinatus*, *Baetis rhodani*, *Baetis niger*, *Ephemerella aurivillii* and *Heptagenia dalecarlica* (partly). The latter species also represents the third group of strategy in which part of the population seems to have a two-year life cycle with the first year spending as egg or quiescent nymphs in the hypohoreal zone. The nymphs grow in the following year and emerge at an age of about two years. Multivoltine life cycle are scarce among mayflies and besides *H. dalecarlica* are described within the genus *Ephemerella* (Svensson 1977), *Hexagenia* and some other species - see Clifford 1982.

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Agonum dorsale (Pont.) (Col., Carabidae) in Norway. Natural expansion and release into new areas 1985-93

Arild Andersen

Andersen, A. 1996. *Agonum dorsale* (Pont.) (Col., Carabidae) in Norway. Natural expansion and release into new areas 1985-93. - Fauna norv. Ser. B 43: 31-34.

Agonum dorsale has expanded its range in eastern Norway in 1985-93. New districts reported are HES, OS and BV, and EIS grid numbers 35, 37, 38 and 47. By mass release the species was successfully established in three locations in western and middle Norway, up to 350 km north of its present natural range. A further natural expansion toward the north and west is therefore expected.

Arild Andersen, The Norwegian Crop Research Institute, Plant Protection Centre, Department of Entomology and Nematology, Fellesbygget, N-1432 Ås, Norway.

INTRODUCTION

Agonum dorsale is a polyphagous predator appearing in agricultural areas all over Europe. By feeding on pest species it is considered highly beneficial to agriculture (Griffiths et al. 1985, Luff 1989, Andersen 1992). It aggregates under stones in field margins during hibernation, which makes it easy to detect in late autumn and early spring. Andersen (1985) gives a summary of the species' biology and appearance in Norway. He showed that *A. dorsale* dramatically expanded its range in Norway during 1965-84.

The present investigation had two aims. Firstly, to follow a possibly continued expansion after 1984, and secondly, to try to enhance the rate of expansion by mass releases into new areas. For all locations, the revised Strand-system (Økland 1981) and the EIS-system for Norway (Økland 1976) are used.

MATERIALS AND METHODS

To check whether an expansion took place, selected fields (mainly cereals) along the border of the species' range were investigated by handpicking at short visits in February-April or September-October 1985-93. A total of 47 locations were visited in 11 EIS grids.

During 1987-88 approximately 6 000 beetles were collected by handpicking in Vestfold and Østfold counties and stored for up to 200 days at +4 °C. For release of the species into new areas, four relatively warm agricultural fields were selected well outside the species' known range (**Figure 1**). On 28 April 1988, 1 200 beetles were released in locality no.1 (RY, Stavanger: Stangeland, EIS7). On 15 April 1989, 1 600 beetles were released in locality no.2 (SFI, Lørdal: Ljøsne, EIS 51). On 17 April 1989, 1600 beetles were released in locality no.4 (STY, Frosta: Logstein, EIS 92). On 20 April 1989, 1 600 beetles were released in locality no.3 (MRY, Molde: Fuglset, EIS 84). The four localities were visited at least once a year in early spring or late autumn during 1988-93 to see if the species was still present in the area.

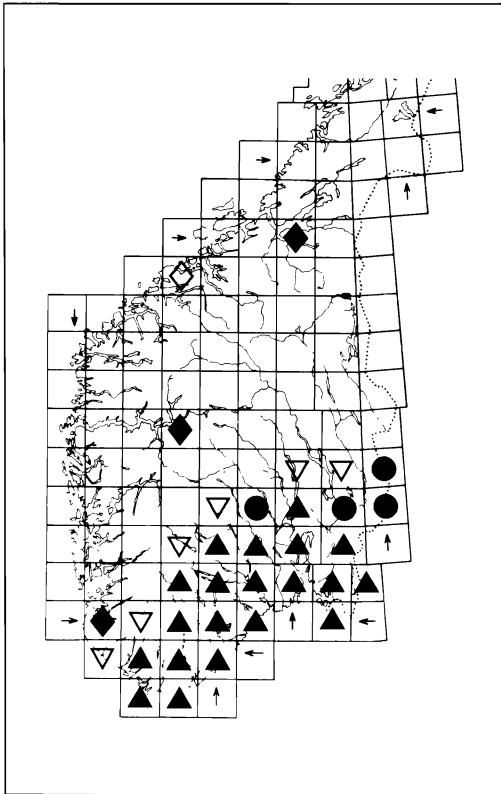


Fig. 1

Distribution of Agonum dorsale in Norway.

▲ *Distribution in 1984.*

● *New areas added 1985-93.*

▽ *Searched areas where it was absent 1985-93.*

◆ *Areas with a successful release.*

◇ *Areas with an unsuccessful release.*

The range of *A. dorsale* has increased northward in the counties Akershus, Buskerud, Oppland and Hedmark in eastern Norway. This is most clearly seen in EIS grid numbers 35 and 37, where five of the six new localities had been searched for *A. dorsale* previously without finding it (Table 1). The area is one of two suitable areas for expansion suggested by Andersen (1985). The other suggested suitable area for expansion was westward to Rogaland county. The species has not been found in this area (Table 1).

RESULTS AND DISCUSSION

Table 1 shows the number of positive and negative searches along the border of the range of *A. dorsale*. The finds in new EIS grids and new areas in the revised Strand-system were: AK, Nes: Udenes, EIS 37, 1 specimen; Nes: Udenes kirke, EIS 37, 4 specimens; Sørum: Frogner kirke, EIS 37, 13 specimens. HES, Eidskog: Skotterud, EIS 38, 2 specimens; Eidskog: Ilag, EIS 38, 1 specimen; Eidskog: Eidskog kirke, EIS 38, 4 specimens; Eidskog: Magnor, EIS 38, 1 specimen; Kongsvinger: Sigernessjøen, EIS 38, 35 specimens; Grue: Grue kirke, EIS 47, 1 specimen. OS, Jevnaker: Nøkleby, EIS 36, 1 specimen. BØ. Modum: Snarum kirke, EIS 35, 3 specimens. BV, Rollag: Størnes, EIS 35, 6 specimens; Rollag: Numedal folkehøgskole, EIS 35, 4 specimens.

In release locality no. 3 the species has not been found again after the release, but it survived in the other three localities. Specimens were recorded several times after the release, but always in low numbers (1-4 specimens per visit). The latest finds are 15 October 1992 in locality no. 1, 27 April 1992 in locality no. 2 and 3 September 1993 in locality no. 4. As the normal lifespan for a carabid beetle is 1-2 years, the registrations 4.5 years after the release strongly indicate that the species has reproduced successfully in the new areas.

The natural expansion of *A. dorsale* in eastern Norway is still going on, and the successful establishments in three of the four release localities clearly indicate that the species may spread further toward the north and west. The final borders will probably be set by the climatic conditions.

Table 1. Survey of *A. dorsale* 1985-93 in locations along the border of its range.

EIS grid number	Negative search	Positive search		
		No. of locations	Previously neg. search	No. of specimens
3	5	0		
7	2	0		
8	3	0		
25	2	0		
34	3	0		
35	3	3	2	13
37	3	3	3	18
38	2	5		43
45	4	0		
46	3	0		
47	5	1		1

ACKNOWLEDGEMENT

Sincere thanks go to Øystein Kjos for technical assistance.

SAMMENDRAG

Agonum dorsale (Pont.) (Col., Carabidae) i Norge. Naturlig ekspansjon og utsetting i nye områder i 1985-93

Agonum dorsale er et nytteinsekt som spiser skadedyr i norske åkre. Arten spredte seg nordover på Østlandet i perioden 1985-93, noe som ble fastslått ved å lete på antatt gode overvintringssteder i åkerkanter i 47 lokaliteter. Den ble funnet i 12 nye lokaliteter, hvorav fem hadde blitt undersøkt tidligere med negativt resultat. De nye områdene var HES, OS og BV, og EIS rutene 35, 37, 38 og 47.

I 1988-89 ble ialt ca. 6 000 biller sluppet ut i antatt gode åkerlokaliteter opptil 35 mil nord for artens nåværende utbredelsesområde. Lokalitetene ligger på Vestlandet og i Midt-

Norge i EIS rutene 7, 51, 84 og 92. På utsettingstedet i EIS rute 84 ble arten ikke funnet igjen, men på alle de tre øvrige stedene ble arten påvist 4,5 år senere. Arten greide altså å overleve i områdene, og da livslengden for løpebiller vanligvis er 1-2 år har den etter all sannsynlighet også reproduisert.

Det konkluderes med at den naturlige spredningen av *A. dorsale* fortsatt foregår på Østlandet, og de tre vellykkede utsettingene tildels langt utenfor artens nåværende utbredelsesområde viser at den enda har potensiale til å bre seg langt nord- og vestover.

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Bokanmeldelse

Eline B. Hågvar:
Det zoologiske mangfoldet
383 sider, kr 285
Universitetsforlaget 1985

Da Eline Hågvars bok om "Det zoologiske mangfoldet" kom på markedet i fjor høst, var dette på mange måter en historisk hendelse. Selv om vi tidligere har hatt tilgjengelig zoologiske standardverk på dansk, var det på tide at det kom en bok på norsk, tilrettelagt for norske forhold, dvs eksemplifisering med bakgrunn i vår egen fauna. Selv om "Det zoologiske mangfoldet" ikke er noen "Boas-Thomsen" eller "Buchsbaum", dekker den det meste av det som med rimelighet kan forventes å gå inn i undervisningen omkring "Dyregruppenes systematikk, bygning og biologi", fra grunnskole til de pedagogiske høyskoler. Jeg vil tro at også mange laveregradsstudenter velger å benytte boken. Det er tross alt behagelig å lese eget morsmål. Den som kan det som presenteres mellom bokens to permer, bør med en viss rett kunne titulere seg zoolog. Bare det å få en så vidt omfattende ordliste over zoologiske faguttrykk (s. 331-338), er en begivenhet.

Som forfatteren påpeker i bokens forord, synes det å ha funnet sted en markert og bekymringsfull nedprioritering av biologiundervisningen i skoleverket, såvel i grunnskole som ungdomsskole og videregående skole. For mange av oss som valgte zoologien som karrierevei, var det vel nettopp vitebegjæret i forhold til hva en fugl, et insekt eller et skjell hadde

for navn, som ofte var en første, sentral drivkraft. Det kunne imidlertid være en tung vei å gå, uten tilgang på grunnleggende systematiske oversikter eller bestemmelseslitteratur, på et forståelig språk. Ikke engang "læreren" hadde alltid svar å gi. "Det zoologiske mangfoldet" bør ha forutsetninger for å bli et standardverk i bokhyllen hos norske biologilærere.

Jeg føler meg trygg på at Eline Hågvar i fremtidige utgaver vil raffinere boken ytterligere, og korrigere en del av de unøyaktigheter og feil som finnes. Det er forøvrig allerede kommet en foreløpig liste over trykkfeil m.m. Forfatteren oppfordrer selv leserne til å kommentere og korrigere boken. En klok oppfordring som alle bør ta på alvor. Og kjenner vi norske zoologer rett, vil Hågvar trolig motta mer post enn vanlig i tiden fremover. Kjepphester, og meninger om hva som er riktig, viktig eller mindre viktig innen biologien, har vi!

Personlig ville jeg valgt en annen tittel på boken. I disse "mangfold"-tider, skal en være nøye med å velge når og hvor begrepet "mangfold" skal brukes. Det er alt for mange som ikke er det.

Det er ikke hver dag tilsvarende norske zoologibøker gjøres tilgjengelig. Vi gratulerer forfatteren med innsatsen og håper boken finner frem til mange kunnskapstørste, naturinteresserte.

Kjetil Bevanger

Distribution and flight periods of Norwegian *Dilophus* Meigen, 1803 (Diptera, Bibionidae), with a key to species

John Skartveit

Skartveit, J. 1996. Distribution and flight periods of Norwegian *Dilophus* Meigen, 1803 (Diptera, Bibionidae), with a key to species. - Fauna norv. Ser. B 43: 35-46.

The distribution of *Dilophus febrilis* (L., 1758), *Dilophus femoratus* Meigen, 1804 and *Dilophus borealis* Skartveit, 1993 in Norway is examined, based on material available in Norwegian museums and some private collections. A key to the Norwegian species is presented. *D. febrilis* is limited to southern Norway, while *D. femoratus* is widely distributed. *D. borealis* has a boreoalpine distribution in Norway. A few records from Sweden are included, based on material from the Museum of Zoology, Uppsala. The flight periods of the species are given. Some observations and literature references on the ecology of the species and their economic significance are presented.

John Skartveit, Zoologisk Museum, Musèclass 3, N-5007 Bergen, Norway.

INTRODUCTION

Bibionidae (sensu Hardy 1981) are compactly built nematocerous flies with soil-living larvae. The family has seven genera worldwide, of which two occur in Norway, *Dilophus* and *Bibio* Geoffroy. The members of the genus *Dilophus* are distributed worldwide and are the dominant bibionids in the Southern Hemisphere (Harrison 1990). In the Northern Hemisphere *Bibio* tends to predominate but a few species of *Dilophus* are present in most areas. *Dilophus* species are most easily differentiated from *Bibio* by two transverse rows of spines on the pronotum and by the fore tibiae having spines near the middle and a ring of spines at the apex. The species group to which all the species treated in this article belong has been revised by Haenni (1982). The immature stages of *D. febrilis* and *D. femoratus* (as *D. albipennis* Meigen) were described by Morris (1922).

Dilophus species frequently visit flowers, particularly open flowers like umbellifers, to feed

on pollen. They are believed to play an important role as pollinators of various plants when they are abundant (Freeman and Lane 1985, Pettersson 1992). The larvae are mainly phytosaprophagous (Morris 1922), but *D. febrilis* has been reported damaging spring barley (Port and French 1984) and amenity grass (Edwards 1941). Edwards reported densities of up to 37 000 larvae/sq.m. in lawns in Wales. Freeman and Lane (1985) gave a summary of damage caused by the species.

Krivosheina (1986) listed 27 species as occurring in the Palaearctic region. Wahlgren (1919) listed *D. febrilis* (L.), *D. femoratus* Meigen and *D. humeralis* Zetterstedt from Sweden. *D. femoratus* is the only species occurring in Finland according to Hackman (1980). *D. femoratus* also occurs in Iceland (Messersmith 1982) and the Faroes (Pedersen 1971). Previous records of *Dilophus* spp. from Norway have been reported by Zetterstedt (1850), Siebke (1853, 1864, 1877), Storm (1907), Greve et al. (1984) and Skartveit (1993).

MATERIAL AND METHODS

Collections of the following institutions and people are included in the survey: the Museum of Zoology, Bergen; Vitenskapsmuseet, Trondheim (VMT); the Museum of Zoology, Oslo (ZMO); Rana Museum (RM); Tromsø Museum (TM); the Museum of Zoology, Uppsala, Sweden (ZMU); private collections of Terje Jonassen (TJ), Knut Rognes (KR) and the author (JS). In the following, specimens referred to are deposited in the collection of the Museum of Zoology, Bergen unless otherwise stated. All identifications of the species treated by Haenni (1982) have been made according to that paper.

Extensive collecting was carried out at RY, Finnøy (EIS 14), South-West Norway, in 1992 and 1993. In 1992 a light trap and eight yel-

low water trays (32 cm diameter) were used during the whole season (April-December), three Malaise traps in the period 5 June-1 July and five Malaise traps in the period 28 August-17 October. In 1993 six yellow water traps and eight Malaise traps (in the spring period, two were removed during the summer) were used. The traps were operated from 10 April until 30 November. Traps were emptied every two to three weeks during the season, except for the Malaise traps in 1992 and three of the Malaise traps in 1993, which were emptied just once in autumn.

RESULTS AND DISCUSSION

Key to the Norwegian species of *Dilophus* (terminology follows Freeman and Lane 1985).

1. - eyes holoptic; abdomen slender with pincer-like terminalia (males).....2
 - eyes not holoptic, smaller; abdomen stout without pincer-like terminalia (females).4
2. - styles strong, curved and pointed (**Figure 1**). Costa and first radial vein black. Tibial spines curved and pointed, one generally more distal to the others. Hypopygium in ventral view as in **Figure 1**.-*febrilis*
 - styles not curved and pointed. Costa and first radial vein brownish. Spines in the middle of the fore tibia more or less on a line.....3
3. - styles strongly knobbed, hammer-like. Hypopygium in ventral view as in **Figure 2**. Apical spines of the protibia strong, seeming narrowly separated. Larger species, thorax length approximately 1.5 mm.-*femoratus*
 - styles not hammer-like. Hypopygium in ventral view as in **Figure 3**. Apical spines of the protibia slender, seeming widely separated. Smaller species, thorax length 1.1-1.4 mm.-*borealis*
4. - legs all black, wings blackish.-*febrilis*
 - legs reddish or yellowish, wings hyaline.5
5. - protibiae rather stout, in lateral view about five times as long as wide (**Figure 4b**); profemora yellowish, protibiae dark. Pterostigmata large and dark brown.....-*femoratus*
 - protibiae more elongate, about six times as long as wide (**Figure 4a**); and profemora reddish brown, protibiae nearly concolourous with the femora. Pterostigmata inconspicuous, light brown.....-*borealis*

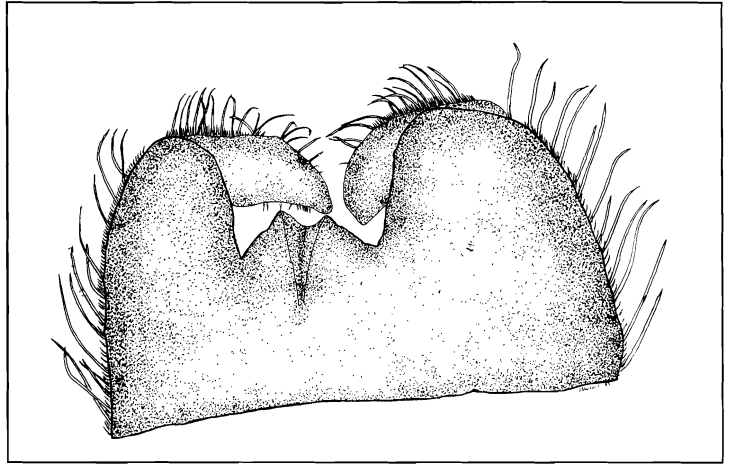


Figure 1
Dilophus febrilis, male hypopygium in ventral view.

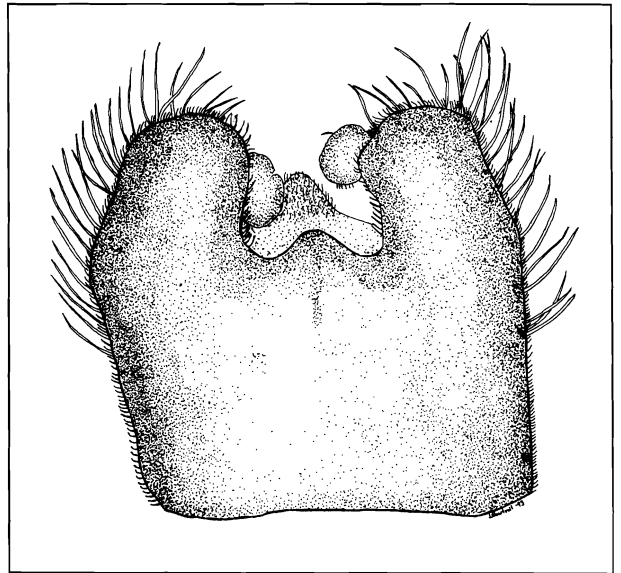


Figure 2
Dilophus femoratus, male hypopygium in ventral view.

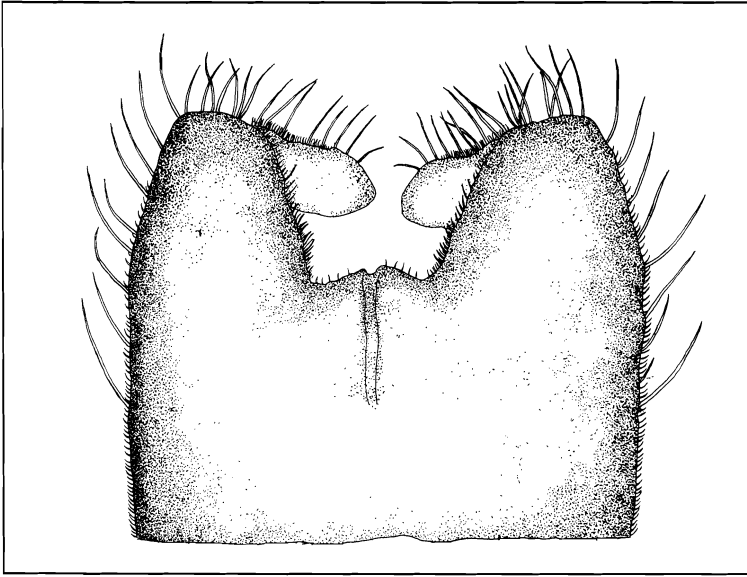


Figure 3
Dilophus borealis, male hypopygium in ventral view.

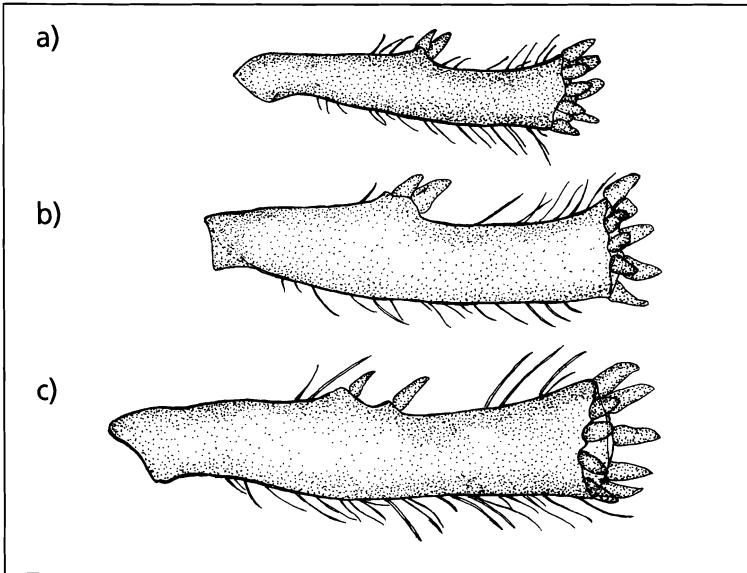


Figure 4
Female protibiae of *D. borealis* (a), *D. femoratus* (b) and *D. febrilis* (c), lateral view.

***Dilophus febrilis* (L., 1758)**
Syn. *Dilophus vulgaris* Meigen, 1818.

Unpublished records, Norway: Ø, Aremark: Bøensætra. (T. J. Olsen pers. comm., not seen). BØ, Hurum: Tofteholmen 1 ♂ 2 ♀♀. VE, Tjøme 1 ♀, Moutmarka 8 ♂♂ 1 ♀, Sandø 2 ♂♂ 5 ♀♀, Fyn Hvasser 1 ♂. TEY, Kragerø: Jomfruland 8 ♂♂ 1 ♀. RY, Finnøy: Sevheim 807 ♂♂ 615 ♀♀, Sevheimsvatnet 35 ♂♂ 18 ♀♀, Sevheimsheia 41 ♂♂ 96 ♀♀, Ladsteinvatnet 172 ♂♂ 292 ♀♀, Kvitevik 24 ♂♂ 13

♀♀, Hauskjevvatnet 7 ♂♂ 12 ♀♀, Bleivatnet 1 ♂ 2 ♀♀. HOY, Fusa: Bogøy 1 ♀.

Sweden: (all in ZMU.) Öl, Hagapark 1 ♂ 5 ♀♀; Öl, unknown locality 1 ♀. Upl, Uppsala: Stadsskogen 2 ♂♂ 2 ♀♀, Predikstolen 1 ♂.

Distribution (Figure 5)

D. febrilis is restricted to the southernmost parts of Norway. One specimen from HOY, Fusa: Bogøy (EIS 31) is the northernmost Norwegian record. The species is often very

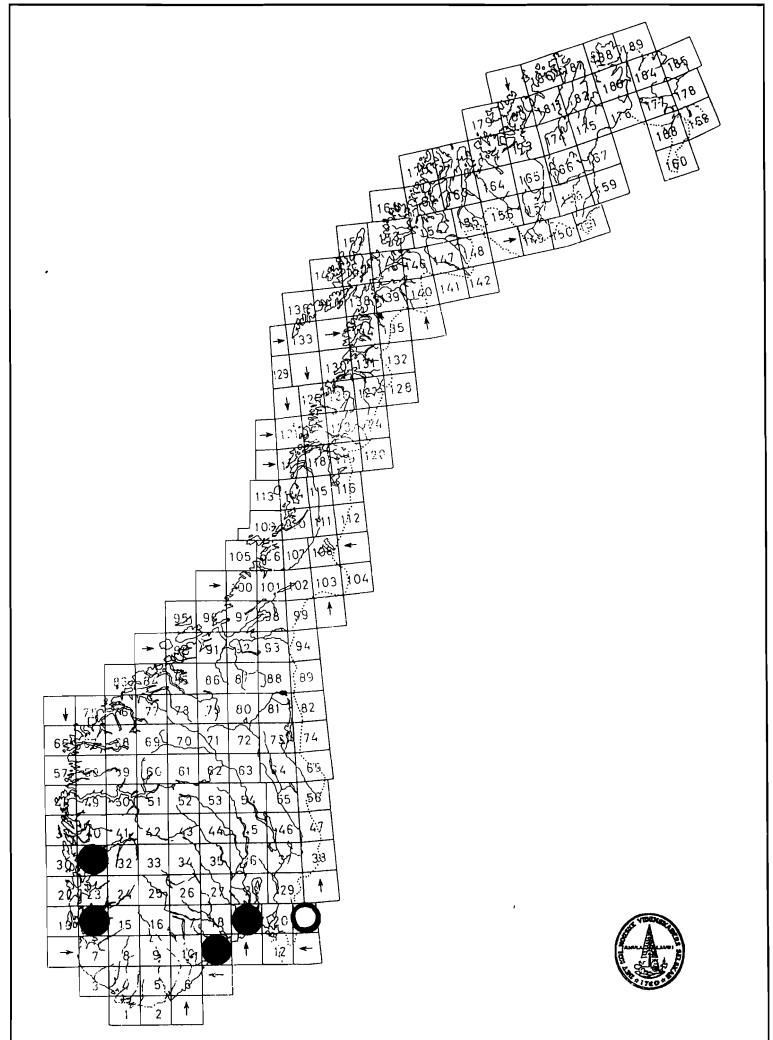


Figure 5
Records of *Dilophus febrilis* in Norway. Open circle: not seen by the author.

abundant. Just one single specimen in the collections examined had been collected prior to 1991, but the sparsity of records may reflect lack of interest from collectors rather than rarity. This species is the most abundant *Dilophus* in central Europe (Haenni 1982) and Great Britain (Freeman & Lane 1985). It is distributed throughout continental Europe (Krivoshchina 1986).

Flight period (Figure 8, Table 1)

D. febrilis has two flight periods each year, one in May to mid-June and one in mid-August to October. This has been interpreted by various authors (Duda, 1930, Freeman and Lane, 1985) to mean that the species has two generations per year. However, Blackshaw and D'Arcy Burt (1992) found that two cohorts of larvae exist, one that grows rapidly in spring and ecloses in May and one that grows slower and ecloses in August. The existence of two distinct flight periods per year may thus indicate two different cohorts of the species and not two generations per year. Collecting with yellow water traps at Finnøy (EIS 14), SW Norway in 1992 and 1993 resulted in altogether 504 specimens collected in May-June and 1442 specimens in August-October. This may indicate that the autumn-flying cohort is the larger one.

Ecology

The species was collected in large numbers from grass fields, heather covered areas and deciduous forests at Finnøy. It was also abundant on pastures and in gardens. All traps used caught at least some specimens of *D. febrilis*, indicating that the species is rather eurytopic. *D. febrilis* larvae were found under tufts of dead grass (ryegrass, *Lolium perenne*, sown for ensilage) at Finnøy in the spring of 1993. The larvae had fed on the roots and the basal parts of the stems of the grass, but it is not known whether they had actually killed the grass or just entered after it was already dead. Only relatively small patches were affected.

The identity of the species was confirmed by breeding some of the larvae.

The light trap at Finnøy caught 102 specimens of *D. febrilis* in 1992. The trap was only operated at night and this indicates that the species is active during the dark.

Dilophus femoratus Meigen, 1804

Syn. Dilophus albipennis Meigen, 1830

Previously published material: STI; Oppdal: Drivstua (Boheman; not seen); near Trondheim (Storm, 1907. Material is destroyed, not seen). NTI, Verdal: Thynæs (Zetterstedt, 1850; not seen).

Unpublished records, Norway: AK, Enebakk: Ekeberg 1 ♀; Nesodden: Fagerstrand 2 ♂♂. BV, Flå: Gulsvik 1 ♂; Gol: Engene 433 ♂♂ 104 ♀♀; . VE, Tjøme 6 ♂♂ 6 ♀♀. TEL, Kviteseid: Morgedal 5 ♂♂ 5 ♀♀, Skredi 1 ♂ (KR). VAY, Flekkefjord (Gyland): Gausdal 1 ♀. RY, Hå: Ognå 3 ♂♂; Klepp: Øksnevad 58 ♂♂ 210 ♀♀; Stavanger: Forus 118 ♂♂ 121 ♀♀; Finnøy: Sevheim 316 ♂♂ 162 ♀♀, Sevheimsvatnet 6 ♂♂ 2 ♀♀, Ladsteinvatnet 8 ♂♂ 8 ♀♀, Hauskjevvatnet 1 ♂, Kyrkjøy 1 ♀ (TJ). HOI, Kvinnherad: Rosendal 3 ♂♂ 3 ♀♀, Ænesdalen 4 ♂♂ 1 ♀; Ulvik: Slondalsvatn 2 ♂♂ 1 ♀; Voss: Mjølfjell 1 ♂ 1 ♀; HOY, Stord: Iglatjønn 1 ♀; Sotra: Sæle 1 ♂; Bergen (Fana): Espegrend 2321 ♂♂ 712 ♀♀, Blomsterdalen 1 ♂ 2 ♀♀, Stend 24 ♂♂ 24 ♀♀; Bergen: Alvøen 1 ♀, Sandviken 6 ♂♂ 8 ♀♀; Bergen (Åsane): Vollane 1 ♂; Askøy: Herdla 47 ♂♂ 41 ♀♀ (including ZMO 11044-11051); Øygarden: Sture 28 ♂♂ 3 ♀♀; Osterøy: Kleppe 1 ♂. SFI, Aurland: Fretheim 1 ♂ 1 ♀; Borgund 1 ♂; Lærdal: Eggum 1 ♂, Hegg 2 ♂♂; Innvik: Briksdal 1 ♂ 1 ♀; Jølster: at Skei towards Kjosnes 1 ♀; Leikanger: Hermannsverk Kleppe 13 ♂♂ 13 ♀♀, Hermannsverk Njøs research farm 1 ♂, Hermannsverk Sanden 1 ♂. HES, Ringsaker: Brumunddal Dæli 2 ♂♂. MRY,

Haram: Løvsøya 4 ♀♀; Hareid: Hareidlandet 2 ♀♀. STI, Oppdal: Kongsvoll 3 ♂♂ 4 ♀♀, Lønset 1 ♂ 1 ♀; Storvatn: Eidum 7 ♂♂ (VMT). NTI, Stjørdal: Stjørdal 2 ♀♀, Vikan 30 ♂♂ 21 ♀♀; Steinkjer 1 ♂. NSY, Sømna: Sandvåg 1 ♂ 1 ♀ (TM); Brønnøy: Brønnøysund 4 ♀♀ (TM), Hommelstø 4 ♂♂ 1 ♀ (TM); Røst 4 ♂♂ 2 ♀♀; Bodø: Bratten 4 ♂♂ 1 ♀, Valnes 88 ♂♂ 13 ♀♀, Urskar, Skuti 1 ♀, Falkflaug 18 ♂♂ 5 ♀♀. NSI, Rana: Svartvashei 1 ♂ 1 ♀ (RM 2208, 2301). TRI, Balsfjord: Aspenes 2 ♂♂ 4 ♀♀ (TM),

Skjåvikør 2 ♂♂ (TM). TRY, Tromsø: Ramfjord 1 ♂ (TM), Tromsø 3 ♂♂ 4 ♀♀ (TM); Karlsøy: Hushattøy 25 ♂♂ 10 ♀♀ (TM). FV, Alta: Gargia 1 ♀.

Sweden (all in ZMU.): Sk, Sövdeborg 1 ♂; Anderslov Sörby 7 ♂♂ 5 ♀♀. Öl, Hagapark 1 ♀. Ög, Källstad Hångerudden 1 ♀.

Distribution (Figure 6)

This species is widely distributed in Norway. Allowing for the uneven collecting effort, the

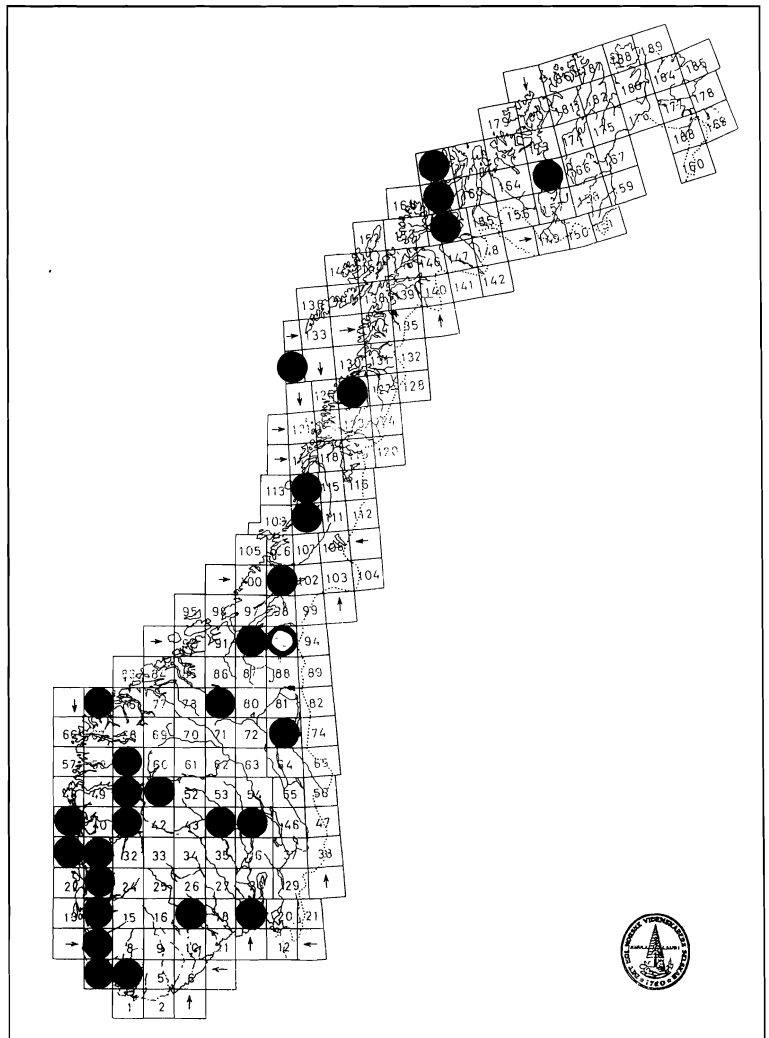


Figure 6
Records of *Dilophus femoratus* in Norway. Open circle: not seen by the author.

map of records indicates that the species is distributed all over Norway. The northernmost record of the species in this survey is from TRY, Karlsøy: Hushattøy (EIS 170, Soot-Ryen leg, TM). The highest altitude record from Norway is 900 m., from STI, Oppdal: Kongsvoll (EIS 79, J. Skartveit leg.). The species is widely distributed throughout Europe and also in the northern parts of Africa and Asia (Haenni 1982).

Flight period (Figure 8, Table 1)

D. femoratus has been collected between mid-May and mid-July in southern Norway, but the flight period ends about 20 June at southern lowland localities (table 1). Northern Norway records originate from late June until early August.

Table 1. *Dilophus febrilis* and *D. femoratus* swarming periods RY, Finnøy (EIS 14), various traps

Period	<i>D. febrilis</i>	<i>D. femoratus</i>
14.-28.V. 1992	11	7
28.V.-5.VI. 1992	31	111
5.-17.VI. 1992	1	44
17.VI.-1.VII. 1992		3
15.-28.VIII. 1992	27	
28.VIII.-16.IX. 1992	133	
16.-24.IX. 1992	3	
24.IX.-1.X. 1992	1	
(28.VIII.-17.X. 1992) ¹	22	
4.-11.V. 1993	6	
11.-29.V. 1993	469	242
29.V.-17.VI. 1993	50	943
17.VI.-9.VII. 1993		22
27.VII.-21.VIII. 1993	7	
21.VIII.-14.IX. 1993	413	
14.IX.-23.X. 1993	323	
23.X.-30.XI. 1993	3	
(21.VIII.-23.X. 1993) ¹	468	

1: all Malaise traps in 1992 and three of the Malaise traps in 1993 were emptied just once in autumn. Only periods in which *Dilophus* spp. have been collected are included.

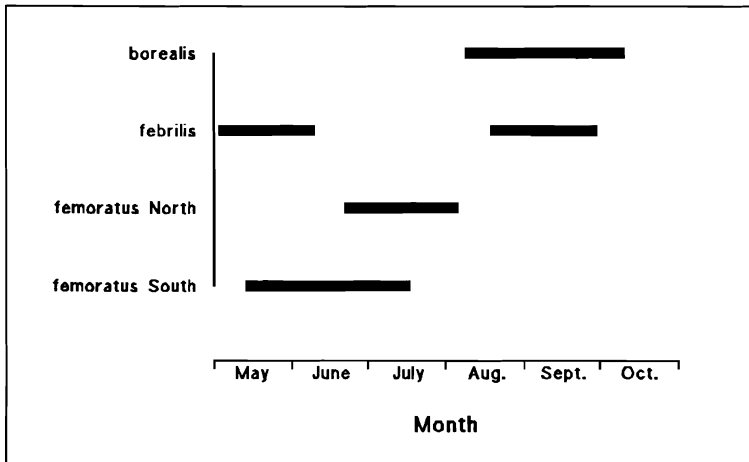


Figure 8

Summary of flight periods of Norwegian *Dilophus* species. Data from northern and southern Norway are separated for *D. femoratus*, all data pooled for *D. febrilis* and *D. borealis*.

Ecology

The species is found in typical coastal habitats as well as inland and subalpine localities. Malaise traps situated in deciduous forest at Finnøy caught only a few specimens of *D. femoratus*, while large numbers were collected on grass fields. This suggests that the species has a stronger preference for open landscapes than *D. febrilis*. One specimen has been bred from a polypore fungus, *Fomes fomentarius*, collected in western Norway (K.H. Thunes pers. comm.). A few specimens of *D. femoratus* have been collected in light traps.

Dilophus borealis Skartveit, 1993

Revised records: OS, Ringeby: Elstad 2 ♂♂ (ZMO 11 980), 1 ♂ (TM) (Siebke, 1853, as *D. vulgaris*). STI, Oppdal: Drivstua 1 ♂ (TM) (Siebke, 1864, as *D. femoratus*), Kongsvoll 112 ♂♂ 18 ♀♀ (VMT) (Greve et al, 1984, as *D. femoratus*).

Previously published records (Skartveit, 1993), Norway: BV, Gol: Engene 1 ♂; Hol: Halnefjorden 9 ♂♂ 1 ♀, Hovet 1 ♂; Uvdal: Geitsjøen 9 ♂♂ 1 ♀. NSI, Rana: Dunderlandsdalen Krokstrand 4 ♂♂ (TM). NSY, Sømna: Sømnes 8 ♂♂ (TM). NNØ, Sørfold: Røsvik 4 ♂♂ 1 ♀ (TM). TRI, Målselv: Kirkesdalen 4 ♂♂ 1 ♀ (VMT); Balsfjord: Malangen 2 ♂♂ (TM), Skjåvikør 1 ♂ (TM); Storfjord: Vassdal 3 ♂♂ (TM). TRY, Harstad: Grunnvassbotn 1 ♂; Ibestad, Ibestad near the church 2 ♂♂, Sørrollnes on Rolla 6 ♂♂ 1 ♀; Tromsø: Ullsfjord 2 ♂♂ (TM).

Sweden: (all in ZMU.) Upl,Uppsala: Nåsten S Håga 12 ♂♂ 3 ♀♀, Sunnersta 2 ♂♂.

Distribution (Figure 7)

It seems that all *Dilophus*-specimens found above the timberline in Norway belong to this

species. The species is known from two lowland localities in Southern Norway: BV, Gol: Engene (EIS 44), altitude 200 m., and OS, Ringeby: Elstad (EIS 63), altitude ca. 250 m. Other records from southern Norway are from altitudes 900 m. or more. In northern Norway the species is recorded down to sea level. *D. borealis* has been collected at altitudes up to 1 300 m. a.s.l. (STI, Oppdal:at Sprænbekken, EIS 79) in Norway.

The Uppsala collection contains specimens from two lowland coniferous forest localities near Uppsala.

Flight period (Figure 8)

D. borealis was collected from mid-August until October in the Dovrefjell mountains (Greve et al 1984), reaching a maximum abundance in September. A few additional specimens from southern Norway are collected in late July to early September. All known specimens from northern Norway are collected in August-September. The Uppsala collection contains specimens collected in August-September.

Ecology

The larva and pupa of this species have not been described. There are no recorded mass-occurrences of *D. borealis*. It has been collected from a flowering meadow, subalpine birch forest, coniferous forest as well as from the lower alpine zone.

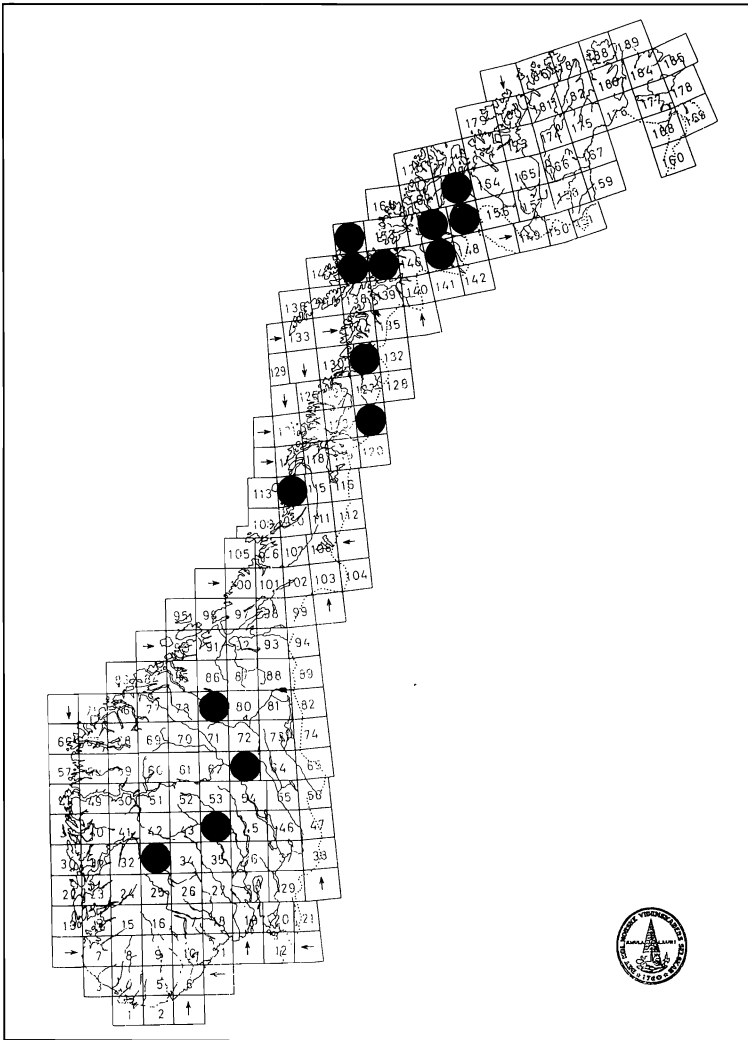


Figure 7
Records of *Dilophus borealis* in Norway.

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SAMANDRAG

Utbreiing og flygetid hos norske *Dilophus* Meigen, 1803 (Diptera, Bibionidae), med bestemmelsesnøkkel

Utbreiinga og flygetida til slekta *Dilophus* i Noreg vert vurdert, og ein nøkkel til dei norske artane vert presentert. Tre artar finst i Noreg: *Dilophus febrilis* (L., 1758), *D. femoratus* Meigen, 1804 og *D. borealis* Skartveit, 1993. *Dilophus febrilis* er funnen rundt Oslofjorden og i Rogaland og er enkelte stader svært talrik. Arten har to flygeperiodar i Noreg, i mai-juni og august-september. *Dilophus femoratus* ser ut til å finnast over heile landet bortsett frå i høgfjellet. Arten flyg mai-juli, seinare i Nord-Noreg enn lenger sør. *Dilophus borealis* flyg i fjellet og i Nord-Noreg i august-oktober. Arten er nyleg beskriven og er foreløpig kjend frå Noreg og Sverige.

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Morphological changes of *Epirrita autumnata* Bkh. and *Operophtera brumata* (L.) (Lep., Geometridae) during a mass outbreak in a subalpine birch forest in Central Norway

Olav Hogstad

Hogstad, O. 1996. Morphological changes of *Epirrita autumnata* Bkh. and *Operophtera brumata* (L.) (Lep., Geometridae) during a mass outbreak in a subalpine birch forest in Central Norway. - Fauna norv. Ser. B 43: 47-57.

The geometrid moths *Epirrita autumnata* and *Operophtera brumata* were studied during a mass outbreak covering six years (1973-78) in a subalpine heath birch *Betula pubescens* ssp. *tortuosa* forest in Budal (about 62°45'N-10°30'E), Central Norway. *E. autumnata* reached a population peak of \bar{x} = 55 and \bar{x} = 51 larvae/100 sweeps in 1975 and 1976, respectively, before the crash in 1977. *O. brumata* had a peak of \bar{x} = 220 and \bar{x} = 195 larvae/100 sweeps in 1976 and 1977, respectively, before the crash the next year. The mean width of head capsules and body weights of the 5th instar (the last) larvae of *E. autumnata* were relative stable during the years 1973-76, but decreased in the crash year. In *O. brumata* the capsule width of the 5th instar larvae decreased evenly from 1974, while the body weight was relatively stable until a reduction in the crash year 1978. The colour of the head capsules as well as bodies of the *O. brumata* larvae changed during the mass outbreak, with an increasing proportion of dark larvae. The dark larvae were smaller than the light ones.

Olav Hogstad, University of Trondheim, The Museum, N-7004 Trondheim, Norway.

INTRODUCTION

Larvae of the geometrid moths *Epirrita autumnata* and *Operophtera brumata* have a cyclicity in density at 9-10 year intervals in northern Fennoscandia (Tenow 1972). There is a parallelism of the outbreaks in these species in the mountain birch forest region, and several hypotheses have been mentioned to be responsible to create this cyclicity, the most current one being the induced response hypothesis, i.e. reduced quality of birch leaves as food as a result of the feeding by the larvae (cf. Haukioja 1991).

Pupal mass varies with density of the *E. autumnata* population (Haukioja 1980, Ruohomäki & Haukioja 1992). Because adults do not feed, the body mass of the

female pupae correlates strongly with the fecundity of the species (Ruohomäki & Haukioja 1992). A reduced pupal mass of *E. autumnata* was also found when the concentration of phenols in the foliage increased due to earlier damaging of birch leaves (Niemelä et al. 1979, Ruohomäki et al. 1992). The larval period protracted when the *E. autumnata* larvae were fed with foliage of low quality (Niemelä et al. 1979, Haukioja & Hanhimäki 1985).

However, little is known about possible changes in larvae size of *E. autumnata* and *O. brumata*. In the present study it is focused on morphological changes of the larvae of these species during a mass outbreak covering six years, i.e. from the population increase to its crash.

STUDY AREA

The study area is situated in a subalpine homogeneous oligotrophic heath birch *Betula pubescens* ssp. *tortuosa* forest in Budal valley (about 62°45'-10°30'E), Sør-Trøndelag county, Central Norway. The forest extends from an altitude of about 750 to 900 m. The general tree height is 4-5 m. The shrub layer consists of birch (0.5-2 m), juniper *Juniperus communis* (0.5-1 m), willows (especially *Salix glauca* and *S. phyllicifolia*, 0.5-1 m) and dwarf birch *B. nana* (0.5 m). The field layer is dominated by *Vaccinium myrtillus*.

The insects were collected within an area of about 10 ha in a south-west slope of the valley, 800-830 m a.s.l.

The area is situated in the transition zone between oceanic and continental climate, and the amount of precipitation is larger and the ambient temperature differences between summer and winter is smaller, than that found in the inland. The mean ambient temperature and the amount of precipitation in the months May, June and July, i.e. the period covering the developmental period for the geometrid larvae, revealed annual differences (**Figure 1**).

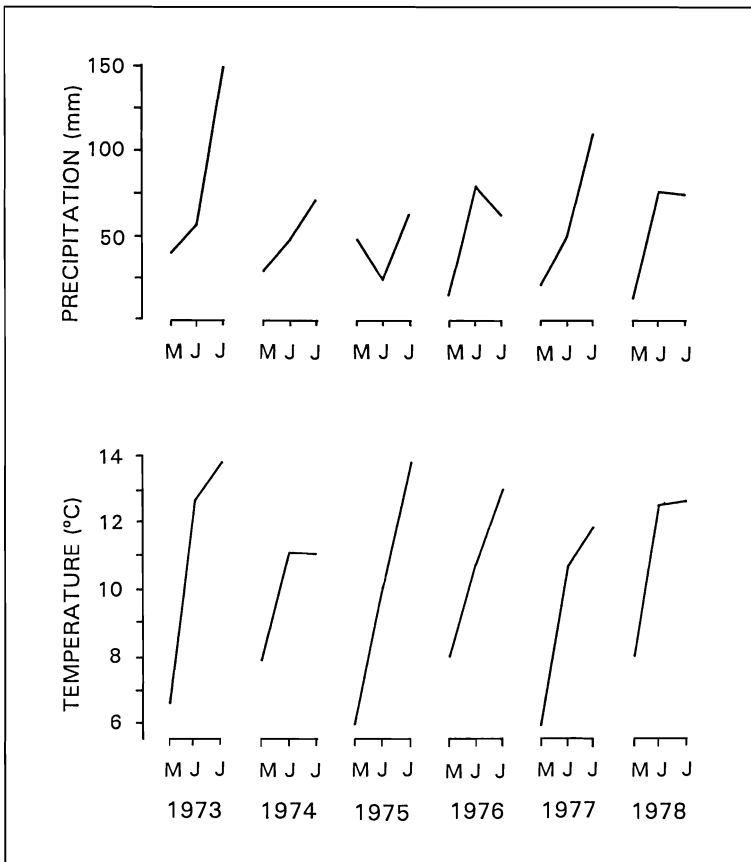


Figure 1

The amount of precipitation (above) and mean monthly temperature in May, June and July for Kvikne (30 km south of Budal) in the period 1973-78 (Det Norske Meteorologiske Institutt 1974-79).

METHODS

Both species have one generation per year, and the larval stages last about one and a half month in summer. The larvae were collected from birch trees, dwarf birches, willows and in the field layer by a sweep-net. Each year, 3-5 collections, each of 100 sweeps, were taken every 5th day during June-July and every 10th day during May in 1973-1978.

The larvae were killed with ether and kept in 70 % ethanol. Their body weight were found by a balance with accuracy 0.1 mg, after being dried on a filter paper. The fresh weight of some of the larvae were compared with their weights after being kept in ethanol for about 18 months, revealing a mean weight loss of 18 % (12-22 %).

The larval body is soft and the larvae grows relatively evenly during the larval development. However, the head capsule is sclerotic

and do not grow within each of the five instars. For every change to a new instar, a new head capsule is formed. This capsule is larger than the previous one. The width of the head capsules were measured by a measuring ocular in a microscope. The width of the head capsules of both species is clearly divided into five instars (**Figure 2**).

The colour of the head capsules of *O. brumata* was recorded as follows: (1) light, one-coloured; (2) medium dark or shaded light/dark; (3) evenly dark.

In total, 5.996 larvae of *E. autumnata* were caught in birch (n = 3.319), dwarf birch (n = 1.356), willow (n = 453) and field layer (n = 868). The total for *O. brumata* was 15 222, birch (10 494), dwarf birch (961), willow (1 207) and field layer (2 560).

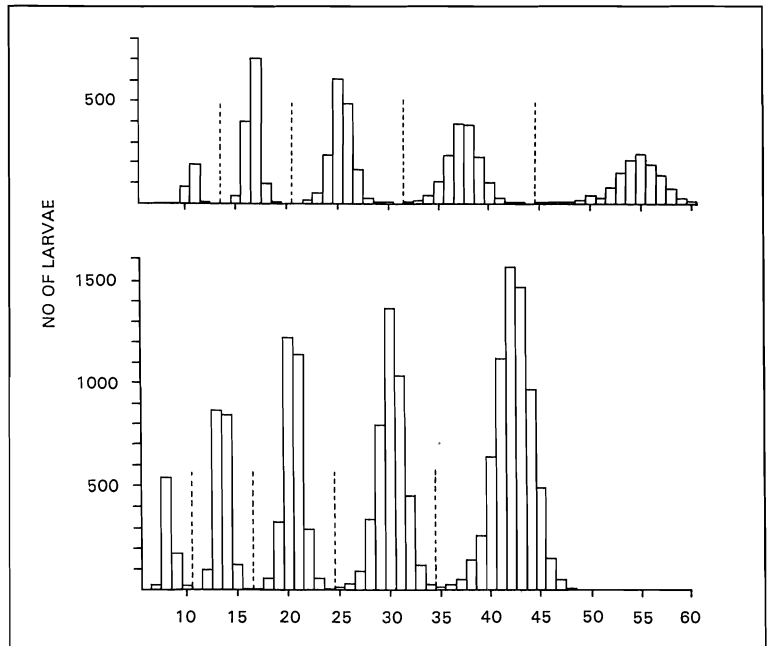


Figure 2
Frequency distribution of width of head capsules of *E. autumnata* (above) and *O. brumata*. Capsule width is given in units of 0.03125 mm.

RESULTS

Population fluctuations

The mean number of larvae of instars 4 and 5 per 100 sweeps in birch trees varied considerably for both species (**Figure 3**). *E. autumnata* reached a population peak of $\bar{x} = 55$ and $\bar{x} = 51$ larvae/100 sweeps in 1975 and 1976, respectively, before the crash the next year. *O. brumata* had a population peak of $\bar{x} = 220$ and $\bar{x} = 195$ larvae/100 sweeps in 1976 and 1977, respectively. Thus, although the two populations fluctuated relatively synchronously (Spearman rank correlation $r_s = 0.49$, $n = 6$, n.s.), the density of *O. brumata* was high also the year after the decrease of *E. autumnata*.

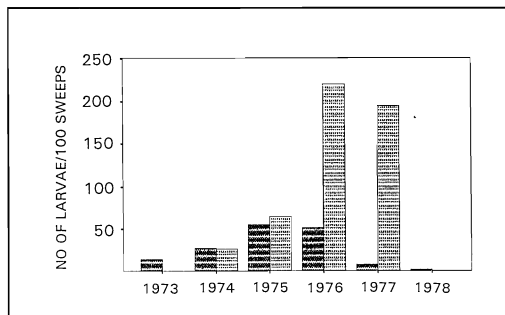


Figure 3
Population fluctuations of *E. autumnata* (black column) and *O. brumata* during 1973-78. Density is mean number of larvae (instars 4 and 5) per 100 sweeps.

Head capsule width

The mean width of the head capsules of the larvae within the different instars was not stable from one year to the next. The most marked change was found for the 5th instar in both species (**Figures 4, 5**). The mean capsule width of *E. autumnata* was approximately the same in 1973, 1975 and 1976, markedly larger in 1974 and lesser in 1977. In 1977, the capsule width was also less in the 4th instar. For the other instars, only small changes were found between years.

In *O. brumata*, it was a marked and even decrease in capsule width of 5th instar from 1974 to 1978 (**Figure 5**). In the period from 1975 to 1977 there was a decrease in capsule width in all instars, but insignificantly so for instars 1 and 2. In 1978 the capsule width of instars 3 and 4 were larger than those in 1977. For the other instars only minor annual differences were found.

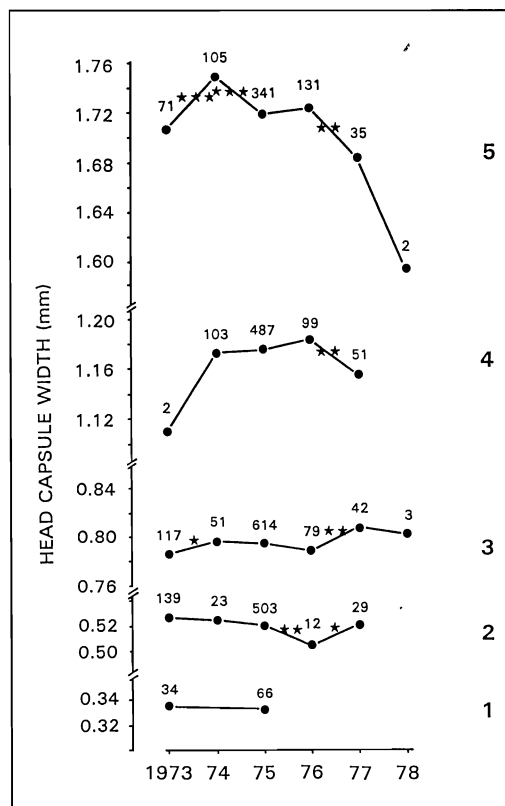


Figure 4
Head capsule width of *E. autumnata* collected in birch trees in 1973-78. Figures denote sample sizes. * = $p < 0.05$, ** = $p < 0.01$ and *** = $p < 0.001$ in a *t*-test. Figures to the right denote larvae instar number.

Also in the larvae caught in dwarf birches, sal-
lows and field layer, the capsule width in the
5th instar decreased during the study period

(Figure 6). For *E. autumnata* the decrease was most marked in the larvae in dwarf birch from 1973 to 1977. In all years the mean capsule width was less of the larvae from dwarf birch than those on birch. The capsule width of *O. brumata* decreased rather parallel and evenly for all layers during 1975-78. From 1975 to 1977 the mean capsule width of larvae from dwarf birch and willows were larger than those from birch and field layer (opposite of *E. autumnata*).

Colour of head capsules of *O. brumata*

The proportion of dark larvae of *O. brumata*, i.e. of head capsules as well as bodies, increased during the larvae mass outbreak (Table 1). The tendency was the same in all vegetation layers, but most marked in the lar-

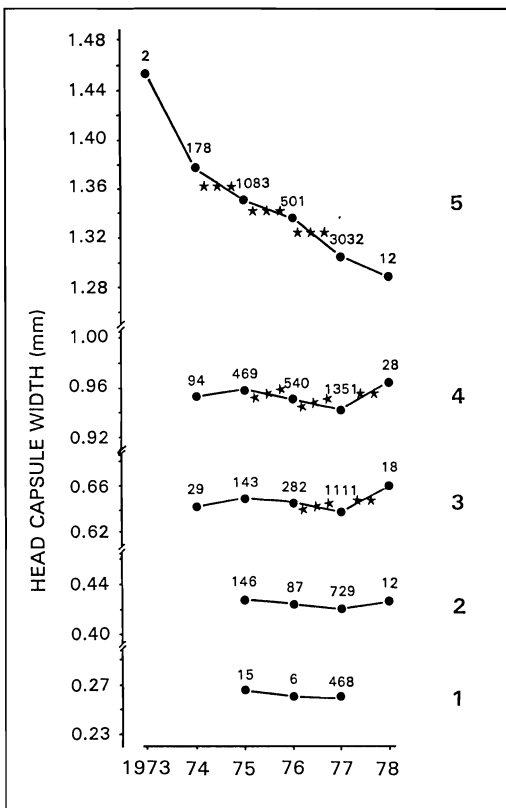


Figure 5

Head capsule width of *O. brumata* collected in birch trees in 1973-78. Figures denote sample sizes. ** = $p < 0.01$ and *** = $p < 0.001$ in a t-test. Figures to the right denote larvae instar number.

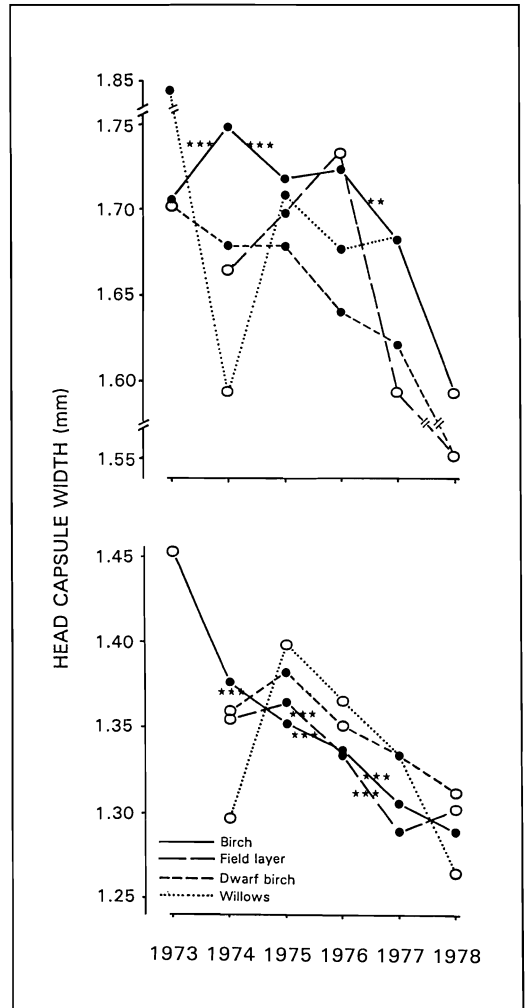


Figure 6

Head capsule width of 5th instar larvae of *E. autumnata* (above) and *O. brumata* collected in different vegetation layers during 1973-78. Open circles denote sample size less than 12. ** = $p < 0.01$ and *** = $p < 0.001$ in a t-test.

vae from birch and the field layer. In these layers, the light larvae was nearly absent in 1977, the year before the population crash. From 1974 to 1977 there was a corresponding change towards darker larvae also in 1-4 instars.

The width of the capsules differed among the different colour phases, the dark larvae being smaller than the light ones (**Figure 7**).

Table 1. Annual distribution (%) of the colour of head capsules of *O. brumata*.

Colour		1974	1975	1976	1977	1978
Birch	Light	9.6	5.7	4.0	0.5	8.3
	Medium	51.7	33.7	36.7	28.2	91.7
	Dark	38.8	60.6	59.3	71.3	0
	(n)	(178)	(1083)	(501)	(3032)	(12)
Dwarf birch	Light	50.0	29.4	22.2	20.6	44.4
	Medium	50.0	47.1	66.7	51.8	55.6
	Dark	0	23.5	11.1	27.6	0
	(n)	(2)	(17)	(9)	(369)	(9)
Sallow	Light	100.0	37.5	30.0	13.8	50.0
	Medium	0	50.0	60.0	29.7	50.0
	Dark	0	12.5	10.0	56.6	0
	(n)	(2)	(8)	(10)	(320)	(2)
Field layer	Light	66.7	54.0	5.8	2.2	0
	Medium	33.3	26.0	31.1	35.1	66.7
	Dark	0	20.0	63.1	62.7	33.3
	(n)	(3)	(50)	(103)	(507)	(3)

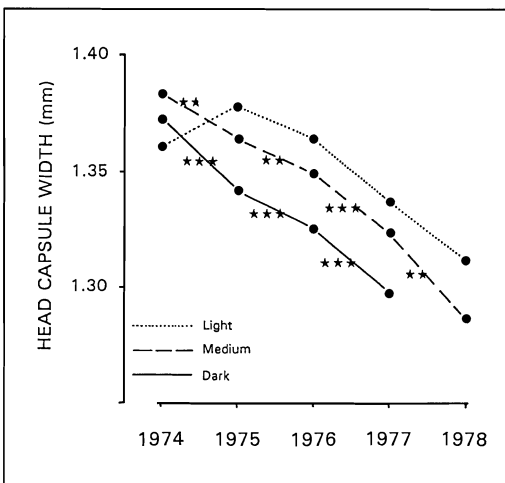


Figure 7

The variation in colour and width of head capsule of *O. brumata* during 1974-78. ** = $p < 0.01$ and *** = $p < 0.001$ in a *t*-test.

Body weight of larvae from birch

The larvae increased their size and body weight during all instars. In the end of instar 5, however, the larvae prepared their pupal stage without eating, and their weight decreased slightly (Figure 8). Although the larval body weight increased within each instar period, and it is less advisable to com-

pare the weight of the different instars from one year to the next, the yearly mean larval body weight of instar 5 is shown in Figure 9, revealing that both species decrease in weight from 1976, especially *E. autumnata*. Also the maximum weight of the 5th instar *E. autumnata* larvae were markedly smaller in 1977 (71.0 mg) and 1978 (31.1 mg) compared to those in 1973-76 (117.3-146.7 mg).

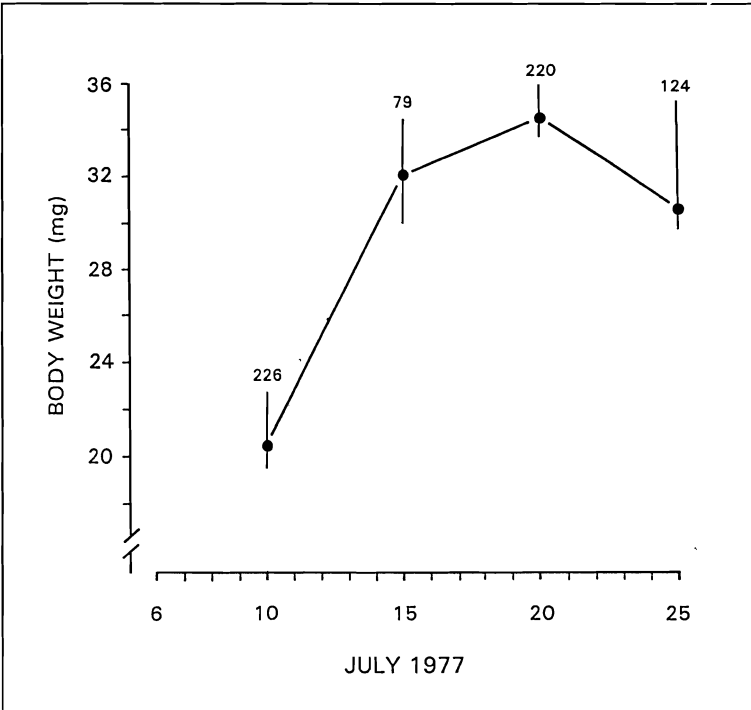


Figure 8
Mean body weight of 5th instar larvae of *O. brumata* collected in birch trees during 10, 15, 20 and 25 July 1977. Figures denote sample sizes and vertical line ± 2 SE (standard error of the mean).

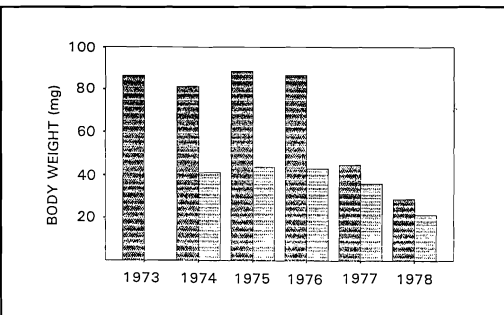


Figure 9
Mean body weight of 5th instar larvae of *E. autumnata* (black columns) and *O. brumata* during 1973-78.

DISCUSSION

The width of the head capsules of the 5th instar larvae decreased gradually in both species during the years, while their body weights did not decrease markedly until 1977. The reduction of the capsule width of *O. brumata* was approximately the same from 1976 to 1977 as that from 1974 to 1975 and from 1975 to 1976, without a corresponding reduction in their body weight. It is therefore reasonable to suggest that the reduction in body weight and head capsule width may be caused by, at least partly, different factors.

The marked reduction in body weight from 1976 to 1977 (c. 50 % in *E. autumnata*, c. 30 % in *O. brumata*) may be due to lack of food in 1977 as a result of the high population density of larvae that year (Hogstad unpubl.). Starvation in the last part of the larval development has been found to lead to a lower body weight (cf. Embree 1965).

The temperature and amount of precipitation varied irregularly during the six years, and no gradually worsening of the climate could explain the evenly reduction in the capsule width.

The food quality affects the larval body weight of several butterfly species, e.g. *E. autumnata* (Haukioja 1979), *O. brumata* (Feeny 1970), *Selidosema suavis* (Geometridae; White 1974) and *Lymantria dispar* (Lymantridae; Wallner & Walton 1979). The digestibility of leaves of birch decreases from about 60 % in June to 10-15 % in August-September because of a reduced content of water and nitrogen and an increase of phenols in the leaves (Haukioja et al. 1978). The phenolic compounds bind proteins and digestive enzymes (Feeny 1979, Rhoades 1979) and the food uptake will be strongly impeded. Simultaneously, an induced increase in the concentration of phenols in the birch leaves

may occur when leaves become damaged or removed from the tree (Niemelä et al. 1979), resulting in a prolonged larval period and reduced pupal mass (Haukioja & Niemelä 1976, 1977, Niemelä et al. 1979). Even a partly defoliation of host mountain birch trees usually reduced significantly pupal mass of *E. autumnata* the next summer (Ruohomäki et al. 1992).

When the population density of larvae increases, the quality and digestibility of the food decreases (Niemelä et al. 1979), and the growth of the larvae is protracted and their mass reduced (Haukioja & Niemelä 1977). The reduction in larval size found in Budal follows this pattern. However, in some species it is also known that the body weight of larvae is negatively correlated with population density of the larvae, without a reduction in food quality (Long 1953, Gruys 1970, Hanna & Azab 1973). Whether and to what extent this is the case in Budal, is unknown. The relative stable yearly differences between the head capsule width of the larvae found on different vegetation types in Budal, may indicate that the larval size is determined of food quality of the different vegetation layers. Although *E. autumnata* normally feeds on birch as well as on dwarf birch, the larvae collected in birch (known as a the best food plant for *E. autumnata*; Niemelä 1979), were larger than those from dwarf birch.

The head capsule width of the *O. brumata* larvae in Budal agrees with that found for larvae of instars 1 to 4 in studies from Central Europe and Canada (Table 2). The 5th instar larvae, however, is significantly smaller in Budal. Also the capsule width of *E. autumnata* instar 5 in the Canadian study (McGuffin 1958), 1.7-2.0 mm, was greater than that in Budal (see Figure 6). In a Finnish study, the mean maximum weight of the 5th instar of *E. autumnata* larvae was 102.8 mg (Haukioja & Niemeä 1974), about the same as that found in

Table 2. Head capsule width (mm) of *O. brumata* recorded in studies from Central Europe (Speyer 1941), Canada (McGuffin 1958) and Budal. The Budal measurements denote the range of yearly mean capsule width during 1974-78.

Larvae instar	Central Europe	Canada	Budal
1	0.26	0.21-0.25	0.26
2	0.43-0.45	0.39-0.42	0.42-0.43
3	0.69-0.71	0.56-0.67	0.64-0.66
4	0.96-1.18	0.88-1.05	0.94-0.96
5	1.8-1.82	1.38-1.61	1.29-1.38

Budal in the years 1973-76 (132.5 mg) but about twice that in the population crash years 1977-78 (51.1 mg).

It is a clear relationship between the pupal size, imago females and number of eggs produced in *E. autumnata* as well as in *O. brumata* (Wylie 1960, Embree 1965, Haukioja 1979, Haukioja & Niemelä 1977). If the 5th instar larvae are small, it is reasonable to suggest that both pupa and imago females will become small, resulting in a reduced reproductive success. If the larvae are very small, it may result in a less successful pupa and further development to imago (Feeny 1970). A large proportion of the 1977 *O. brumata* larvae was very small, and probably died before development to pupa or imago. Similarly, the body weight reduction of the *E. autumnata* was so marked that probably only a small proportion of the population could work out a further development.

There was a gradual change from mostly light to dark larvae of *O. brumata* during the mass outbreak in in Budal. The last instar of the species appears in a light and a dark variant (Tenow 1972), and in other geometrids it is found a positive correlation between the degree of dark colour and increasing population density (Gruys 1970). In *Plusia gamma*

(Noctuidae), the darkness of the larvae is dependent of the larvae population density (Long 1953), and intraspecific competition is suggested as an important factor (Gruys 1970).

The size of the larvae as well as the pupal mass of the geometrids *E. autumnata* and *O. brumata* are obviously related with their food resources. Severe leaf damage and partially defoliation of birches result in a reduced food quality for the larvae the same and also the following years (Haukioja et al. 1988). It may therefore be suggested that repeated leaf damages by the moths induce deterioration of the quality of leaves as food (cf. Haukioja & Neuvonen 1987) with a reduced larval size as result.

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SAMMENDRAG

Morfologiske endringer hos larver av fjellbjørkemåler *Epirrita autumnata* og liten frostmåler *Operophtera brumata* i løpet av en masseforekomst i et fjellbjørkeskogsområde i Budal, Sør-Trøndelag

Fjellbjørkemåler og frostmåler har masseforekomst omtrent hvert 10. år i Fennoskandia. I løpet av 1973-78 hadde disse artene en slik masseforekomst i fjellbjørkeskog i Budal, Sør-Trøndelag. Nedbør og temperatur i undersøkelsestida (mai-juli) varierte uregelmessig mellom årene (Figure 1). Larvene ble fanget

med slaghåv, 3-5 serier a 100 håvslag, hver 10. dag i mai og hver 5. dag i juni og juli. Larvene hadde fem larvestadier som var lett å bestemme ut fra bredden av den sklerotiserte hodekapselen (**Figure 2**).

Den gjennomsnittlige tettheten (antall larver i stadium 4 og 5 pr. 100 håvslag) av fjellbjørkemåler i bjørk økte fra 14 larver i 1973 til 55 og 51 i henholdsvis 1975 og 1976, for deretter å avta til 8 og 2 larver i henholdsvis 1977 og 1978 (**Figure 3**). Tettheten av liten frostmåler økte fra ingen larver i 1973 til 220 og 195 i henholdsvis 1976 og 1977, for deretter å ende med ingen larver i 1978.

Hodekapselbredden og kroppsvekta av fjellbjørkemålerlarvene i 5. stadium var relativt stabile gjennom årene 1973-76, men avtok sterkt i 1977 (**Figure 4, 9**). Hos liten frostmåler avtok bredden av hodekapselen jevnt fra 1974, mens kroppsvekta var relativt stabil inntil tetthetsreduksjonen i 1978 (**Figure 5, 9**). Også hos larvene fanget i dvergbjørk, vier og feltsjiktet avtok hodekapselbredden i løpet av undersøkelsesperioden (**Figure 6**).

Frostmålerlarvene fantes i to fargevarianter, lyse og mørke. Andelen av mørke larver økte i løpet av undersøkelsesperioden (**Tabell 1**). De mørke larvene var mindre enn de lyse (**Figure 7**). Larvene av liten frostmåler økte i størrelse og vekt innenfor hvert larvestadium, bortsett fra slutten av det 5. og siste da de sluttet å spise og forberedte puppestadiet.

Hodekapselbredden hos Budal-frostmålere i larvestadium 1-4 var omtrent den samme som hos larver fra Sentral-Europa og Canada, mens larver i stadium 5 var klart mindre (**Tabell 2**).

Målerlarvenes skader på løvverket resulterer i redusert næringskvalitet i bjørkebladene, i samme såvel som i påfølgende år. Det antas derfor at gjentatte årlige skader av målerlarve-

ne induserer en kvalitetsforverring i næringen til larvene, med redusert larvesørrelse som resultat.

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Short communications

Mallota megilliformis (Fallén, 1817) and *Chrysotoxum cautum* (Harris, 1776) (Diptera: Syrphidae) new to Norway

Morten Falck

Morten Falck, Karl Flods vei 5, N-0953 Oslo, Norway.

The hoverflies *Mallota megilliformis* (Fallén, 1817) and *Chrysotoxum cautum* (Harris, 1776) are reported new to Norway. The specimens were captured at S. Bjanes, Fetsund in Fet in Akershus, and Åsebu friområde, Asmaløy, Hvaler in Østfold, south-eastern Norway, on 25. May 1990 and 9. and 17. Jun. 1994.

INTRODUCTION

In Enumeratio Insectorum Norvegicorum Siebke (1877) lists the foxy red, bumble bee mimicking hoverfly species *Mallota megilliformis* (Fallén, 1817) as Norwegian. He writes that Mr. Grimsgaard has captured a female at "Hvideseid in Thelemarken", but gives no date. This is probably the reason why Peck (1988) is listing the species as Norwegian in Soós & Papp's catalogue of Palaearctic Diptera.

The specimen is not in the collections of the Zoological Museum, University of Oslo, which contains the collections of Siebke, Esmark and other Norwegian nineteenth century collectors. Other Norwegian specimens is not known. Therefore the existence of this species in the Norwegian fauna has been rather doubtful.

A male *Mallota megilliformis* was captured at AK, Fet: Fetsund, S. Bjanes, EIS 29, 9. Jun. 1994 on flowering *Crataegus*.

The genus *Mallota* is closely related to *Myathropa*. The larvae are of the rat tail type with a breathing tubercle in the rear end. They

are living in rot holes in trees, in moist, moulded wood of birch and aspen. The adult flies are seldom seen and difficult to capture, because they, like several other hoverflies, are staying high in and around the crowns of the trees.

The area where the *M. megilliformis* specimen was captured is an old agricultural area, where the river Glomma runs into the lake Øyeren, forming the greatest inland delta in northern Europe. The area is rich in old, deciduous trees, such as birch (*Betula*), ash (*Fraxinus*), maple (*Acer*), aspen (*Populus*), alder (*Alnus*), willow (*Salix*) and bird cherry (*Prunus padus*), and thus should constitute a good biotope for *Mallota* species. *Myathropa florea* (Linnaeus, 1758), which has the same habitat preference, is numerous in the area.

The genus *Mallota* contains several Palaearctic species. *M. megilliformis* is recorded from Finland (Hackman 1980) and Southern Sweden, (Östgötaland and Uppland districts) (Hedström 1990). It is not recorded from Denmark. In Germany it is considered a northern species, and rare and local in Central Europe (Röder 1990). It is further recorded from France, Poland, Russia and throughout Siberia from the Ural mountains to Kamtchatka.

As Siebke's record can not be supported by any existing specimen, it can not be fully accepted. If we chose to accept it, his data would be: TEI, Kviteseid, EIS 17, a female without date, leg. Grimsgaard.

A female specimen of *Chrysotoxum cautum* (Harris, 1776) was collected at Ø, Hvaler: Asmaløy, Åsebu Friområde, EIS 20, 25. May 1990 by Øistein Berg. Two females were also collected at AK, Fet: Fetsund, S. Bjanes, EIS 29, 9. Jun. 1994, and another two females 17. Jun.. The species is new to Norway. The number of *Chrysotoxum* species in Norway is thus 6, as in Denmark, while Finland has got 7 and Sweden 9 species.

The genus *Chrysotoxum*, which are all wasp mimicks, belong to the subfamily Syrphinae, whose larvae are predators on aphids. The larvae of *Chrysotoxum* are supposed to be predators on root aphids, though Stubbs & Falk (1983) describes the life of the larvae as "a mystery". Rotheray (1993), in his recent review of Syrphidae larvae, do not solve this mystery, but notes that females have been reported ovipositing about ant nests and puparia found under stones close to nests. Röder (1990) poses the question if the larvae prey on ant larvae as well.

According to Peck (1988), *Chrysotoxum cautum* is recorded from Great Britain to Finland, from Spain to Italy and Bulgaria, and Eastwards to the Altai mountains. According to Röder (1990) it is the most common species of the genus in many places, but clearly more common in the southern parts of the area. It is common in great parts of Denmark (Torp 1994), and is recorded from Skåne in Sweden (Hedström 1990).

The specimens are all in the author's collection.

ACKNOWLEDGEMENT

My thanks are due to Øistein Berg, who presented me with the specimen of *C. cautum*, and to Tore R. Nielsen, Sandnes, who have read the manuscript and suggested several corrections and emendations, and also for his patient help and never failing support during many years of work with the Syrphidae.

SAMMENDRAG

***Mallota megilliformis* (Fallén, 1817) og *Chrysotoxum cautum* (Harris, 1776) (Diptera: Syrphidae) nye for Norge**

En hann av den humleliknende blomsterflua *Mallota megilliformis* (Fallén, 1817), ble fan-

get i AK, Fet: Fetsund, S. Bjanes, EIS 29 den 9 juni 1994 på Fetsund i Akershus, på blomstrende hagtorn. Området er et naturreservat ved Glommas delta i Øyeren, midt i et gammelt jordbruksområde. Det er rikt på løvtrær som ask, bjørk, osp og or, hegg og andre, som får stå i fred i naturreservatet, og utgjør en egnet biotop for arten.

Arten ble registrert som norsk av Siebke i 1877, men eksemplaret har gått tapt, og det har vært tvilsomt om arten virkelig tilhører den norske faunaen. Den er registrert som norsk hos Peck (1988) i Soós & Papp, antakelig på grunnlag av Siebke, ettersom andre funn ikke er kjent. Det nye funnet bekrefter at arten er norsk. Det er ikke mulig å godta Siebkes registrering fra TEI, Kviteseid, EIS 17 når eksemplaret ikke finnes.

Arten er funnet i det østlige Sør-Sverige og i Finland, såvel som i Tyskland, Polen, Frankrike og i Russland, og gjennom Sibir fra Ural til Sakhalin. Den er ikke tatt i Danmark. Ifølge Röder (1990) er det en nordlig art, som er meget sjelden og lokal i Sentral-Europa.

Arten *Chrysotoxum cautum* (Harris, 1776) ble funnet ny for Norge i Ø, Hvaler: Asmaløy, Åsebu friområde, EIS 12, 25 mai 1990 av Øistein Berg, og også i AK, Fet: Fetsund, S. Bjanes 7 juni 1994, og på samme sted en uke seinere. Arten er registrert fra Skåne (Hedström, 1990), og fra Finland og Danmark. Ifølge Peck (1988) lever den i Europa fra Storbritannia til Finland og sørover til Middelhavsområdet, og går østover til Altai. De norske funnene ser slik ut til å representere artens nordgrense.

Slekta hører til underfamilien Syrphinae, som har larver som lever av bladlus. *Chrysotoxum*-larvene antas å leve på rotlevende bladlus, som ofte gjetes av maur. Det er ikke kjent om maurene har noen betydning for *Chrysotoxum*-larvenes utvikling, og Röder

(1990) spekulerer over om de lever som rovdyr på maurarvene også.

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Tephritis arnicae (L.1758) (Diptera, Tephritidae) new to Norway

Kristina Bjureke & Lita Greve

Kristina Bjureke, Botanical Garden and Museum, Trondheimsveien 23 B, N-Oslo 5, Norway.

Lita Greve, Zoological Museum, Zoological Institute, University of Bergen, Muséplass 3, N-5007 Bergen-Univ., Norway.

INTRODUCTION

During an investigation of *Arnica montana* L. (Fam. Asteraceae) made by one of us, KB, in the summers of 1994 and 1995, the Tephritid fly *Tephritis arnicae* L. 1758 was found in nearly all populations of the species.

The localities were AK Nes: Bjørndalen UTM (ED50) PM 490617, Haukelia UTM (ED50) PM 513598, Rakeie UTM (ED50) PM 541565; Aurskog-Høland: N.Mangen UTM (ED50) PM 567537, S.Ovlien UTM (ED50) PM 519527, N.Ovlien UTM (ED50) PM 518536, Øysjøen UTM (ED50) PM 572484, Øisjøfoss UTM (ED50) PM 567492, Haveråtangen UTM (ED50) PM 563520, Bunes UTM (ED50) PM 499379, Mikkelsrud UTM (ED50) PM 490518, Enebakk: Omberg UTM (ED50) PM 179238. HES Eidskog: Haveråen UTM (ED50) PM 565519. For reference are specimens from AK Nes: Haukelia deposited in Zoological Museum, University of Bergen.

T. arnicae can be distinguished in having the posterior orbital setae and the notopleural setae black and not white as in other species of *Tephritis*. Both the scutum and the abdomen are mostly with black hairs in this species, while at least the scutum in other species of *Tephritis* is with pale hairs. The black areas of the wings have many very small white dots. In Norway the larvae live on *Arnica montana*. Other host plants, *Doronicum* spp., are known from Middle Europe.

T. arnicae has been recorded from Småland, Västergötland and Närke in Sweden (Janzon 1984). Merz (1994) reports it as widely distributed in North- and Middle-Europe as far east as Ukraine. In Switzerland *T. arnicae* is common in all parts where *A. montana* is distributed. *T. arnicae* has not been recorded from the British Isles (White 1988).

The records of *T.arnicae* are the first for Norway. *T.arnicae* was found in 13 out of 15 investigated populations of *A.montana*. This fits very nicely with the observations made by Janzón (1984) for Sweden where *T.arnicae* was found in all populations of *Arnica montana* even when the population was small.

In our investigation the plant-populations ranged from 1 to 1600 flowering individuals of *A.montana*. The two smallest populations with 1 respectively 3 flowering individuals had not been attacked by the larvae of the fly. 65 % of the investigated capitulae of *A.montana* (n = 268) in 1994 were attacked by the larvae of *T.arnicae*. Oviposition occurs very early in the bud stage. As the larvae grow, more and more of the developing flowers, and parts of the receptacle, are destroyed. The larvae of *T.arnicae* do not induce an abnormal host-tissue growth which is common for other species of Tephritid flies.

The maximum number of pupae found in one capitula was 13, but even then some achenes were left uneaten and undamaged. The pupae were fastened on and in the receptacle. The larvae could also pupate in the uppermost 0.5 cm of the stem. Many seeds cling together and stop developing as a result of the sticky faeces of the larvae. Those capitulae which were attacked very early during the bud development were the worst damaged. The larvae destroy most of the capitulae, often only the involucral bracts were left. The inside of the capitulae was a gritty black mass, consisting of the excrements of the larvae and rotting plant material.

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We are grateful to Dr. Bernhard Merz, Zürich, who verified the determination of *T.arnicae*.

SAMMENDRAG

Tephritis arnicae (L.1758) (Diptera, Tephritidae) ny for Norge.

Tephritis arnicae (L.1758) (Diptera: Tephritidae) rapporteres her fra Norge for første gang. Larvene av denne fluearten lever i kurvene av solblom *Arnica montana* L. (Fam. Asteraceae) hvor frøanleggene blir oppspiste og ødelagte. Larver av fluen ble funnet på 13 av 15 lokaliteter, i Akershus (12) og i Hedmark (1).

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Mezira tremulae (Germar) from stands of old aspens in South Norway (Hemiptera, Meziridae)

Arne Fjellberg, Oddvar Hanssen & Stig Otto Hansen

- Arne Fjellberg, *Gonveien 38, N-3145 Tjøme, Norway.*
 Oddvar Hanssen, *NINA, Tungasletta 2, N-7004 Trondheim, Norway.*
 Stig Otto Hansen, *Gamle Stavernsvei 28, N-3250 Larvik, Norway.*

INTRODUCTION

The wood-living barkbug *Mezira tremulae* (Germar) has so far not been reported from Norway. During the last five years there has

been several records in the Larvik district in Vestfold county (VE: Larvik):

Solum (UTM:32VNL5049): Under bark on large, dead aspen (*Populus tremula*), still standing, 28.IV.1990, S.O. Hansen leg.

Vestmarka, Røysås (UTM:32VNL5853): Under bark on fallen, hollow aspen, 1.V.1991, S.O. Hansen leg. The bug was associated with several other rare species like the beetles *Ampedus nigroflavus* Goeze and *Plegaderus caesus* Herbst. Same locality, 17.IV.1992, under bark on large, dead aspen, still standing, S.O. Hansen leg. Same locality, 20.III.1993, under bark, fallen aspen, A. Fjellberg leg.

Vemnansås (UTM:32VNL5455): Numerous specimens (adults and juveniles) under bark on fallen aspen, still partly fresh, 1.IX.1995, A. Fjellberg & O. Hanssen leg.

Mezira tremulae is a mainly boreal species distributed through Siberia, Russia, Baltic area, Poland and Northern Germany with southern extensions to Hungary, Italy and former Yugoslavia. It is absent from Denmark and Finland, but has scattered populations in southern Sweden north to Hälsingland (Coulianos & Ossiannilsson 1976, Coulianos 1989). It is absent from the western provinces of South Sweden. The Norwegian area is thus quite isolated.

Ehnström & Waldén (1986) consider the species to be vulnerable in Sweden, and modern forestry has without doubt reduced the area of the species in recent time. The Norwegian records are all from an area which, due to difficult topography, has small remnants of mixed coniferous and broadleaf forests which have escaped modern forestry. Over the last ten years a number of very rare forest species have been found here (Borgersen et al. 1985, Hansen 1991, Hansen & Borgersen 1991). *Mezira tremulae* is another member of this exclusive fauna which supports an idea of establishing a nature reserve in the area.

SAMMENDRAG

Mezira tremulae (Germar) fra bestander av gamle ospetrær i Sør-Norge (Hemiptera, Meziridae)

Barktegen *Mezira tremulae* blir rapportert for første gang fra Norge der det nå er flere funn fra Larvikdistriktet i Vestfold. Arten er funnet flokkvis under bark på døde, grove osper i bestander av gammelskog som også huser en rekke andre sjeldne insekterarter, i første rekke biller. Arten er truet av det moderne skogbruket og har gått tilbake i Sverige i senere tid. Den finnes ikke i de vestlige provinsene i Sør Sverige, og den norske forekomsten er isolert. Den rike faunaen aktualiserer ideen om å skape et reservat for skogsinsekter i Larviksområdet.

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Dates should be given as 10-20 Aug. 1970 (except March, April, May, June, July).

All Latin names of genera and species in the text and tables should be in italics. The approximate position of tables and figures in the text should be indicated in the margin. All acknowledgements should be gathered under a single heading at the end of the text.

Figures and Tables. Each illustration must be clearly numbered, and an abbreviated title and the name(s) of the author(s) must be written lightly on the reverse side. If the article is in Norwegian, the figures and tables must have both Norwegian and English text. Write **Table** and **Figure** both in the running text and above/beneath tables and figures.

Figures should be no larger than 20x28 cm. Lettering should be large enough to withstand reduction. Choose contrasting patterns.

Nomenclature. The first time a binomen of an invertebrate or a less known vertebrate is used in the text the name of the author should be included. Names of authors should be written in full, except L. for Linnaeus. Dates of description can be included when considered necessary, i.e. *Rhynchophila nubila* (Zetterstedt, 1840).

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Book:

Haftorn, S. 1971. Norges fugler. - Universitetsforlaget. Oslo.

Article published in a book or collection:

Corbet, G.B. 1974. The distribution of mammals in historic time. - Pp. 179-202 in Hawksworth, D.L. (ed.). The changing flora and fauna of Britain. Academic Press, London.

Report:

Myrberget, S. 1990. Wildlife management in Europe outside the Soviet Union. - NINA Utredning 18: 1-47.

Thesis:

Harvey, H.H. 1963. Pressures in the early history of the Sockeye Salmon. - Ph.D. thesis, University of British Columbia, Vancouver.

Conference proceedings:

Spong, P., Bradford, J. & White, D. 1970. Field studies of the behavior of the Killer Whale (*Orcinus orca*). - Pp. 169-174 in Poulter, T.C. (ed.). Proceedings of the Seventh Annual Conference on Biological Sonar and Diving Mammals, Menlo Park, Calif., October 23 and 24, 1970. Stanford Research Institute, Menlo Park, Calif.

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Attention

Please control that the former issue of Ser B (Vol 42 no 2) is received. We regret that some few subscribers have received another issue of vol 42 no 1 instead of no. 2.