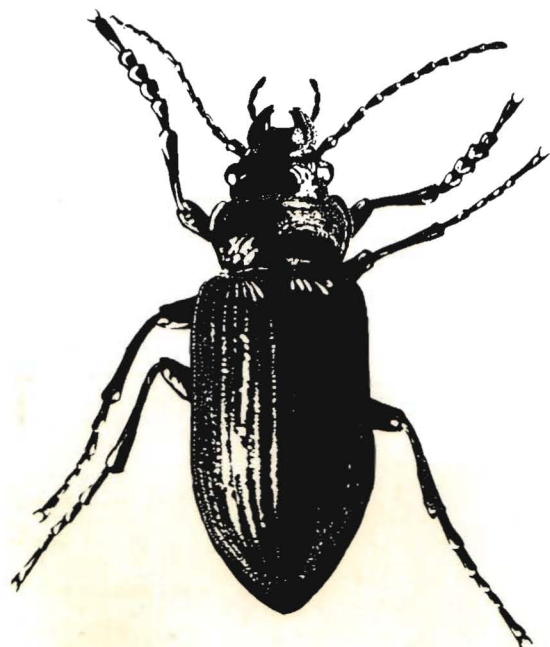


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Beetle fauna associated with scats of Brown bear (*Ursus arctos*) from Trysil, South Norway 1974

IVAR MYSTERUD & RICHARD WIGER

Mysterud, I. & Wiger, R. 1976. Beetle fauna associated with scats of Brown bear (*Ursus arctos*) from Trysil, South Norway 1974. *Norw. J. Ent.* 23, 1-5.

The beetle fauna from 16 scats of Brown bear from Trysil, South Norway, were investigated. Of the 44 species of Coleoptera collected there were 27 species of Staphylinidae, 10 Ptiliidae, four Hydrophilidae, and three Scarabaeidae.

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An earlier investigation of the coleopterous fauna from scats of Brown bear (*Ursus arctos*) in Norway was reported by Mysterud (1974). 30 species were identified, but the sample was handpicked and was non-quantitative. Consequently an additional investigation was carried out, reported in this paper, where both hand plucking and a Berlese funnel on both scats and substratum were used.

MATERIAL AND METHODS

Sixteen Brown bear scats were collected from four areas associated with sheep carcasses during field investigations of sheep predation in Hedmark county in 1974. The scats from the carcass areas were collected in *Vaccinium myrtillus* spruce forests (Nos. 1-16) at altitudes varying from 620 to 660 m a.s.l. Scat No. 17 was located at the edge of a large, open bog in a pine (*Pinus sylvestris*) bog forest, 625 m a.s.l. The locations, elevations, and date of find are presented in Table I.

Most of the scats were fresh, and none older than 3 weeks.

In the field the scats were collected in individual plastic bags. The substratum was then removed to a depth of 6 cm and stored in plastic bags. In the laboratory 0.5 g of faeces was dissolved in 10 ml distilled water, and pH measured. The scats were in different stages of drying, but the fluid scats were in very good condition.

Both the scats and substratum samples were handpicked and most of the latter were also treated in a Berlese apparatus. An overwhelming majority of the Coleoptera was found in the substratum (Table II).

RESULTS AND DISCUSSION

The scat weight, colour, texture/consistency, and substratum varied considerably (Table I). Scat pH values ranged from 7.7 to 8.4 and weights when collected between 5 and 744 g. Many of the scats were unstructured dark olive green fluids originating from 'diarrhoea'

2 I. Mysterud & R. Wiger

Table 1. Data on 16 Brown bear scat groups collected in Trysil, Hedmark, South Norway 1974.

Scat No.	Date	UTM location	Height (m a.s.l.)	Substratum	Weight(g)		Colour	pH	Consistency ²⁾	Content
					Wet ¹⁾	Dry				
1	30 June	UJ 579995	620	<u>Vaccinium myrtillus</u> , <u>Deschampsia flexuosa</u> , mosses (in path)	111.6	35.9	Black-yellow brown	8.0	FS-P	Mainly sheep wool.
2	"	" - "	"	<u>V. myrtillus</u> , <u>Sphagnum</u> spp.	48.1	19.3	" - "	7.8	"	" - "
3	"	" - "	"	<u>V. myrtillus</u> , <u>Pleurozium schreberi</u> .	158.5	39.6	" - "	8.1	"	" - "
4	"	" - "	"	" - "	35.2	15.1	" - "	7.8	"	Mainly sheep wool, partly unstructured
6	01 July	UJ 580996	630	<u>V. myrtillus</u> , <u>Pleurozium schreberi</u>	26.8	9.6	Black-yellow brown	7.7	FS	Mainly sheep wool.
7	"	" - "	"	" - "	5.3	4.0	Black	7.7	C	Unstructured, a few ants.
8	"	" - "	"	<u>V. myrtillus</u> , <u>Hylocomium</u> spp. and <u>Dicranum</u> spp.	58.3	9.3	Dark olive-green to brown	8.4	F	Unstructured.
9	"	" - "	"	" - "	56.6	6.1	" - "	8.0	"	Unstructured except for one undigested piece of sheep meat
10	"	" - "	"	" - "	97.8	22.2	" - "	8.1	"	Unstructured
11	"	" - "	"	<u>V. myrtillus</u> , <u>Hylocomium</u> spp.	93.7	21.6	" - "	8.1	"	" - "
12	"	" - "	"	<u>V. myrtillus</u> , <u>Deschampsia flexuosa</u>	71.3	23.2	Black	8.2	F-PC	Plant particles, a few ants, but in general unstructured.
13	"	" - "	"	<u>Sphagnum</u> spp.	103.5	24.7	Dark olive-green to brown	8.2	F	Unstructured, except for a few small pieces of sheep meat
14	16 Sept.	UJ 540094	670	<u>V. myrtillus</u> , <u>Hylocomium splendens</u>	385.0	60.5	Black-yellow brown	7.8	FS	Sheep wool and wasps
15	"	" - "	"	<u>Pleurozium schreberi</u> , <u>Empetrum</u> spp., <u>V. myrtillus</u>	194.0	30.1	Dark olive-green to brown	8.0	F	Unstructured, except for a few pieces of undigested sheep
16	17 Sept.	" - "	"	<u>V. myrtillus</u> , <u>Pleurozium schreberi</u>	231.0	38.0	" - "	7.3	"	" - "
17	"	UJ 589069	625	Mosses indet.	744.0	143.8	Black	7.6	FS	Hymenoptera (wasps) and berries

1) All the fluid scats could not be completely collected from substratum, therefore the weights are too low.

2) F - fluid, FS - firmly-shaped, P-porous, PC - partly crusted, C - crusted, originally fluid.

following meat-eating, whereas others contained sheep wool and were firmly shaped. The entire sample of scats probably originates from the same bear, which had established its summer range in forested hills E of Innbygda, Trysil (Mysterud in prep.).

The beetle populations which had colonized the scats and the underlying substratum are presented in Table II. The sample contained 44 species, 27 species belonging to Staphylinidae, four to Hydrophilidae, three to Scarabaeidae, and ten to Ptiliidae.

The majority of beetles were collected from the substratum and not the faeces. Nevertheless it is felt that the size of the scats has a direct influence upon the physical property of the underlying vegetation. This is especially the case when precipitation is great, as it was during the summer of 1974. Therefore scat weights will be used in assessing the relationship between numbers of staphylinid beetles and scat mass.

The scats were collected during two periods; samples 1-13 were found 30 June-1 July,

Table II The Coleoptera species associated with 16 scat samples of Brown bear (*Ursus arctos*) in Trysil, South Norway, 1974. (Species found earlier in association with wild mammals, Ba = Badger, M = Moose, R = Reindeer, U = bear.) H = Handplucked, B = Berlese funnel.

Sampling method	H	B	H	-	H	B	H	-	H	-	-	B	H	B	H	B	H	B	H	B	H	B	H	B	Other						
Scat number	1	2	3	4	6	7	8	9	10	11	12	13	14	15	16	17	Total	Species													
FAMILY - SPECIES																															
STAPHYLINIDAE																															
<i>Megarthus depressus</i> Payk.	1		1																							5					
<i>M. fennicus</i> Laht.				2				1		1		1														6					
<i>M. sinuaticollis</i> Lac.			1																							1					
<i>Proteinus crenulatus</i> Pand.										1				1	1	2										13	Ba				
<i>Omalius brevicolle</i> Th.																										2	2				
<i>O. rivulare</i> Payk.																										6	6	M, Ba, P			
<i>Deliphrum tectum</i> Payk.	4			3																						14	25				
<i>Oxytelus laqueatus</i> Mrsh.																										2	2	M, R, U			
<i>Philonthus fimetarius</i> Gr.																										1	2	M, Ba			
<i>P. puella</i> Nordm.	2			1						2																3	9				
<i>Tachinus laticollis</i> Gr.	9										4	1	1													5	5	4	2	4	35
<i>T. pallipes</i> Gr.	3	2											1													3	2	11	23		
<i>T. proximus</i> Kr.																										4	1	1	6		
<i>Autalia impressa</i> Ol.	1																									4	1	1	7		
<i>Atheta allorcerca</i> Epp.																										4	4	M			
<i>A. brunneipennis</i> Th.																										1	1				
<i>A. celata</i> Er.																										1	1	M			
<i>A. cinnamoptera</i> Th.	1																									3	4				
<i>A. dwinensis</i> Popp.																										2	2				
<i>A. laevana</i> M. & Rey																										1	1				
<i>A. lapponica</i> J. Sahlb.																										1	1				
<i>A. lateralis</i> Mnh.	1																									1	2				
<i>A. nigripes</i> Th.	1				1																					2	2	M			
<i>A. parapicipennis</i> Brd. ♂																										1	1	1	3		
<i>A. picipennis</i> Mnh. ♂																										6	10	16			
<i>A. picipennis - parapicipennis</i> ♀																										7	2	28	37		
<i>A. subtilis</i> Scriba																										7	2	2	19	30	
<i>Oxypoda nigricornis</i> Mtsch.																										1	1				
Fam. totals	23	2	8	1	0	1	1	7	3	2	1	24	31	9	16	118	247														
HYOROPHILIDAE																															
<i>Cercyon lateralis</i> Mrsh.	1				2	1																						8			
<i>C. impressus</i> Sturm	12			1																							1	1	1	37	
<i>C. melanocephalus</i> L.																											1	1			
<i>Megasternum obscurum</i> Mrsh.	24	7	4		5	14	2																						70		
Fam. totals	37	7	5	7	15	2		6	9	1	4	20		1	1	1	116														
SCARABAEIDAE																															
<i>Geotrupes stercorosus</i> Scriba	1	1	1																									3			
<i>Aphodius piceus</i> Gyll.																											1	4	U, M		
<i>A. rufipes</i> L.																										1	1	2			
Fam. totals	1	1	1					1	1			3					9														

Continued

PTILIIDAE

<i>Eurptilium saxonicum</i> Gillm.																					1		1		
<i>Baeocrara variolosa</i> Muls.																								2	
<i>Acrotrichus cognata</i> Matth.	20	5	41	1	7	1	7	71	1	4	87	1												28	274
<i>A. dispar</i> Matth.	1		1																						2
<i>A. grandicollis</i> Mnh.			2				1				1														5
<i>A. rugulosa</i> Rossk.	6										1														15
<i>A. sericans</i> Heer	2		1																						4
<i>A. silvatica</i> Rossk.																								2	2
<i>A. volans</i> Mtsch.	2										1													2	9
<i>Nanoptilium Kunzei</i> Heer																								1	3
Fam. totals	31	5	47	1	7	2	7	76	1	4	103	1												32	317
Grand totals	92	15	61	9	22	5	8	90	14	7	108	48	31	10	49	120	689								

whereas 14–17 were collected 16–17 September. The mean number of Staphylinidae per 100 g scat weight for the two periods was $\bar{x}_{1-13} = 7.94$ and $\bar{x}_{14-17} = 8.87$, a non-significant difference (using Student's t test; $t = 0.268$, $8 > P > 5$). Consequently the material will be treated as a single sample. There was a very close linear correlation between scat size and number of staphylinid individuals and/or species per 100 g scat ($r = 0.938$ and $r = 0.855$, respectively, $p > .001$.) Similar tests were not performed for Hydrophilidae and Ptilidae because these two families occurred in much greater numbers in June/July than in September.

Nine species of Staphylinidae, nine species of Ptilidae, two species of Scarabaeidae, and one Hydrophilidae species were not collected in the previous bear scat study (Mysterud 1974). Both *Aphodius piceus* and *Oxytelus laqueatus* have been collected earlier in association with Brown bear scats (Landin 1957, Palm 1961, Mysterud 1974). Several other species have previously been found on the faeces of various wild mammals in Scandinavia (Palm 1948, 1961).

Nine of the ten species of Ptiliidae have not been found previously in association with Brown Bear scats (Mysterud 1974). This is undoubtedly the result of sampling differences; in the present study Berlese funnels were used in addition to hand plucking. Scats 3, 9, and 12 contained numerous acrotrichids which were not identified. Consequently the number of *Acrotrichus* sp. are semi-quantitative and will not be treated statistically. The

♀♀ *Atheta picipennis* and *A. parapicipennis* cannot be separated and have been listed together in Table II. Of the *Acrotrichus* species nine individuals, among these an unknown male, could not be identified.

Thus the present study revealed an additional 21 Coleoptera species which were not reported in the previous bear scat study (Mysterud 1974). Seventeen of the scatophilous species must be characterized as well known in the Norwegian beetle fauna and will receive no further comment. Of the other four species, *Omalium brevicolle*, *Atheta brunneipennis*, and *Atheta dwinensis* are less common, while *Atheta lapponica* f. Sahlbr. is rare (Lindroth 1960, Palm 1948 and 1970). It is a northern species that has only been sampled in a few climax spruce forest localities, among others in Vassfaret, Buskerud and in Otta and Vågå in Gudbrandsdalen (Andreas Strand, pers. comm.).

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The phenology of *Mitopus morio* (Fabr.) (Opiliones) in Norway

TORE SLAGSVOLD

Slagsvold, T. 1976. The phenology of *Mitopus morio* (Fabr.) (Opiliones) in Norway. *Norw. J. Ent.* 23, 7–16.

The cosmopolitan *Mitopus morio* (Fabr.) can be caught without difficulty in Barber pitfall traps. Its growth period, from a tiny nymph in the spring to a long-legged adult in late summer, makes it suitable for phenological studies. The femur length of the fourth pair of walking legs was measured on 5350 specimens from several parts of Norway. Five juvenile stages were found in the traps. Growth began later with increasing altitude and latitude; in dense old forest compared to a more open woodland and a clear-felled area; on north-facing slopes; and was related to the time of onset of spring. A significant correlation was found between the time of snow disappearance and the time of birch leafing. The retardation of the onset of growth of *M. morio* and the development of birch leaves was of the same magnitude or slightly smaller for the former.

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Mitopus morio (Fabr.) has a world-wide distribution, being found in North America, Asia, North Africa, and Europe (Meinertz 1964a, 1973, Sankey & Savory 1974). It is one of the most common species of harvestmen trapped in Scandinavia, occurring from sea-level to high up in the mountains (Lehtinen 1964, Meinertz 1962, 1964a and b, 1973, Kauri 1966a, Hauge 1972, Hågvar & Østbye 1972, Solhøy 1972, Solem & Hauge 1973). Nymph stages and adults can be caught without difficulty in Barber pitfall traps. The species has an annual life-cycle and probably overwinters as eggs laid during the period August–October. It undergoes several ecdyses throughout the spring and summer, becoming fully adult during the summer and early autumn (Todd 1949, Phillipson 1959, Williams 1962, Meinertz 1964c, 1973). *M. morio* lives mainly amongst low vegetation (the field layer), but the young stages, especially the very early instars, occur under stones, under logs, in moss, and in plant debris (Sankey 1949). The adults, at least, are carnivorous (Phillipson 1960, Sankey & Savory 1974).

In the present paper its phenology has been studied in a variety of localities in Norway, from Bore in Rogaland in the south (59°N) to Tana in Finnmark in the north (70°N), from sea-level to an altitude of 1250 m.

MATERIAL AND METHODS

The data for the 23 localities are listed in Table I. 2–20 Barber pitfall traps with formalin were used in each locality, and the specimens were preserved in alcohol. Trapping period length was usually 4–10 days. The femur length of the fourth pair of walking legs (right or left), measured under a 16 × 4 binocular, was used as a measure of size. A total of 5350 specimens was measured.

The growth of *M. morio* is not smooth, but occurs in steps at each ecdysis. However, when the average values for a population are plotted, the graph becomes smoothed and may be used to compare the growth patterns in various localities. Average femur size, for all

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Table I. Altitude, slope and habitat of the various localities in Norway at which *Mitopus morio* was caught in Barber pitfall traps, together with the dates on which femur growth curve crossed the mean length for those of the juvenile stages 1 and 2.

Locality	UTM	m a. s. l.	Slope	Habitat	Year	Stage 1-2
a Bore	32VLL0322	30	NW	Mixed conifer	1975	21 May
b Røa	32VNM9145	120	SW	Mixed wood	1971	23 May
					1972	16 May
					1975	21 May
c Sørkedal 1	32VNM8951	210	flat	Spruce forest	1971	27 May
					1972	26 May
					1975	29 May
d Sørkedal 2	"	"	flat	Dense spruce forest	1972	30 May
					1975	5 Jun
e Sørkedal 3	"	200	E	Spruce forest	1971	27 May
f Kvale 1	32VNN0078	700	NNE	Clearing planted with spruce	1971	7 Jun
g Kvale 2	"	"	NNE	Spruce forest	1971	11 Jun
h Valdresflya	32VMP8810	1250	NW	Phyllodoce-Vac- cinion myrtilli	1973	-
i Tangen	32VMP9119	955	flat	River delta	1973	-
j Håskelia	32VMP9219	990	flat	Subalpine birch forest	1973	16 Jun
k Hindflya	32VMP9529	1120	E	Kobresieto- Dryadion	1973	15 Jun
l Russlia	32VMP9629	900	ENE	Prealpine pine forest	1973	20 Jun
m Hjerkin	32VNP2998	920	E	Subalpine birch forest	1975	14 Jun
n Budalen	32VNR7655	830	SW	Subalpine birch forest	1975	19 Jun
o Tiller	32VNR7024	120	flat	Spruce forest	1973	5 Jun
					1974	28 May
					1975	11 Jun
p Bratsberg	32VNR7525	160	flat	Spruce forest	1973	6 Jun
					1974	4 Jun
					1975	7 Jun
q Steinan	32VNR7230	200	flat	Spruce forest	1975	8 Jun
r Bymarka 1	32VNR6232	430	S	Spruce forest	1975	23 Jun
s Bymarka 2	32VNR6332	350	SE	Spruce forest	1975	22 Jun
t Bymarka 3	32VNR6633	170	flat	Mixed wood	1975	5 Jun
u Leangen	32VNR7335	10	E	Mixed wood	1975	19 May
v Saltfjellet	33WWQ0425	500	N	Subalpine birch forest	1975	2 Jul
w Tana	35WNU4403	10	flat	Heath birch forest	1975	6 Jun

individuals, was calculated for each trapping period and plotted against the mean date of the trapping period.

The date on which the first nymphs appeared in the traps is not a convenient measure of the start of growth of *M. morio* in spring because it is influenced by the chance of members of the population being caught. This chance is not the same in each locality but is related not only to the local population density, but also to degree of activity (e.g. the prevailing temperature) during those particular days of the trapping period. I have

instead used the date on which the smoothed growth curve for femur length crosses a certain value, this chosen value being the average femur length for stages 1 and 2 (called Stage 1-2), i.e. at this time stages 1 and 2 are being trapped in equal numbers. Such a value was calculated for the localities for each year (Table I, frequency distribution corresponding to that in Fig. 1 was made for each locality each year and the average femur length of stages 1 and 2 calculated).

Measurements were also made of plant phenology. At a few days interval the lengths

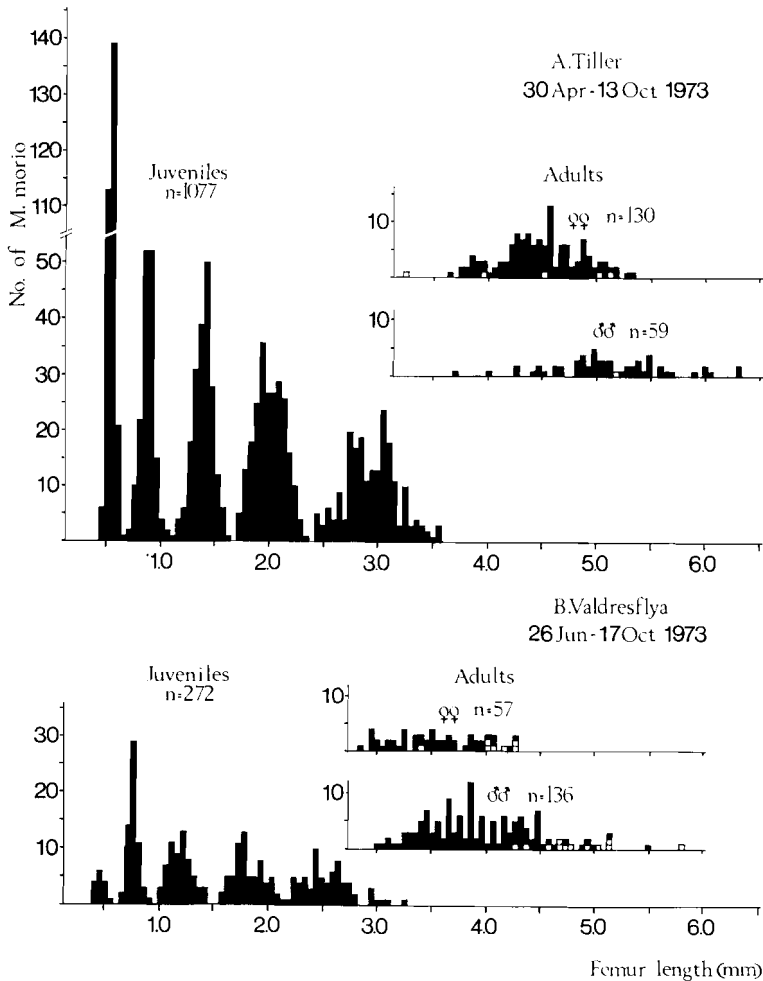


Fig. 1. Frequency distribution of the femur lengths of the fourth pair of walking legs of *Mitopus morio* from Tiller and Valdresflya. Open symbols show the values for adults trapped before 6 August at Tiller and 9 August at Valdresflya; n is the sample size.

of leaves and shoots were measured and growth curves constructed. To compare the localities, the dates on which the birch leaves attained 75% of their final length were estimated (called Leafing; the mean date for 2-9 trees, full (100%) length used for the leaves was that measured by the end of June - middle of July). *Betula pubescens* was used, except for some trees of *B. verrucosa*.

RESULTS AND DISCUSSION

Stages and size

Fig. 1A shows the frequency distribution of the femur lengths of the fourth pair of walking legs of all the *M. morio* trapped at Tiller in Trondheim during the period 30 April to 13 October in 1973. The length distribution for the 1077 juveniles shows five distinct peaks, indicating the presence of at least five discrete size-classes (here called stages 1-5), i.e. at least five ecdyses to take place. There were probably further, smaller stages which were not trapped, since for British harvestmen ecdysis is said to take place seven or eight times (Sankey 1949, Sankey & Savory 1974). Five size-classes were also found in the other Norwegian localities studied, e.g. the highest locality Valdresflya in Sjødalen (Fig. 1B). At this locality femur lengths of each successive stage were shorter than the corresponding ones caught at Tiller, as well as of the adults; they were in fact the shortest femurs of all localities together with

those from the northernmost locality at Tana. The longest femurs were found at Røa in Oslo (Table II).

The femur of the adult male was in general longer than that of the female, and this was true for each locality (cf. Meinertz 1962), although length variation within one sex was very great, especially among the males (Fig. 1, Table I). The femur lengths of the last juvenile stage showed two peaks in the frequency diagram, probably already a reflection of sexual divergence. Femur lengths of the adults from high-altitude localities were, in general, smaller than those from lower-lying sites. Nevertheless, variability in length was great - remarkably large values for both sexes - in the subalpine birch forest at 990 m a.s.l. in Håskelia in Sjødalen (20 ♂♂: 5.13 mm, 9 ♀♀: 4.67 mm). Shorter legs in cool climate have also been found in Finland (Lehtinen 1964) and for other eurythermal Opiliones in South Africa and on the Aleutian Islands, varying inversely to the body length (Kauri 1966b).

Femur length tended to be greater for the earliest developed adults, of both sexes of *M. morio*, than for those trapped later in the autumn, though this was only statistically significant (t-test, $P < 0.01$) for Valdresflya (Fig. 1). Furthermore, there was a significant difference between the femur lengths of adult females at Bratsberg in Trondheim in 1973 and 1974, 4.45 mm and 4.78 mm respectively (t-test, $P < 0.02$).

Table II. Femur lengths (in mm) of the fourth pair of walking legs of *Mitopus morio* from three localities in Norway (see also Fig. 1 and Table I). Mean length, square root of unbiased variance and sample size is given, as well as min. and max. femur lengths of adults.

Locality & years		Juvenile stages					Adults					
		1	2	3	4	5	♂♂	Min.	Max.	♀♀	Min.	Max.
b Røa 1971-72, 75	\bar{x}	0.57	0.97	1.57	2.37	3.77	5.84	4.97	7.11	5.45	4.52	5.96
	\sqrt{v}	0.04	0.06	0.11	0.16	0.23	0.59			0.42		
	n	51	62	51	58	20	11			14		
o Tiller 1973	\bar{x}	0.53	0.87	1.38	1.99	2.94	5.12	3.72	6.31	4.49	3.26	5.34
	\sqrt{v}	0.03	0.06	0.09	0.14	0.24	0.52			0.38		
	n	280	159	195	136	206	59			130		
h Valdresflya 1973	\bar{x}	0.46	0.76	1.19	1.81	2.55	3.99	3.00	5.80	3.57	2.85	4.28
	\sqrt{v}	0.05	0.05	0.11	0.14	0.23	0.54			0.40		
	n	15	60	63	67	68	136			57		

Occurrence of nymphs and adults

When traps were checked in early spring, only stage 1 nymphs were found, and in the autumn only adults. In the intervening period the traps contained a mixture of size-classes, due to incomplete synchronization of development and, to a certain degree, to the lapse of days between each time the traps were emptied. Stage 1 was found in the traps during a period of one month, starting early in May at the lowland localities in South Norway, the earliest being trapped during the period 29 April to 3 May 1974 (Bratsberg). At higher altitudes and in North Norway the period started at the end of May—beginning of June, as in South Greenland; this is a month later than in Denmark (Meinertz 1973). The latest one was trapped during the period 15 July to 9 August 1975 (Saltfjellet).

The first adults appeared in the traps by the end of July, both in Sjødalen as well as at Tiller and Bratsberg, as has been reported in Finland (Lehtinen 1964). At Saltfjellet they were found in the middle of August in 1975. Females tended to appear earlier than males in the traps (Fig. 1). By the second week of August in 1973, a total of 25 females and 25 males had been trapped in the five plots (localities h-1 in Table I) in Sjødalen. Later on, only a further 92 females were caught, compared to 187 males. This difference in the time of occurrence was significant (X^2 -test, $P < 0.025$).

Numbers trapped

The numbers of specimens trapped were closely related to the mean air temperatures (Fig. 2). Great annual variation in population densities was found, e.g. much smaller numbers at the Tiller and Bratsberg localities in Trondheim in 1974 compared to 1973 (15 and 46% respectively by ca. 10 July). The numbers taken in 1974 may have been influenced by the trapping of adults in 1973, but this is not very likely for two reasons; the six traps on each plot were at least 20 m apart and numbers increased once more in 1975. The difference was probably not due to a greater degree of activity, and so to increased chances of being trapped, in 1973, because air temperatures were higher in 1974, during both May and June (Table III). The number of adults trapped in the autumn of 1973 was

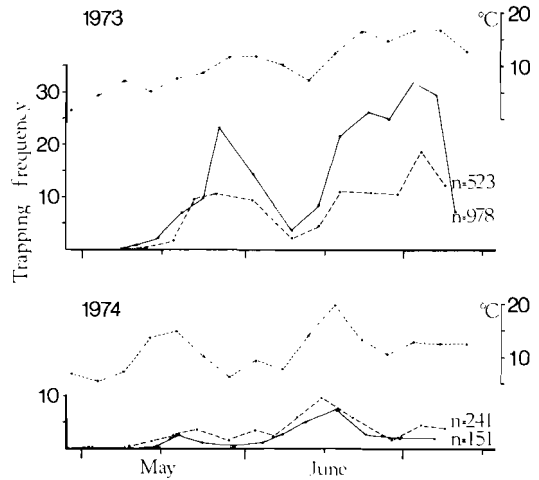


Fig. 2. Trapping frequency of *Mitopus morio* at Tiller (solid line) and Bratsberg (broken line) in 1973 and 1974. The average numbers trapped per day in six Barber pitfall traps have been plotted against the mean dates of the respective trapping periods. n is the sample size. The five-day mean values for air temperature at Trondheim-Tyholt have been added (taken from the tables issued by the Norwegian Institute of Meteorology).

high and the number of stage 1 nymphs in the spring of 1974 was low (12 and 38% on the two plots respectively, of the 1973 numbers). A heavy mortality therefore probably occurred in the period between. A possible explanation may be the low precipitation in 1974 (Table III). The temperature for the last four months of 1973 was lower than normal but with high precipitation. The population decrease may also have been due to other circumstances such as egg predation, but this was not studied.

The adult sex ratios (males : females) at both Tiller 69 : 140) and Bratsberg (22 : 47) in 1973 were practically 1 : 2, in contrast to Sjødalen, where the opposite ratio was found (136 : 58 for Valdresflya, 76 : 59 for the other plots). In 1974 the last trapping period at Tiller was 9 July to 9 August, and no adults were found. At Bratsberg the last period during that year was 10 July to 27 October, during which 12 adults were caught, all females. 11 males and 14 females were trapped at Røa 12 August to 23 September 1975. At Kvale in Valdres a total of 9 adults had been trapped by 16 August in 1971; all were females. At Saltfjellet, trapping ended 3 September in 1975 and the ratio was 10 : 189.

Table III. Monthly means of air temperature and depth of precipitation at Trondheim-Tyholt (taken from the tables issued by the Norwegian Institute of Meteorology, Oslo).

Month	1973		1974	
	Temp. (°C)	Precip. (mm)	Temp. (°C)	Precip. (mm)
Jan	2.5	94	1.6	47
Feb	-2.1	101	0.2	28
Mar	3.3	74	1.2	3
Apr	1.7	75	4.5	72
May	7.8	70	9.5	34
Jun	11.9	66	12.7	58
Jul	14.2	99	12.2	113
Aug	11.6	83	12.5	81
Sep	8.3	134	10.9	50
Oct	3.2	174	3.7	72
Nov	-1.2	121	0.0	30
Dec	-1.5	122	0.3	81

In a collection from Denmark the sex ratio was 922 : 621 and 144 : 505 in one from Greenland (Meinertz 1973). According to Meinertz, a possible explanation for the difference was that the Danish material had been captured with forceps throughout the year over a period of several years, while that from Greenland was collected in traps during only one and a half months of a single year (July–August, 1970). Most of the Greenland females were caught at a single locality (ratio 72 : 381). Perhaps the females reach the adult stage earlier than the males in Greenland as well, resulting in a low sex ratio in summer. The low ratio from Greenland may suggest a dominance of females in a cold climate. However, an opposite tendency was found in Norway, with a high ratio in the mountain of Valdresflya, for which I have no explanation at present.

Growth phenology

Growth curves for *M. morio* from some of the localities are given in Figs. 3–5. A phase displacement of the growth pattern was found with altitude and latitude. This was also found between adjacent traps in the spruce forest in Sørkedal, Oslo (Fig. 3). Four of the traps were located in a relatively open habitat, but two traps were situated in denser forest, about 135 m away. The snow disap-

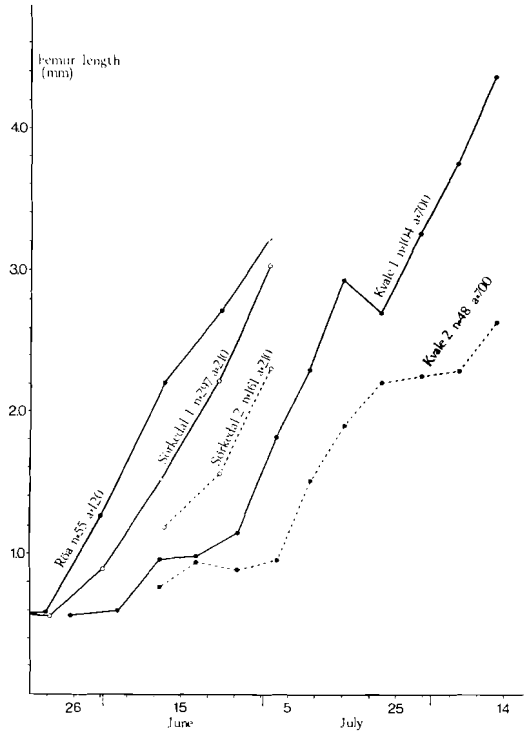


Fig. 3. Growth curves for populations of *Mitopus morio* in 1971. n is the sample size, a the altitude in m a.s.l. (see Table I for further site details).

peared from the denser habitat 8 days later in 1971 and 1972. Leafing and flowering of *Vaccinium myrtillus* and *Anemone nemorosa* in the second half of May 1975 were seen to be delayed by approximately 8 days in the denser habitat, and this corresponded to the delay found in the start of growth of *M. morio* (7 days in 1975, Table I).

At Kvale, Valdres in 1971, the start of growth was delayed by approximately 10 days, at the beginning of July, in old spruce forest, compared to the adjacent clear-felled area. This delay persisted and even appeared to increase during the summer (Fig. 3).

In Sjødalen the development of *M. morio* was 10–14 days further delayed at the 1250 m locality than at 1120 m a.s.l. (Fig. 4). However, this delay was probably also due to the north-western exposure of the higher locality, compared to the eastern exposure of the lower one. The birch forest at 990 m a.s.l. showed an even earlier development of *M. morio*. In Trondheim the growth pattern

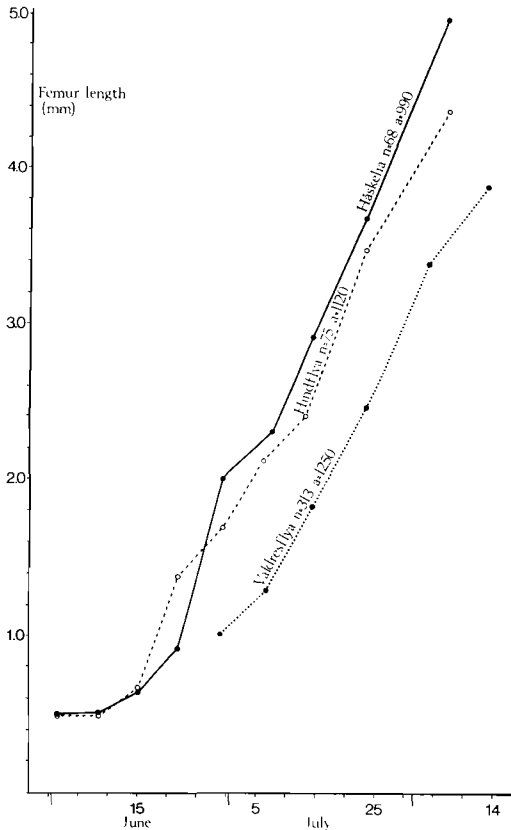


Fig. 4. Growth curves for populations of *Mitopus morio* in 1973. n is the sample size, a is the altitude in m a.s.l. (see Table I for further site details).

was the same at Tiller as at Bratsberg. Stage 1 made an early appearance, but probably because the climate was oceanic, further growth was delayed in comparison with Sjødalen, the same stages being reached by the end of June in 1973, in spite of a 900 m difference in altitude (Fig. 4 and 5). Furthermore, the final adult stage seems to have been reached at an even earlier date at 1250 m in Sjødalen than at 120 m in Trondheim in 1973, viz. only 6 adults had been trapped at the beginning of August at Tiller compared to 19 at Valdresflya, even though the trapping frequency for *M. morio* in the former area was much higher (Fig. 1).

Except for an earlier start of growth in 1974, compared to 1973, at both Tiller and Bratsberg, development was similar at both localities in both years (Fig. 5B), despite the

lower spring temperatures in 1973, with a corresponding delay in the development of the vegetation (Fig. 5A). This delay amounted to 13 days at the beginning of June 1973, compared to the warm spring of 1974. Some measurements of leaf development on *Vaccinium myrtillus* and *Dryopteris linnaeana* indicated a corresponding phenological delay of this lower layer. One explanation for the relatively delayed growth of *M. morio* in 1974 may have been the low precipitation that winter and spring, although the values for the month of June were similar and near the normal (Table III). In comparison, the growth of the Homopteran *Oncopsis flavicollis* (Det. Holger Holgersen), living on birch, was retarded by 14 days on Tiller and Bratsberg at the beginning of June in 1973 (Slagsvold, in prep.).

The growth of *M. morio* at Tana in 1975 (Fig. 5 B) was exceptionally early compared to the other localities, if one bears in mind its northern latitude and late vegetational development (Fig. 5 A).

Growth of M. morio, snow disappearance, and birch leafing

Fig. 6 A shows the relationship between the start of growth of *M. morio* in spring (Stage 1–2) and the time of snow disappearance (estimated as the date on which 80% of the plot became snow free) for the localities and years for which both pairs of observations are available. The correlation proved to be significant and Stage 1–2 was reached, on average, 31 days after the date of snow disappearance.

A close correlation was also found between the development of *M. morio* and the time of birch leafing (Fig. 6 B). On average, *M. morio* reached Stage 1–2 on the same day as the birches reached the 75% stage. However, the variation was great, with Stage 1–2 being reached 12 days after the leafing stage at Bratsberg in 1974 (point p74) and 21 days before the leafing stage at Tana in 1975 (point w75). In particular, the latter point is exceptional. The temperature in June 1975 was 2–3°C lower than average in North Norway, and the development of the birch leaves was very late at Tana, but, as for Tiller and Bratsberg in 1973 compared to 1974, I cannot satisfactorily explain why the growth of *M. morio* was not more delayed.

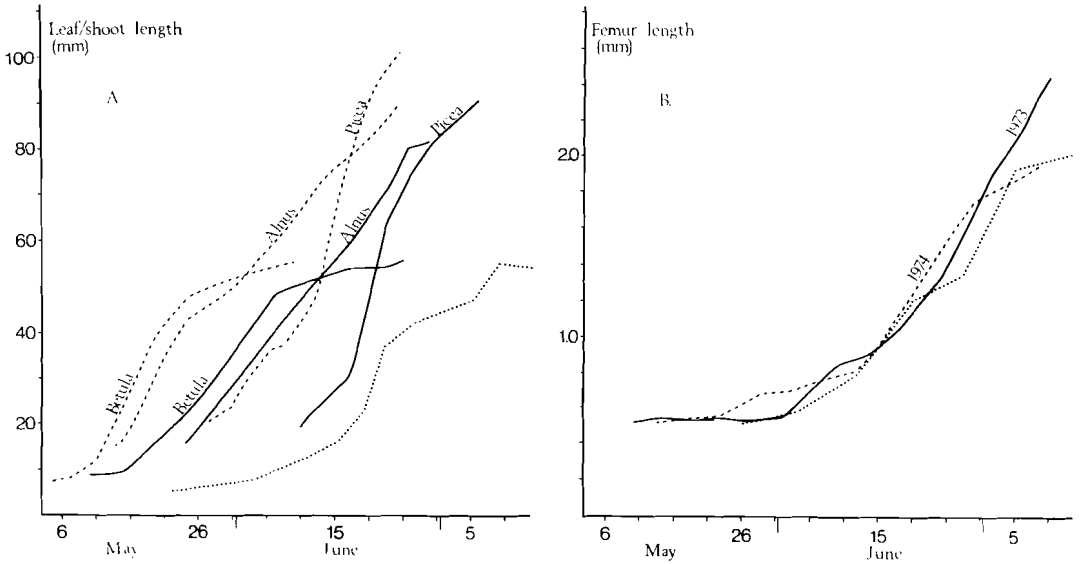


Fig. 5. A. Tree phenology at Tiller and Bratsberg in 1973 (solid line) and 1974 (broken line). Based on leaves of 5 trees of *Betula pubescens* and 3 trees of *Alnus incana*, and shoot extension of 3 trees of *Picea abies*. Dotted line: leaf development of 4 trees of *B. pubescens* at Tana in 1975. B. Average growth curves for *Mitopus morio* at Tiller and Bratsberg in 1973 (1401 specimens measured) and in 1974 (390 specimens measured). Dotted line: the growth curve at Tana in 1975 (66 specimens measured).

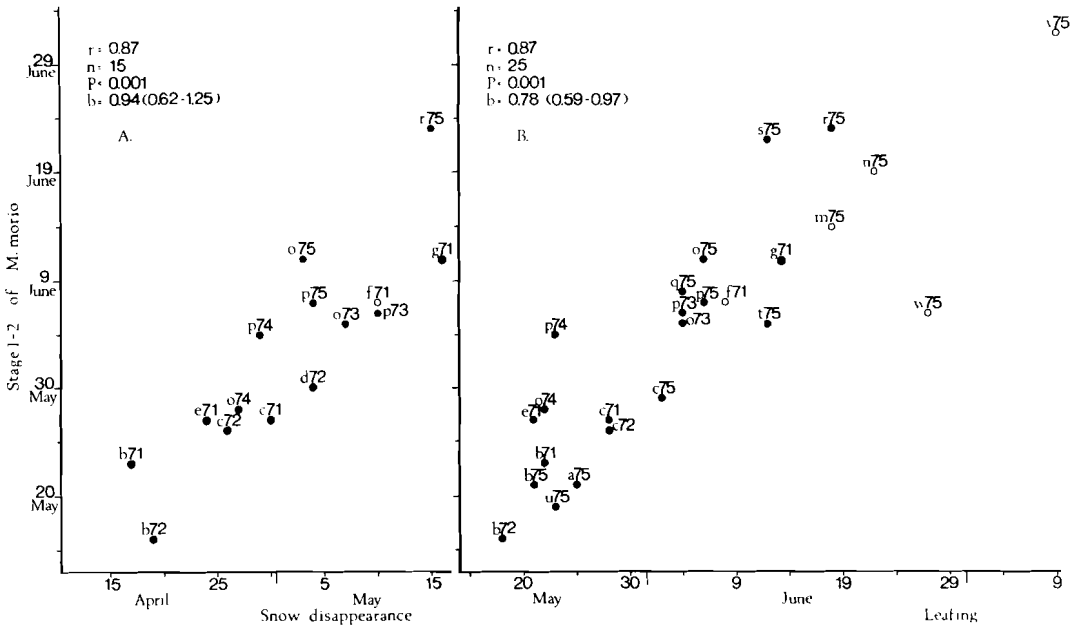


Fig. 6. Correlation of the onset of growth of *Mitopus morio* with the date on which 80% of the locality was free of snow (A) and with the date on which the birch leaves had reached 75% of their full development (B). The letter beside each point refers to the locality and year, as listed in Table I. Open circles: open habitat, much of the ground exposed to solar radiation. r is the correlation coefficient, n the number of points, P the significance level, b the regression slope with a 95% confidence interval.

Leafing was measured nearby the 10 traps. Increased solar radiation received by the ground in this open and northernmost habitat may be involved, as early *M. morio* growth was also found in the clear-felled area in Valdres and in the subalpine and alpine areas (Fig. 6 B, open circles). In the alpine region at Finse, Hågvar (1975) found that the litter surface temperatures in the *Salix herbacea* communities exceed 40°C in sunshine. However, the interval between the Stage 1–2 of *M. morio* and the 75% leafing stage of the birch was drastically changed from the open habitat at Saltfjellet to Tana, both stations located north of the polar circle.

The data from Tana may suggest that the growth of *M. morio* has a slightly smaller latitudinal retardation than the development of the vegetation. The regression slope in Fig. 6 B was lower than unity (0.78; equal to 0.88 if the value from Tana is omitted), which means that for each ten days delay of leafing, the delay of *M. morio* growth was 7.8 days. However, it should be noticed that leaf development in the 'unexposed' localities was measured on birch trees standing generally more open and exposed than the actual traps, probably giving a too early leafing date and so a too low regression slope. The growth of *M. morio* does not directly depend on the birch trees, but together with the vegetation is probably related to the climate. We may therefore change the coordinates and also look at this regression. We find a regression slope of 0.97 (the 95% confidence interval being 0.74–1.21), meaning that for each 10 days delay in the growth of *M. morio*, the delay in birch leafing was 9.7 days, i.e. of the same order.

M. morio lives on the ground and its growth should preferably be compared to the development of the lower vegetation. However, the latitudinal and altitudinal retardation in the development of these plants did not seem to be smaller than for birch leaves: viz. leaf development of *U Vaccinium myrtillus* was delayed by ca. 37 days at Saltfjellet compared to Bratsberg in 1975 (75% leaf elongation of *U. myrtillus* was found 9 July and 2 June respectively). This corresponded approximately to the delay in birch leafing (32 days).

Conclusions

A retardation in the time of growth of *M. morio* nymphs was found at higher altitudes; in dense, old forest compared with more open woodland, or a clear-felled area; on a north-west facing slope; in years with a delayed onset of spring, with concurrent delay in snowmelt and leaf development of the birch trees.

This retardation is probably mainly due to variation in the climate, primarily variation in air temperature besides solar radiation. Precipitation, too, may influence both start of growth and population size. Experiments have shown that *M. morio* survival fell sharply with decreasing humidity (Todd 1949). There may also be an effect on growth through food availability.

M. morio seems very useful when studying the phenology of an invertebrate in different habitats from year to year, relationships with microclimate, dates of snow disappearance and development of the vegetation, since it is both widely distributed and shows high trapping frequencies, besides its rapid growth from tiny nymphs to long-legged adults. As Savory said, 'the study of harvestmen is a study of legs' (Bristowe 1949).

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Species composition of Oribatei (Acari) on oceanic mountain ground in western Norway

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Solhøy, T. 1976. Species composition of Oribatei (Acari) on oceanic mountain ground in western Norway. *Norw. J. Ent.* 23, 17–22.

A list of Oribatei (Acari) from a NNE-facing slope (460 m a.s.l.) near Bergen, western Norway, is given. Relative abundance and biomass were calculated. *Liochthonius hystricinus* (Forssl.) and *Suctobelba similis* (Forssl.) are recorded for the first time in Norway, and *Ovonothrus septentrionalis* (Selln.), *Ceratoppia bipilis* (Herm.), *Sphaerozetes piriformis* (Nic.), *Chamobates cuspidatus* (Nic.) for the first time in western Norway.

Taxonomical notes are given on *Paulonothrus longisetosus* (Willm.), *Ovonothrus septentrionalis* (Selln.) and *Nanhermannia coronata* Berl.

The structure of the Håstefjell Oribatei community is shown to have certain affinities to a subalpine community in southern Norway and some arctic/alpine ones in western Greenland.

Of the species found, 11% must be regarded as mountain forms, 22% as lowland forms, while the remaining species are relatively euryoec.

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At present there is an increasing interest in the study of soil and litter microarthropods. In view of their numerical abundance, they are supposed to have certain effects on the soil forming processes. Oribatid mites form a group with a high diversity, a world wide distribution, and probably reach their highest densities in northern coniferous forests and some alpine and arctic habitats.

In western Norway about 67 oribatid species have previously been recorded (Willmann 1929, Forsslund (in Løken 1966), Karppinen 1971). According to Løken (1966) another 15 species were found by Forsslund but not published. Records given in the above-mentioned papers are based on a relatively small number of samples from a few habitats. Consequently the oribatid fauna of western Norway is poorly known and data on relative abundance and biomass have not been published. The aim of this paper is to present species list and data on relative abundance and biomass of the oribatid mites found on an oceanic mountain site in western Norway.

STUDY AREA

The sampling plot (60°29'N, 5°18'E) is situated on a gentle NNE-facing slope near the top of the mountain Håstefjell (460 m a.s.l.) about 12 km north of Bergen (Fig. 1). The area is hilly with steep slopes toward the lowland.

The mountain slopes are treeless down to about 200 m a.s.l. due to the oceanic climate, grazing by sheep, and, in former days, regular burning of the vegetation.

The vegetation of the sampling plot is dominated by mosses: *Pleurozium schreiberi*, *Hylocomium splendens*, *Polytrichum commune*, *Dicranum scoparium*, *Dicranella heteromalla* and *Sphagnum* cf. *quinquefarium*. Scattered specimens of vascular plants e.g. *Galium saxatile*, *Uccinium vitis-idea*, *Dechampsia flexuosa*, *Alchemilla alpina* are interspersed in the moss carpet.

A few temperature measurements have been made on Håstefjell during five days in July 1974 about 3 cm below the surface of the

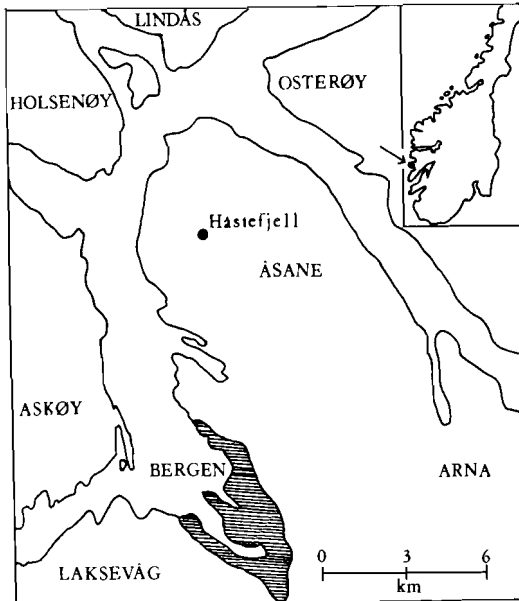


Fig. 1. The location of the habitat investigated.

moss cover (Fig. 2). The temperature fluctuated quite uniformly between 6°C and 10°C and was 5–6°C lower than the air temperature measured at the same time at the Meteorological Station in Bergen (43 m a.s.l.).

METHODS

One sample consisting of 100–200 cm² of the moss layer and to about 6 cm depth was taken on two occasions (14 February and 22 May 1974). The samples were extracted in

modified Tullgren funnels. Only adult specimens of oribatid mites were identified. Biomass (dry weight) was calculated using my own unpublished data on weights and in a few cases data from Luxton (1975) of species of the same size.

Species recorded

At least 31 species were recorded and of these 27 could be identified. The most common species were *Chamobates* (*borealis* and *cuspidatus*), *Phthiracarus* spp., *Ovonothrus septentrionalis*, *Oppia translamellata*, *Nanhermannia coronata*, *Carabodes minusculus*, *Quadroppia quadricarinata*, *Suctobelba* (*similis* and *subcornigera*) (Table I). The large species *Ovonothrus septentrionalis*, *Phthiracarus* spp., *Platynothrus peltifer*, *Ceratoppia bipilis* and *Edwardzetes edwardsi* accounted for most of the biomass (Table I).

Two of the species have not been previously recorded from Norway, i.e. *Liochthonius hystericinus* and *Suctobelba similis*. Four species were for the first time recorded in western Norway, i.e. *Ovonothrus septentrionalis*, *Ceratoppia bipilis*, *Sphaerozetes piriformis* and *Chamobates cuspidatus*.

DISTRIBUTION OF THE SPECIES NEW TO WESTERN NORWAY

L. hystericinus is recorded in the other Nordic countries (however as subsp. *tuxeni* in Iceland (Forsslund 1957)) and seems to be common elsewhere in Europe (Niedbała 1972). It is also found in Japan (Chinone & Aoki 1972).

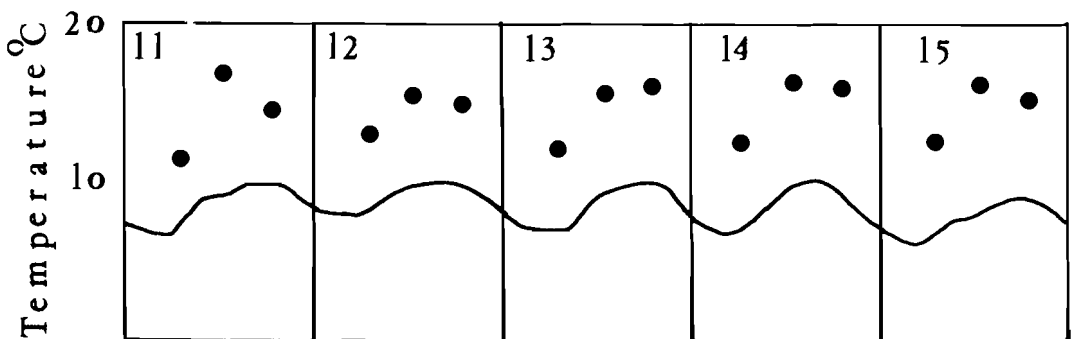


Fig. 2. Temperature records (solid line) from Håstefjell 11–15 July 1974 measured 3 cm down in the moss carpet. Dots show temperatures (at screen height) recorded at Bergen Meteorological Station.

It occurs in the soils of both deciduous and coniferous forests of different types.

S. similis is, according to our present knowledge, confined to Europe where it is widely distributed. It is found in Sweden, Finland, Denmark but not in Iceland, and occurs in about the same types of habitats as *L. hystricinus*.

Karppinen (1971) recorded *O. septentrionalis* in four localities in northern Norway. The only other published Fennoscandian record is from the Åland Islands in Finland. However, I can add two other localities from Norway viz. (1) Aust-Agder, Vegusdal, Hovlandsdalen 270 m a.s.l. (58°35'N, 8°03'E). A south-facing slope with mixed forest of *Pinus*, *Quercus* and *Populus*. In sifted material of litter (9 September 1973, leg. T. Solhøy). (2) Telemark, Vinje, near the eastern end of lake Sessvatn, 920 m a.s.l. (59°40'N, 7°31'E). A small hill with a few scattered birches, some willow thickets, herbs and mosses. In sifted material of litter (10 September 1973, leg. T. Solhøy).

Thor (1937) considered *C. bipilis* to be a common species in central Norway, but Karppinen (1971) found it to be rare in the northern parts of Norway and absent in samples from western Norway. However, my own investigations suggest that *C. bipilis* is a common species around Bergen.

S. piriformis is previously only recorded in mosses at Dovre, central Norway (Thor 1937).

TAXONOMICAL NOTES

A revision of the genera *Phthiracarus* and *Eupelops* is much needed (Forsslund pers. comm.) and no attempt has been made to identify the specimens found in this study. Since there is some confusion about some of the other species listed in Table I, I shall briefly discuss some of the problems of identification.

Paulonothrus longisetotus (Willm.)

Willman (1925) described a variety (*longisetotus*) of *Heminothrus paolianus* (Berl.). Kunst (in litt., see Kunst (1971)) is of the opinion that *longisetotus* and *paolianus* are different species. He has also erected a new

Table I. Numbers and biomass of the adult Oribatei species found on Håstefjell, Western Norway

Species	Number	Biomass µg d.w.
<i>Liochthonius hystricinus</i> (Forssl.)	20	4
<i>Phthiracarus</i> spp. (2 species)	108	2160
<i>Steganacarus striculus</i> (C.L.K.)	4	32
<i>Hypochothonius rufulus</i> (C.L.K.)	3	33
<i>Camisia biurus</i> (C.L.K.)	4	176
<i>C. lapponica</i> (Träg.)	5	105
<i>Paulonothrus longisetotus</i> (Willm.)	1	17
<i>Platynothrus peltifer</i> (C.L.K.)	18	630
<i>Ovonothrus septentrionalis</i> (Selln.)	92	3220
<i>Nanhermannia coronata</i> Berl.	52	468
<i>Paradamaeus clavipes</i> (Herm.)	1	58
<i>Ceratoppia bipilis</i> (Herm.)	30	600
<i>Carabodes marginatus</i> (Mich.)	4	64
<i>C. minusculus</i> Berl.	43	344
<i>Tectocephus velatus</i> (Mich.)	5	9
<i>Quadropia quadricarinata</i> (Mich.)	42	29
<i>Oppia translamellata</i> (Willm.)	93	65
<i>Suctobelba similis</i> Forssl.	} 56	28
<i>S. subcornigera</i>		
<i>Hemileius initialis</i> Berl.	3	30
<i>Oribatula tibialis</i> (Nic.)	2	16
<i>Chamobates cuspidatiformis</i> (Träg.)	6	48
<i>C. borealis</i> (Träg.)	} 125	375
<i>C. cuspidatus</i> (Mich.)		
<i>Edwardzetes edwardsi</i> (Nic.)	18	504
<i>Melanozetes mollicomus</i> (C.L.K.)	2	18
<i>Sphaerozetes piriformis</i> (Nic.)	4	88
<i>Parachipteria punctata</i> (Nic.)	1	18
<i>Eupelops</i> spp. (2 species)	6	120
Total	748	9259

genus *Paulonothrus* for the species described by Willmann (1925). This view is followed here.

Ovonothrus septentrionalis (Selln.)

Sellnick (in Hammer (1944)) described a variety (*septentrionalis*) of *Heminothrus capillatus* (Berl.). Van der Hammen (1959) claimed that the differences between the nominate form and this variety are of minor importance. Dr. F. Bernini (Siena, Italy) has kindly compared some specimens from Håstefjell with the typus of *capillatus* at the Berlese Collection in Florence and with two other Italian populations. He confirms the differ-

ences in the cuticular microsculpture of notogaster described by Sellnick, and informs me that *septentrionalis* should be considered as a taxon of a higher rank. In accordance with this I propose that the variety *septentrionalis* should be regarded as a good species and placed in the genus *Ovonothrus* erected by Kunst (1971).

Nanhermannia coronata Berl.

In the literature there is much confusion about the nomenclature of the *Nanhermannia* species. Forsslund (1963) called attention to the fact that *N. nana* (sensu Willm. 1931) is not *N. nana* Nic. 1855 but identical with the type of *N. coronata* Berl. 1913. The *Nanhermannia* specimens from Håstefjell completely agree with specimens of *coronata* kindly given to me by Prof. Forsslund.

COMPARISON WITH OTHER AREAS

Several attempts have been made to establish more general species-associations of microarthropods (Haarlöw 1960) but the results have been rather discouraging. Only places which are, for instance, very dry or wet seem to have distinct species-associations (Haarlöw 1960).

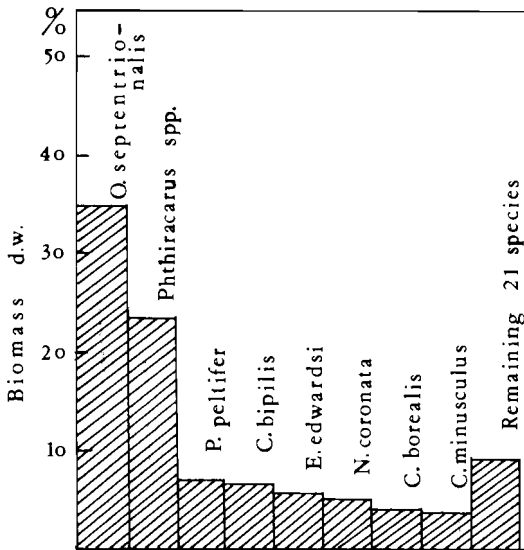


Fig. 3. Biomass dominance of adult Oribatei in the Håstefjell habitat.

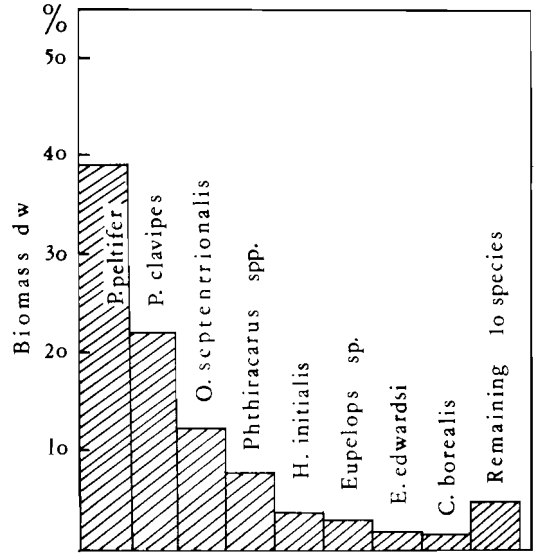


Fig. 4. Biomass dominance of adult Oribatei in the Sessvatn habitat.

In the habitat investigated on Håstefjell *O. septentrionalis* accounted for about 35% of the total adult Oribatei biomass (Fig. 3). In other habitats investigated by me this

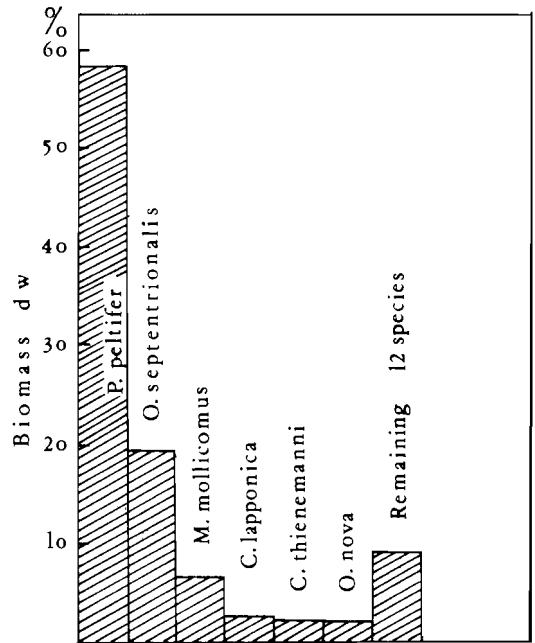


Fig. 5. Biomass dominance of adult Oribatei in the southwestern Greenland habitats (Calculated from Hammer 1944).

species was found to be fairly abundant only at the Sessvatn locality described above. At Sessvatn it accounted for about 12% of the adult Oribatid biomass (Fig. 4). In the south-western parts of Greenland, Hammer (1944, Tab. 15, pp. 80–81) found the species in one sample from Jacobshavn and two samples from Godthaab. From her data I have calculated that *O. septentrionalis* constituted about 20% of the total biomass of adult Oribatei (Fig. 5).

Another species which is common to the three above-mentioned areas is *P. peltifer*, which accounts for 7% of the biomass on Håstefjell, 39% at Sessvatn, and 58% on Greenland.

The species composition of the three habitats is, however, not very similar. The differences in species composition can be illustrated by calculating the Sørensen quotient of similarity (Sørensen 1948). The quotient is 0.45 between the two Norwegian habitats and about 0.20 in both cases between the two Norwegian and the Greenland one (the two samples treated as one). In the comparisons I have excluded the genera *Phthiracarus*, *Eupelops*, *Achipteria*, *Parachipteria*, *Mycobates*, and *Tectocephus* due to inadequate data.

On the Åland Islands, *O. septentrionalis* was found in a dry heathy forest of *Vaccinium* type (Karppinen 1955). However, this description of the habitat is a very broad one, and the sample could possibly have been collected in a relatively wet microhabitat. The same applies to my sifted sample from the south-facing slope in Hovlandsdalen mentioned above, which also positively included material from some wetter spots. Two of the localities from northern Norway are classified as birch meadows while no details are given for the other two (Karppinen 1971). On Svalbard the species were found on a mountain slope with patchy vegetation of *Papaver*, *Dryas*, *Erigeron*, *Taraxacum* etc. (Karppinen 1967).

DISCUSSION

The structure of the Oribatei community on Håstefjell mountain with the abundance of *O. septentrionalis* and the presence of the

predominantly alpine species *C. lapponica* and *C. cuspidatiformis* certainly reflect the cool and moist microclimate of the habitat.

The species list of Håstefjell has certain affinities to that of Sessvatn and those from western Greenland as *O. septentrionalis*, *P. peltifer*, and *O. translamellata* are common to all these habitats. The low similarity between the habitats with regard to total species composition is, however, striking. This is apparently only to a minor extent due to real geographical differences. All the species from the Sessvatn locality and about 75% from those in Greenland are found in different places in western Norway (Willmann 1929, Løken 1966, Karppinen 1971, Solhøy unpubl.). Therefore, the low species similarity found may be explained by differences in microhabitats or differences in the surroundings of the sampling localities. Furthermore, the small number of samples taken means that data on the relatively rare species can easily be biased.

Of the species found on Håstefjell *C. bipilis*, *C. cuspidatus*, *H. rufulus*, *P. punctatus*, *S. piriformis*, and *S. similis* can be regarded as lowland species, whereas *C. lapponica*, *C. cuspidatiformis*, and *O. septentrionalis* are arctic/alpine or subalpine species, while the remaining species are found both in lowland and mountain areas.

The abundance of *O. septentrionalis* is difficult to explain. Admittedly, the distribution of Fennoscandian Oribatei is insufficiently known, but the species was not found by Thor (1937) in his survey of the Oribatei of Norway, nor in Sweden according to the paper on Camisiidae by Sellnick & Forsslund (1955), and in Finland only from the Åland Islands, although most of the country was extensively surveyed (Karppinen 1955). Neither has it been found in Finland in recent years (Karppinen pers. comm.). Only four samples (of about 200) from northern Norway contained the species (Karppinen 1971) and it was not found in Swedish Lapland by Dalenius (1960). Further research may show that *O. septentrionalis* is more common in Fennoscandia but that it is a relatively stenoecc species. At present the amount of data on the ecology of oribatid mites is inadequate, especially data concerning the ecological factors 'of the mites' own dimension' as Haarløv (1960, p. 83) puts it.

ACKNOWLEDGEMENTS

Prof. S.-A. Bengtson, Bergen and Dr. A. Lillehammer, Oslo have offered valuable criticism of the text. I am also indebted to Dr. M. Hammer (Roland, Denmark) for confirming the identification of *O. septentrionalis* and to Dr. P. Dalenius (Hedemora, Sweden) for identifying material of *C. cuspidatiformis*. I acknowledge the loan of specimens of *O. septentrionalis* from Dr. E. Karppinen (Helsinki), Dr. P. I. Persson (Stockholm) and Prof. S. L. Tuxen (Copenhagen). Dr. F. Bernini (Siena, Italy) kindly confirmed the differences between *O. septentrionalis* and *O. capillatus*. My thanks are also due to Dr. D. O. Øvstedal, Bergen for his identification of the moss species.

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Studies on the behaviour of adults of *Phryganea bipunctata* and *Agrypnia obsoleta* (Trichoptera)

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

Field studies on behaviour of emergence, swarming, and copulation are reported. The emergence and swarming of *Agrypnia obsoleta* had a definite daily periodicity and both features occurred around midnight. Both species performed swarming only when air temperatures exceeded 14–15°C. When wind was steady, *Agrypnia obsoleta* did manage to swarm in wind velocities up to 1.5–2.0 m/sec, but in gusty conditions lower values inhibited swarming. The behaviour patterns during swarming and copulation of both species treated were very much alike. Copulation of *Agrypnia obsoleta* was not strictly dependent upon swarming as copulation occurred over a wider range of environmental factors than swarming.

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In the literature I have found very little about the behaviour of adult caddisflies. Authors that have mentioned behaviour have given general information like that of Ross (1944) about the emergence of caddisflies, or they have given small notes on a behaviour pattern observed, like Botosaneanu (1957). The general description of emergences given by Ross (1944) may fit some caddisflies but not all, e.g. fam. Phryganeidae. One of the reasons for this lack of information may be that it requires a lot of patience and time in the field to learn about behaviour. The nearly complete ignorance of behaviour of caddisflies motivated the present study. Besides that, more exact information of the behaviour of different species may be of taxonomic or systematic value.

STUDY AREA AND METHODS

The study was mainly carried out during 1964–1965 in Trøndelag county, Norway, 63°N. In the field, continuous direct observa-

tions were made for several 24-hr. periods. Temperature was measured both manually and with a thermohygrograph, on which humidity was also recorded. The thermohygrograph was located at the water line, about 10–20 cm above water surface. Wind measurements were taken manually. Data on light intensities were taken from measurements carried out with an AEG lux meter in the years 1971–1972.

DIEL PERIODICITY

Agrypnia obsoleta

Diel periodicity of emergence and swarming for four dates in 1965 and one date in 1964 are shown in Fig. 1. Emergence and swarming had a clear daily periodicity. Both activities occurred around midnight. On the dates around 20 July the starting time was just after midnight and on 7 August about 2230 hrs. Emergence was confined to the first part of the activity period. When using the 5 lux level as a fixed limit between day and night, emergence and swarming started within an

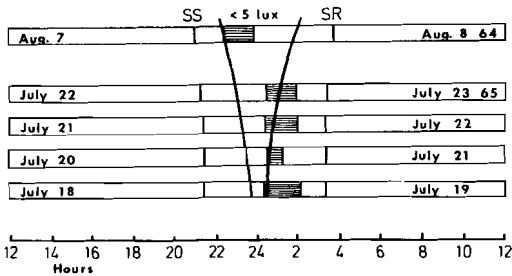


Fig. 1. Diel periodicity of emergence and swarming of *Agrypnia obsoleta* in the area of Trondheim. The shaded areas show the periods of activity. SS = Sun set. SR = Sun rise. The curved lines show the approximate time for light intensities of 5 lux.

hour after the light intensity had dropped below the 5 lux level.

Both emergence and swarming were carried out for only a short time, 1–2 hrs., during a 24-hr period. At the end of swarming a high number of pairs were seen in copula, and when mass emergence and swarming occurred, copulation also had a definite diel periodicity. Brindle (1957b) found *A. obsoleta* to aggregate in great numbers on the shore of the pond early in the night.

Hickin (1967) reported that *A. obsoleta* in England on 23 August 1953 emerged at 1000 hrs, and from noon several pairs were seen copulating. Emergence in daytime was not recorded in the present investigation. But in a long period with unsuitable climatic conditions, males were once observed performing swarming procedures in daytime, on a sunny day with no wind at an air temperature exceeding 14–15°C.

Phryganea bipunctata

The flight period of *P. bipunctata* covers the latter half of June and early July. Observations around summer solstice did not give any definite periodicity in emergence, swarming or copulation, as the few observations made range over the whole 24-hr period when the air temperature exceeded 15°C.

EMERGENCE

The results presented here show that *P. bipunctata* follows a very definite procedure during emergence. This was also the case for *A. obsoleta*, but the procedure seemed to be more simple than that of *P. bipunctata*.

The emergence procedure for *P. bipunctata* was as follows (Table I): 1. The pupa reached the water surface and the pupal skin burst at once. After 25–30 seconds the adults were free. 2. The adults crawled around on the water surface for about 5–10 seconds. 3. The adults stretched their wings. The wings were lifted high up in the air, and held in the same position as those of a mayfly. After 20–30 seconds, the wings were taken down and put into the position typical of a caddisfly. Afterwards the individuals crawled or flew to the shore.

The behaviour of *A. obsoleta* was more simple than that of *P. bipunctata*, but due to the fact that *A. obsoleta* emerged during night, it was difficult to follow the procedure in detail. However, two complete observations were made. After the pupae reached the water surface, the adults were free of the pupal skin within 25–30 seconds. Afterwards the specimen crawled straight to the vegetation belt along the shore. Newly emerged specimens of *A. obsoleta* were never seen flying, and the same was also noted by Brindle (1965).

SWARMING

Following the definition of Dahl (1965), the swarming is a flight pattern, which is repeated over and over again until the controlling microfactors or physiological exhaustion force the individual to a resting place.

Table I. The time in seconds for specific behaviour patterns at the emergence of *Phryganea bipunctata*

Observation no.	Emergence	Crawling	Stretching of wings
1	25–30	--	--
2	25–30	--	--
3	25	10	20
4	20	8–10	30
5	--	5–10	30
6	--	5–10	30
7	--	--	15
8	--	--	20
9	25–30	8–10	30

For *P. bipunctata* and *A. obsoleta*, it is difficult to state that the swarming behaviour was confined to a certain procedure, which was repeated over and over again, but the swarming of the two species was so unlike all other flight activities that it was easily recognized.

The swarming of *P. bipunctata* occurred both on land and above the water surface, while that of *A. obsoleta* was observed only above the water or at the water line. When the species were swarming above the water surface, the general features of the swarming were similar for both species. The individuals flew only about 10–20 cm above the water surface, and at short intervals they changed flight direction, exhibiting a zig-zag flight. During this zig-zag flight, the insect might suddenly descend and shortly touch the water surface. This water touching could be repeated several times, but between each time the insect flew a bit further forward. After the described flight pattern, one or two other patterns started.

1. The individual settled on the water surface and immediately started to crawl around. This pattern seemed to be very similar to that of the gyrids (Coleoptera, Gyrinidae). During their crawling on the water surface, they could jump about 10–15 cm up in the air and repeat this procedure several times within very short time intervals.

2. The individuals settled on the vegetation along the shore, and climbed up to the top of the plants (in this case *Carex rostrata*), dropped down to the water surface, crawled to another plant and climbed to the top, and repeated this several times.

The behaviour described is, according to the observations, mostly carried out by males. However, females were seen to carry out at least parts of the procedure performed at the water surface.

During the crawling on the water surface or on the vegetation, there was one particular pattern that was only confined to the males, and that was the rushing, ruffling, sound of the wings. The males lifted both the fore- and the hind-wings half way up and half way out (making 45° both with the horizontal and vertical line), and as they put the wings into rapid movements, they made a sound that was easily registered by the human ear. Rapid movements of the wings were most

commonly carried out in the vegetation belts, but could also occur for short intervals when they were crawling on the water surface.

RESTING PLACES AND HABITAT OF SWARMING

At two ponds and two lakes where the investigation was carried out, *P. bipunctata* and *A. obsoleta* had different resting places but partly similar swarming places. When coniferous trees surrounded the ponds and lakes, they were the resting places for *P. bipunctata*. In the mountainous area where coniferous trees were scanty or rare, *P. bipunctata* was found in the ling vegetation (*Caluna vulgaris*). *A. obsoleta*, on the other hand, was found closely allied to the pond and lake shores and mostly in the shore vegetation belt at resting time.

For the two species in question it is very difficult to define certain sites at which swarming occurred, as has been done by Mori & Matutani (1953) for e.g. leptocerids and molannids. As swarming is dependent on climatic conditions (see below), some localities may be suitable more frequently than others. But it was impossible to define the swarming sites more precisely than the following indication: swarming of *A. obsoleta* normally occurred along the water line and that of *P. bipunctata* along the water line and on land close to the ponds.

SWARMING AND CLIMATIC CONDITIONS

When studying the animals and their behaviour in the field, it is very often difficult to decide which factor is the main controlling factor at a given observation, as nearly always several factors are acting at the same time. To follow Dahl (1965), the influence of one of the factors can only be observed in the field when it acts as an activity controller, which has reached a critical level – a restricted zone – in the gradient.

As several environmental factors normally act together in all field observations, observations that have one main controlling factor will be few. In the following, only those observations with strong evidence that only one factor acted as the controlling one are treated.

No traps were used to collect swarming adults, but to get information about the intensity of the swarming, the following scale was used: mass swarming, little swarming, and no swarming. Little swarming was noted when 1–10 individuals were in activity. The most intense flight period of *P. bipunctata* is around summer solstice and that of *A. obsoleta* in late July and early August.

Agrypnia obsoleta

In none of the observations was humidity acting as a main controlling factor. The range of humidity at which swarming occurred was about 70–90%. The results agree with those of Yasumatsu (1938) and Brindle (1957a), who also found that humidity was of minor importance in controlling flight activity of caddisflies.

Wind velocities about 1.5–2.0 m/sec. acted as a controlling factor, while velocities of about 1.0–1.5 m/sec. could be a controlling factor when the wind was gusty, but did not control the swarming when the wind was steady.

The swarming was strongly influenced by air temperature. On the dates 22 and 23 July 1965, swarming occurred, and the temperature was above 14°C. On both dates mass swarming was observed when the temperature exceeded 15°C, while in the range of 14–15°C, little swarming activity was exhibited. On the date 24 July 1965, no swarming occurred at the same times as on 22 and 23 July 1965. The only factor which was found to differ from those measured 22 and 23 July 1965, was the air temperature, which on the night in question, commenced at 15°C and decreased to 12°C some hours later. From the observations presented, it is concluded that in the lowland of Trøndelag, *A. obsoleta* is swarming when the temperature exceeds the level of 14–15°C at the time of night when swarming may occur. Any maximum limit of the air temperature for swarming was not found, but a lower limit, the 10°C level, affected the behaviour of the animals. Below 10°C, *A. obsoleta* was very inactive and kept quiet both during day and night. The specimens were found sitting in the shore vegetation and were difficult to discover. On cloudy days, they stayed the whole day and night close to the ground or water surface. On days when the sun was shining,

they moved up, but not to the very top of the vegetation, which consisted mainly of *Carex rostrata*.

In the temperature range of 10–14°C, the specimens were found on the top of the vegetation (mostly *Carex rostrata*), and some individuals tried to start swarming at night. In contrast to the behaviour observed below 10°C, a typical pattern was that the individuals swept their antennae around. Pairs in copula were frequently found, but no swarming was observed.

Phryganea bipunctata

In some features, the swarming of *P. bipunctata* and *A. obsoleta* differed. *P. bipunctata* swarmed for short intervals, spread throughout the whole 24-hr period, while *A. obsoleta* had a diel rhythmic pattern. Usually swarming occurred at small restricted areas (a few m²) only, but could also cover much larger areas. The swarming of *P. bipunctata* resembles the patterns described by Botosaneanu (1957). *P. bipunctata* could suddenly start swarming, and also suddenly stop it. To the observer, no change in the climatic conditions could be registered when they appeared and disappeared.

Due to the behaviour of *P. bipunctata*, it was difficult to carry out exact measurements on temperature and other climatic factors. However, all registrations of swarming were done when the air temperature exceeded 14–15°C, and like *A. obsoleta*, this limit may be expected to be the lower level for swarming.

COPULATION

The females of *P. bipunctata* and *A. obsoleta* were ready for copulation only a few minutes after the emergence. Females of *P. bipunctata* started copulation about 4 minutes after emergence. Exact time for *A. obsoleta* cannot be given but newly emerged females were seen in copula 10–15 minutes after emergence. The females have well developed eggmasses at the time of emergence, which is in contrast to that of the limnephilid species, reported by Novak & Sehnal (1963). Just after the emergence, specimens of both species had a pale colour. Hickin (1967) reported that 'normal' colour is obtained from about 24

hours after emergence. Several pale coloured females were observed in copula, while males were always of 'normal' colour. This indicates that the females mature before the males.

Copulation always started and proceeded on the ground or in the vegetation, never in the air. As the mating started, the male had his head up against the apical end of the wings of the female, and he rapidly moved his wings and a ruffling sound could be heard. If the female was ready to mate, she lifted her wings and the male walked up on her abdomen. He then bent his abdomen and grasped the female genitalia with the claspers. At this moment, the sternites of the last abdominal segment of the male was in the position of the abdominal tergites of the female. Thereafter, the male turned around 180°, and the male and female were in opposite direction. During mating the pair might move around, but in all observations it was the female that was the leading partner.

There is evidence to believe that behaviour at copulation is also affected by temperature. At suitable climatic conditions for swarming, the male made a ruffling sound with the wings. At temperatures below 14–15°C, no such ruffling sound was heard, although copulation occurred within a very short distance of the observer. To a certain degree copulation seemed to be independent of swarming.

In four observations of copulation of *A. obsoleta*, followed from the very start to the very end, the variations in time were in the range of 73 to 104 minutes. A fifth couple was followed for 82 minutes, but in this case the starting of copulation was not seen. Only two observations of this kind were made on *P. bipunctata*, and the copulations lasted for 50 and 67 minutes.

CONCLUSION

Regarding *A. obsoleta*, emergence and swarming were confined to a short time period in the early night (when night is defined as the time period having light intensity below the 5 lux level). Swarming was performed at temperatures above 14–15°C when other climatic factors were suitable. After swarming, a great number of pairs were found in

copulation. Copulation also occurred at temperatures below the level suitable for swarming and did not follow the same diel periodicity as swarming. Newly emerged females seemed to be very attractive to males.

P. bipunctata followed the behaviour of *A. obsoleta* except that swarming was not found to have a clear diel periodicity, as it occurred in short intervals over the whole 24-hr period. Emergence and copulation also occurred over a wide time interval. *P. bipunctata* has a flight period around summer solstice at a time when the lowest light intensities during a 24-hr period are in the range of 15–30 lux.

The females of both species had developed eggs at the time of emergence, and were shortly afterwards ready for mating. Although pairs in copulation were frequently found at the end of, and after, swarming, the relationship between swarming and copulation is a bit obscure, because copulation also occurred when swarming did not occur. Two observations of *P. bipunctata* indicated that female pheromones acted as an attractant to males. In both cases, two newly emerged females approached the shore and from the surroundings, males came flying in straight lines to the females. The males started the swarming dance and after a while copulation began.

If female pheromones are present, they may explain the peculiar behaviour pattern of *P. bipunctata*, which suddenly appeared and started swarming for a short period on limited sites, and also suddenly disappeared again. In all these observations it could be a newly emerged female that attracted the males and made them start swarming. Also, it may explain the fairly weak relationship found between swarming and copulation. Copulation seemed more strongly connected to emergence, but this may be a secondhand effect because of the attractiveness of the newly emerged females.

With regard to temperature, emergence and copulation of *A. obsoleta* occurred over a wider range than swarming. In other words, copulation can occur without previous swarming. The importance of this feature is obvious – it may allow the species to inhabit areas otherwise unsuitable; copulation may be a key factor as to whether or not the species will survive in a particular area, e.g. in a high mountainous area. *A. obsoleta* clearly

expands its limits of tolerance greatly, both against abiotic environmental factors and also in competition with other species.

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Development of *Anthocoris sibiricus* Reuter (Het., Anthocoridae) at constant and fluctuating temperatures with the green peach aphid *Myzus persicae* (Sulzer) as prey

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Hofsvang, L. 1976. Development of *Anthocoris sibiricus* Reuter (Het., Anthocoridae) at constant and fluctuating temperatures with the green peach aphid *Myzus persicae* (Sulzer) as prey. *Norw. J. Ent.* 23, 29-34.

Time of development of *Anthocoris sibiricus* Reuter was studied at temperatures fluctuating from 8° to 28°, and at constant temperatures of 8°, 18°, and 28°C. *Myzus persicae* (Sulzer) was used as prey. Development at fluctuating temperature was slightly but significantly faster than at 18° in spite of the fact that development was not carried through at 8°C. Hatching per cent and mortality at the different temperatures were studied. Females had a significantly longer developmental time than males at all temperatures.

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Anthocoris sibiricus Reuter, synonym with *Anthocoris pilosus* Jak. (Péricart 1972, Ossiannilsson pers. comm.), is distinguished from the other anthocorid species by its long, projecting hairs, especially at the lateral sides of the pronotum (Stichel 1959, Péricart 1972). According to Péricart (1972), *A. sibiricus* is a Euro-siberian species. In Finland the species was first found in 1946 by Linnavuori (Valle 1947). In 1960 *A. sibiricus* was reported from Drammen and Oslo by Ossiannilsson (1962) and was then new to Norway. In 1961 he found the species for the first time in Sweden (Arvika), and it is suggested that *A. sibiricus* is in fact a recent immigrant into the Scandinavian countries (Ossiannilsson 1962).

The specimens of *A. sibiricus* used in this investigation originate from the laboratory at Department of Zoology, The Agricultural University of Norway, where as intruders they entered cages with cultures of parasitic Hymenoptera during the autumn 1969. The Hymenoptera were parasitizing the green peach aphid *Myzus persicae* (Sulzer), reared

on swedes, *Brassica napus napobrassica* (L.) Rchb. During the winter 1969-70, specimens of *A. sibiricus* were put into a cage (0.3 × 0.3 × 0.3 m) and reared on *M. persicae*. Since the biology of *A. sibiricus* is poorly known and since *M. persicae* is a serious pest in paprika and tomato greenhouses, *A. sibiricus* was investigated as a predator on *M. persicae*. This paper deals with developmental times, hatching, and mortality at different temperatures. On the basis of microclimatic field investigations made at Ås in the period from May to September 1966 (Sundby, pers. comm.), a fluctuating temperature, 8°-28°C, was chosen. Constant temperatures used were the two extremes, 8° and 28°, and the mean temperature, 18°C. The investigation was carried out in 1970 and 1971.

MATERIAL AND METHODS

Female bugs were taken from the stem culture in the cage and reared individually for oviposition in glass petridishes (6 cm diameter)

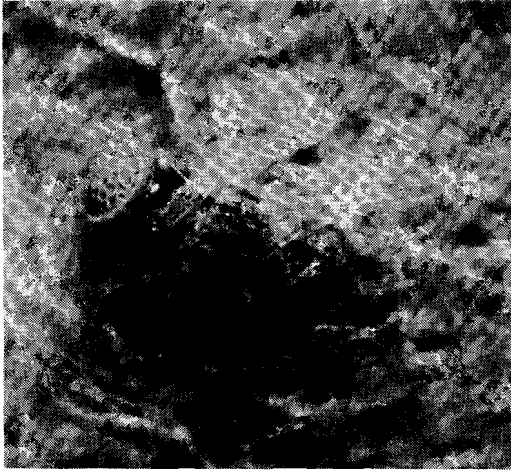


Fig. 1. Egg of *A. sibiricus* inserted between moistened paper filaments. Only the operculum is clearly visible.

at room temperature. A disc of moist filter paper was given a turned up edge in the middle and was placed in each petridish. Hill (1957) found that moist filter paper was accepted for oviposition by adult females of *A. nemorum*, and this was also the case for females of *A. sibiricus*. The eggs were inserted between the moistened paper filaments with only the operculum visible (Fig. 1). They were generally placed along the edges on the underside of the paper, single or in small groups. The eggs could be identified as small swellings in the paper (Fig. 1). The paper discs were renewed daily, and discs with eggs were put in 4-dram vials with perforated plastic lids. Nymphs were kept individually in similar vials. These vials contained a rectangular filter paper with a turned up edge in the middle. Just a corner of this paper was moistened. If more water was supplied, condensation was produced in the vials, and this could kill the smallest nymphs.

The nymphs were daily fed with *M. persicae*, the filter papers were moistened and changed if necessary, and excuvia were noted. Hatching per cent was calculated from fertilized, yellow eggs. Sometimes there were dead nymphs in the vials with eggs at the daily control of hatching. These nymphs had obviously died from starvation and low humidity or perhaps from predation by other nymphs. For this reason, mortality was calculated from nymphs which were alive at the

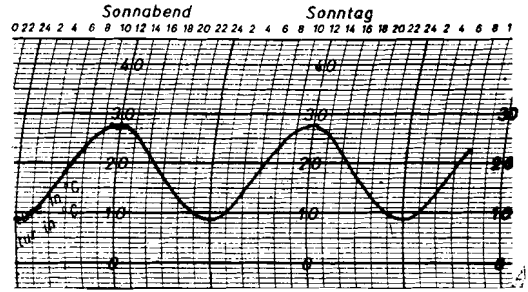


Fig. 2. Fluctuation of the temperature in the 8°-28°C incubator.

daily control of hatching and which from that moment on were reared individually in vials.

Eggs and nymphs were reared in incubators at 8°, 18°, 28° and 8° to 28°. The fluctuating temperature changed from 8° to 28° and back to 8°C again during 24 hours (Fig. 2).

At each temperature the same specimens were followed through the five instars. These specimens are also included in the studies on duration of egg stage, per cent hatching of eggs, and adult mortality.

The photoperiod was 18 hrs. Humidity in the incubators varied between 35 and 90% r.h. In the statistical treatment two samples were regarded as significantly different if $P \leq 0.05$ (Student's test).

RESULTS

Time of development

At 8°C only the egg stage was completed. The developmental time of the eggs was between four and five times longer at this temperature than at 18° and 8°-28°C (Table I).

Table I. Mean duration in days of the egg stage of *A. sibiricus* at constant and fluctuating temperatures. Standard error (SE) and range are given.

Temp. °C	n	Days	SE	Range
8	7	13.6	0.20	13-14
8-28	128	3.0	0.06	2-4
18	253	2.9	0.04	2-5
28	67	1.6	0.06	1-2

Table II. Mean duration in days of the nymphal instars and total nymphal stage of *A. sibiricus* at constant and fluctuating temperatures. Standard error (SE) and range (in brackets) are given.

Temp. °C	n	1st instar		2nd instar		3rd instar		4th instar		5th instar		Total	
		Days	SE	Days	SE	Days	SE	Days	SE	Days	SE	Days	SE
8-28	57	3.6 (3-6)	0.09	2.4 (2-4)	0.08	2.8 (2-4)	0.06	3.1 (2-4)	0.06	6.6 (5-8)	0.13	18.5 (16-24)	0.22
18	60	3.5 (3-5)	0.07	2.6 (2-3)	0.06	2.9 (2-4)	0.05	3.4 (3-7)	0.09	6.8 (5-8)	0.10	19.1 (17-22)	0.14
28	31	2.1 (2-3)	0.04	1.1 (1-2)	0.04	1.3 (1-2)	0.08	1.6 (1-2)	0.09	2.8 (2-4)	0.08	8.9 (8-10)	0.12

Four of the seven nymphs which hatched at 8°C died during the first 24 hours after hatching. One of the three nymphs left died five days old, and the second died nine days old. The last nymph lived for 14 days, but then the experiment was broken.

Mean duration of developmental time of the egg stage and the total nymphal stage was more than halved at 28°C compared with the corresponding values at 18° and 8°-28°C (Tables I and II). The relative duration of the different stages was slightly changed at 28°C compared with 18° and 8°-28°C (Table III). Thus the egg stage and the first instar occupied a relatively larger part of total nymphal time at 28°C.

Duration of the egg stage was slightly longer at fluctuating temperature than at 18°C, but the difference was not significant (Table I). The first nymphal instar showed the same result (Table II). The last four instars had a shorter duration at fluctuating temperature than at constant, but the difference was significant only in the second (P≤0.02) and the fourth instar (P≤0.05). Development time of the entire nymphal stage

was significantly shorter at fluctuating temperature (P≤0.05). The rates of development of the different stages at constant and fluctuating temperatures are shown in Fig. 3.

Time of nymphal development was different for male and female of *A. sibiricus* as shown in Table IV. It was significantly longer for the female at all three temperatures and this was because of the fifth instar.

Table IV. Average duration in days of the nymphal instars and total nymphal stage of males and females of *A. sibiricus* at different temperatures. The results are based on experiments with 29♀♀ and 28♂♂ at 8°-28°, 31♀♀ and 29♂♂ at 18°, and 17♀♀ and 14♂♂ at 28°C. Significant differences between the developmental time of the sexes are marked with asterisks.

Instar	Sex	8°-28°C		18°C		28°C	
		Days	SE	Days	SE	Days	SE
1st	♀	3.7	0.12	3.6	0.10	2.1	0.06
"	♂	3.5	0.12	3.4	0.09	2.1	0.07
2nd	♀	2.4	0.10	2.6	0.09	1.1	0.06
"	♂	2.4	0.12	2.6	0.09	1.1	0.07
3rd	♀	2.9 ^x	0.07	2.9	0.06	1.4	0.12
"	♂	2.7	0.10	2.8	0.08	1.2	0.11
4th	♀	3.3 ^{xx}	0.08	3.4	0.12	1.6	0.12
"	♂	3.0	0.06	3.3	0.15	1.5	0.14
5th	♀	7.3 ^{xxx}	0.13	7.4 ^{xxx}	0.09	3.1 [*]	0.06
"	♂	5.8	0.12	6.1	0.40	2.6	0.14
Total	♀	19.6 ^{xxx}	0.27	20.0 ^{xxx}	0.14	9.2 ^{xxx}	0.10
"	♂	17.3	0.23	18.1	0.20	8.4	0.17

x: P≤0.05, xx: P≤0.01, *: P≤0.005, xxx: P≤0.001

Table III. Relative duration of the developmental stages of *A. sibiricus* at constant and fluctuating temperatures.

Temp. °C	Egg stage	Instar				
		1st	2nd	3rd	4th	5th
8-28	0.14	0.17	0.11	0.13	0.14	0.31
18	0.13	0.16	0.12	0.13	0.15	0.31
28	0.15	0.20	0.11	0.12	0.15	0.27

Table V. Hatching per cent of eggs of *A. sibiricus* at constant and fluctuating temperatures.

Year	Temp. °C	Exp.no.	n	Hatching per cent
1970	18		347	59.1
1970	8-28		336	60.1
1971	8-28		555	75.7
1971	8		121	9.9
1971	28	I	106	23.6
1971	28	II	125	48.0
1971	28	I+II	231	36.8

At fluctuating temperature, the difference in development time was significant also at the third and fourth instar.

Hatching

At 8°C the percentage of hatching was low (Table V) and the few eggs which hatched came from the same female.

In 1970 the hatching per cents at 8°-28° and 18°C were about the same. The eggs at the two temperatures derived from the same females (n = 8) and were laid in the same period. In 1971 the hatching at fluctuating temperature was about 15 per cent higher, eggs of 12 females were then used.

At 28°C the hatching per cent was extremely dependent of moisture. In experiment I at this temperature, the filter paper was handled as at the other temperatures, that is, no extra supply of water was added after the papers were put in the vials. In experiment II, the papers were moistened daily and the hatching per cent was then doubled.

Table VI. Mortality of *A. sibiricus* at constant and fluctuating temperatures. n = number of specimens in the beginning of a stage, d = number of specimens that died during the stage.

Instar	d/n			Per cent mortality		
	8°-28°C	18°C	28°C	8°-28°C	18°C	28°C
1st	14/82	3/72	1/34	17.1	4.2	2.9
2nd	4/68	1/69	0/33	5.9	1.4	0.0
3rd	1/64	2/68	0/33	1.6	2.9	0.0
4th	3/63	1/66	2/33	4.7	1.5	6.0
5th	0/60	2/65	6/31	0.0	3.1	0.0
Total	22/82	9/72	3/34	26.8	12.5	8.8

Mortality

Except for the one first instar nymph which was killed after 14 days, mortality at the first instar was 100 per cent at 8°C. Mortality of the nymphs of *A. sibiricus* was higher at fluctuating than at constant temperatures (Table VI).

At 8°-28° the mortality was twice the mortality at 18°C, mostly because of the low survival of the first instar at fluctuating temperature. At 28°C the mortality was very low (Table VI).

DISCUSSION

A. sibiricus seems to have a shorter time of development than its most closely related species. At 18°C and fed on *M. persicae*, nymphs of *Anthocoris nemorum* (L.) used 30.5 days (n = 71) on the average to reach maturity (Hofsvang, unpublished). This is 11.4 days longer than the developmental time of *A. sibiricus* reared at the same conditions (Table II). Anderson (1962) examined 6 species of *Anthocoris* on different prey at 23 ± 2°C, *M. persicae* not included. He found that the shortest value of nymphal development was 23.7 days for *A. nemorum*, 14.9 days for *Anthocoris nemoralis* (F.) and *Anthocoris sarothamni* Douglas and Scott, 16.2 days for *Anthocoris gallarum ulmi* (DeG), 17.2 days for *Anthocoris confusus* Reut., and 17.9 days for *Anthocoris minki* Dohrn. At 23°C and being fed on *M. persicae*, the length of total nymphal development of *A. sibiricus* would be about 12 days. This value, which is very approximate, is calculated from the rate of development at 23°C. This rate is found by drawing a straight line between the rates at 18°C and 28°C for the total nymphal period. The author (unpublished) found that *A. nemorum* developed slower when fed on *M. persicae* than on some of the prey species investigated by Anderson (1962). If the different prey species have the same effect on *A. sibiricus* as on *A. nemorum*, *A. pilosus* has an even shorter time of development compared with the other anthocorid species than demonstrated from the values above. On the other hand, *M. persicae* could also be a specially favourable prey species just for *A. sibiricus*, in which case comparison with the other anthocorid species is difficult.

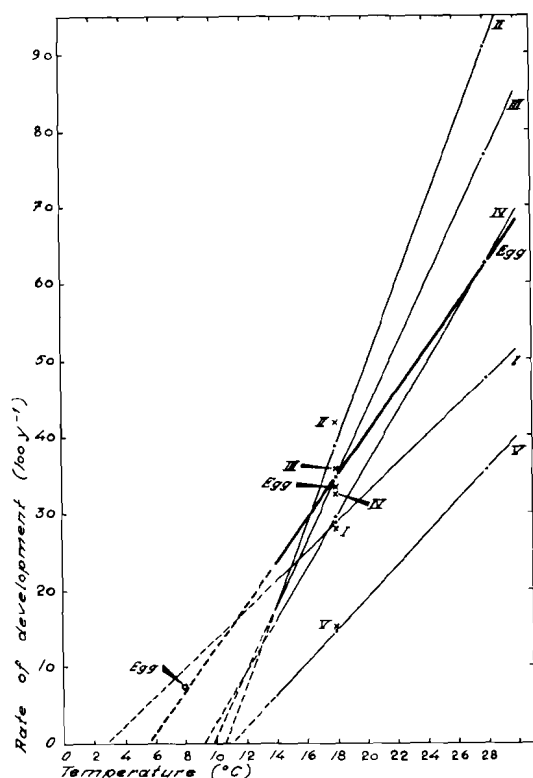


Fig. 3. Rates of development, $100.y^{-1}$, of the egg stage and nymphal instars of *A. sibiricus* at constant and fluctuating temperatures. y = time of development. Straight lines are drawn through the rates at 18° and 28°C (marked with dots). The rates at 8° – 28° are marked with asterisks, the rate at 8°C with a circle.

Because of the low hatching per cent (Table V) and 100 per cent mortality of the nymphs except for one specimen, it seems that 8°C does not belong to the temperature range of tolerance of *A. sibiricus* even though the egg stage and perhaps also the first instar may be carried through at this temperature. Suggesting that 18° and 28°C are within the favourable range of temperature and that development rate is proportional to temperature in this range, a straight line (Wigglesworth 1965) is drawn through the points of development rate at 18° and 28°C . This is done for each stage of development (Fig. 3). When prolonged, this line meets the temperature axis at a point, a , where the development would cease if the curve did not in fact turn upwards in this region. This temperature

represents the theoretical 'developmental zero' (Wigglesworth 1965). Although these lines are based on only two values of developmental rate, they might, together with the a -values found, help to explain some of the results obtained at 8° – 28° and 8°C .

The a -values of the egg stage and the first instar in Fig. 3 are 5.7° and 3.0°C respectively, and indicate that development of these stages are possible at 8°C . This does not agree with the results, but if the range of temperature where the rate is supposed to be linear does not include one of the two temperatures chosen and most probably the highest, the lines of the egg stage and the first instar in Fig. 3 reach the temperature axis too far to the left and indicate an a -value which is too low. Both 18° and 28°C seem to be favourable temperatures for *A. sibiricus*. The increase in development rate when the temperature is raised from 18° to 28°C is lowest for the first instar (Fig. 3). The relative duration of this instar has also a clear increase at 28°C (Table V). It is possible that, at the first instar at 28°C , the growth of developmental rate has started to decrease. Assuming that 18°C belongs to the range of temperature of the first instar where the rate of development is about linear and that 28°C does not belong to this range, the straight line in Fig. 3 belonging to this instar will be steeper and the a -value higher. If the first instar nymph that lived for 14 days at 8°C had moulted after that 14 days, the rate of this nymph would have been lower at 8°C than indicated for this instar in Fig. 3, and though uncertain, it confirms the results and assumptions above. Similar assumptions can be done for the egg stage.

The a -value of the last four instars lies between 9.1° and 11.0°C (Fig. 3) and indicates that it would be difficult to rear these instars at 8°C . But as the theoretical minimum is higher than the real developmental minimum (Wigglesworth 1965), development is perhaps possible after all. At 28°C the relative durations of these instars are shorter than at 18°C (Table III), and it seems that the favourable range of temperature of the four oldest instars are displaced to higher values than the egg stage and the first instar. This confirms that different stages in the life cycle may have different limits to the favourable range and may respond differently to

temperature within the favourable range (Andrewartha & Birch 1954). Andrewartha & Birch (1954) confirm that healthy development may proceed during short or intermittent exposures to extreme temperatures which would be harmful or even lethal if experienced continuously. It seems that fluctuating temperature between 8° and 28°C has a small but significant favourable effect on the development time of *A. sibiricus* in spite of the fact that the lowest temperature, 8°C, does not seem to belong to the temperature range of tolerance of the nymphs.

Baskerville & Emin (1969) have made a rapid estimation of heat accumulation by using daily maximum and minimum temperatures and assuming the sine curve as an approximation of the diurnal temperature curve. When daily minimum is below a lower threshold, as in this paper, a table for estimating heat accumulation is given. The lower threshold used is 51°F (10.6°C). The highest a-values in Fig. 3 are very near this threshold value. Using the table of Baskerville & Emin (1969) at a temperature fluctuating from 8° to 28°C in a day, the daily heat accumulation, using °F, is 14 day degrees. The thermal summation (Andrewartha & Birch 1954, Wigglesworth 1965) at 18°C, using the same lower threshold and °F, is 13.4 day degrees. It is assumed that the response of the animal to temperature is linear, and that this response is constant over a growth period (Andrewartha & Birch 1954, Wigglesworth 1965, Baskerville & Emin 1969). Even though these conditions are not quite fulfilled, and the lower threshold used in these calculations will differ a little from the real threshold value of the total development time of *A. sibiricus*, there is probably

a difference in thermal summation between fluctuating and constant temperature. This is obviously the reason why development is faster at fluctuating temperature.

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Species composition and distribution of spiders (Araneae) in Iceland

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Spiders were collected by hand and pitfall trapping on four plots (each 30 × 30 m), between early June and November for three years. The plots represent different biotopes: tall herb meadow, grass meadow, hayfield, and birch wood. The number of species of spiders was 16, 6, 6, and 21, respectively. The species composition is discussed. A list of species includes one species new to Iceland (*Bathyphantes gracilis* (Blw.)) and eight species previously found only once or twice on the island.

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The present knowledge of the spiders of Iceland is almost entirely based on faunistic collecting. The most detailed account was published by Brændegård (1958), who listed 78 species. During an ecological and zoogeographical study of the Skaftafell area in southeastern Iceland, Lindroth (1965) was able to add four species to the list. Later Lindroth et al. (1973), in connection with studies of the faunal colonization on the new volcanic island of Surtsey, made extensive collections of spiders on the Vestman Islands (including Surtsey), and on the south coast of Iceland. This field work yielded valuable information on the distribution, and to some extent the ecology, of many spiders and another five species new to Iceland were recorded.

This paper is based on data collected during the course of a study of the dispersal and population ecology of certain Icelandic terrestrial invertebrates. Spiders were not the primary object of the study, but since we worked intensively in four different biotopes it was possible to gain some insight into the

species composition of the spiders. We also collected in a number of other localities all over Iceland, and were thereby able to extend our knowledge of the distribution of several species of spiders.

STUDY AREAS AND METHODS

The field work was concentrated on four permanent study plots (each 30 × 30 m); two at Vík on the south coast of Iceland (approx. 63°25'N, 19°W) and two inland at Mývatn in the north (approx. 65°35'N, 17°W). These plots can be described as follows:

1. Rich tall *herb meadow* at Vík in Mýrdal. A southeast facing talus beneath a sea-bird cliff. Vegetation consists mainly of *Anthoxanthum odoratum* L., *Poa pratensis* L., *Angelica archangelica* L., *Rumex acetosa* L., *Plantago lanceolatum* L., and *Ranunculus acris* L. Bryophytes are abundant. The plot is protected from grazing.

2. *Grass meadow* at Vík in Mýrdal. A south facing talus slope which is dominated by *A. odoratum*, *P. pratensis* and a thick

layer of bryophytes (about 70% coverage). Grazing by sheep occurs.

3. *Hayfield* (tún) at Reykjahlíð, Mývatn. Relatively level ground used for haymaking and grazing and intensively managed (including use of fertilizers). The vegetation is dominated by *Poa annua* L., *P. pratensis*, and *Festuca ovina* L. but there are no bryophytes.

4. *Birch wood* in a lava field at Vogahraun, Mývatn. Sparse trees and shrubs of *Betula pubescens* Ehrh. (3–6 m high) and a field layer with patches of *Betula nana* L., *Vaccinium uliginosum* L., *Arctostaphylos uva-ursi* (L.) Spreng., and *Empetrum* sp. Grasses and bryophytes are poorly represented and the litter layer thin. Some grazing by sheep occurs.

The plots at Vík are situated within one km from the sea and at about 30 m a.s.l. The climate is mild and rainy; the coldest months are January and February with a mean temperature of about 1.2°C. The annual mean precipitation is about 2200 mm. The plots at Mývatn are situated inland at about 300 m a.s.l. and have a more continental climate. The coldest months are January and February with a mean temperature of about -4°C. The annual mean precipitation is about 400 mm.

Between early June and November 1973–1975 we sampled lumbricids (the main object of our work; see Bengtson et al. 1975) 4–6 times each year on each plot. On each sampling occasion the vegetation was carefully removed by hand from 20 squares (each 0.25 m²) and all invertebrates encountered were preserved. In 1974 and 1975 we also employed varying numbers of pitfall traps on each plot.

We also collected in a number of other localities using the same methods, i.e. removal of vegetation and collecting by hand and sometimes by pitfall trapping.

Despite the fact that our lumbricid sampling was quantitative, our sampling of spiders can by no means be regarded as such. Differences in size, mobility, and phenology of the spiders make it impossible to quantify and compare numbers on the basis of our collecting. Collecting by pitfall traps is of little quantitative value (see e.g. Southwood 1966, p. 195), but remains a convenient method of obtaining spiders. Therefore, we have refrained from calculating any figures on density or dominance. However, it ought to

be possible to use the data to indicate whether a species is 'regular and common', 'regular but less common' or 'rare' (below denoted + + +, + +, and +, respectively).

The field work was conducted by the first four co-authors, while E. Hauge identified all spiders included in this paper.

The nomenclature mainly follows Locket & Millidge (1951–53). For *Pardosa sphagnicola* (Dahl), *Pardosa hyperborea* (Thor.), *Latithorax faustus* (Cbr.), *Heterocornicularia cuspidata* (Blw.), *Walckenaeria nodosa* (Cbr.), and *Parawideria melanocephala* (Cbr.) we refer to other sources (Holm 1943, 1947, Holm & Kronstedt 1970 and Wunderlich 1972). We here find it most natural to give Wunderlich's subgenera of the complex genus *Walckenaeria* Blackwall 1833 their status as genera.

RESULTS AND DISCUSSION

In describing and discussing the species composition of the spiders, we will mainly restrict ourselves to those four 30 × 30 m plots that were studied intensively in 1973–1975. As stated above, the two localities, Vík in Mýrdal (the herb meadow and grass meadow) and Mývatn (the hayfield and birch wood), differ markedly with respect to climate, latitude, and altitude. The four plots represent distinctly different biotopes.

The following 16 species (598 adult specimens) were found in the tall herb meadow:

<i>Pardosa sphagnicola</i>	+ + +
<i>Savignya frontata</i> (Blw.)	+ + +
<i>Gonatium rubens</i> (Blw.)	+ + +
<i>Lepthyphantes zimmermanni</i> Bertkau	+ + +
<i>Haplodrassus signifer</i> (C. L. Koch)	+ +
<i>Pardosa palustris</i> (L.)	+ +
<i>Cnephalocotes obscurus</i> (Blw.)	+ +
<i>Centromerita bicolor</i> (Blw.)	+ +
<i>Lepthyphantes mengi</i> Kulcz.	+ +
<i>Xysticus cristatus</i> (Cl.)	+
<i>Ceratinella brevipes</i> (Westr.)	+
<i>Walckenaeria nodosa</i> (Cbr.)	+
<i>Trachynella nudipalpis</i> (Westr.)	+
<i>Centromerus prudens</i> (Cbr.)	+
<i>Latithorax faustus</i> (Cbr.)	+
<i>Erigone atra</i> (Blw.)	+

The list mainly consists of species with a wide ecological amplitude. There are, however, several species which are known to

favour places with a relatively high and constant moisture; e.g. the two most dominant species *P. sphagnicola* and *S. frontata*, but probably also *C. obscurus*, *E. atra*, and *T. nudipalpis*. None of the species are typical of higher vegetation such as shrubs or woods. Several of the species have only been recorded a few times in Iceland; e.g. *W. nodosa*, *C. bicolor*, *L. faustus*, and *C. prudens* (see also annotated list below).

The following 6 species (214 adult specimens) were found in the grass meadow:

<i>P. palustris</i>	+++
<i>X. cristatus</i>	+++
<i>S. frontata</i>	+++
<i>H. signifer</i>	++
<i>G. rubens</i>	+
<i>E. atra</i>	+

The dominance of *P. palustris* and *H. signifer* is characteristic of areas with open vegetation.

The following 6 species (23 adult specimens) were found in the hayfield:

<i>Erigone arctica maritima</i> Kulcz.	+++
<i>E. atra</i>	++
<i>Heterocornicularia cuspidata</i>	+
<i>Silometopus curtus</i> (Sim.)	+
<i>Hilaira frigida</i> (Thor.)	+
<i>Meioneta rurestris</i> (C. L. Koch)	+

Only *E. a. maritima* appears to occur regularly in any numbers. It is an arctic and north palearctic species which occurs on arctic and alpine tundra, but also on seashores in Fennoscandia and Germany. It is abundant in Iceland, especially in the northern districts. *H. frigida*, *E. atra*, and *M. rurestris* are northern and alpine species, whereas *S. curtus* is a south- to mid-boreal species. It is worth noting that no lycosids have been found on the hayfield.

The following 21 species (193 adult specimens) were found in the birch wood:

<i>H. signifer</i>	+++
<i>H. frigida</i>	+++
<i>X. cristatus</i>	+++
<i>Dismodicus bifrons</i> (Blw.)	+++
<i>P. palustris</i>	+++
<i>Pardosa hyperborea</i>	++
<i>Bolyphantes index</i> (Thor.)	++
<i>Agyneta decora</i> (Cbr.)	++
<i>Maso sundevalli</i> (Westr.)	++

<i>Parawideria melanocephala</i>	++
<i>L. mengei</i>	++
<i>E. atra</i>	+
<i>P. sphagnicola</i>	+
<i>Agyneta subtilis</i> (Cbr.)	+
<i>C. brevipes</i>	+
<i>Cornicularia karpinskii</i> (Cbr.)	+
<i>Tiso aestivus</i> (L. Koch)	+
<i>L. zimmermanni</i>	+
<i>Diplocentria bidentata</i> (Em.)	+
<i>Gnaphosa lapponum</i> (L. Koch)	+
<i>G. rubens</i>	+

This is the kind of species composition one might expect to find in a northern subalpine sparse, to moderately dense, birch wood as this one. The arctic and/or alpine components are *H. frigida*, *P. hyperborea*, *C. lapponum*, *C. karpinskii*, *T. aestivus*, and *B. index*. All species are northern except *P. melanocephala*, which is apparently rare in Iceland (see annotated list below). Some of the species are usually associated with open ground, e.g. *H. frigida* and *P. palustris*, although they may occur in sparse woods. A few species, such as *M. sundevalli*, *D. bifrons*, *L. mengei*, and the two species of *Agyneta*, are more often associated with shrubs and woods.

When comparing the four plots it is obvious that vegetation and structural diversity of the vegetation is reflected in the number of spiders found. The two plots at Vík are situated only 2.5 km apart and have the same type of macroclimate. However, the grass meadow is subjected to grazing and has a lower, much more homogenous vegetation with much fewer species of spiders than the herb meadow. *P. palustris* is the commonest species on the grass meadow where *P. sphagnicola* seems to be missing. On the herb meadow the latter is much more common than the former (17:1 based on total numbers). Possibly some more species are still to be found in the thick moss layer of the grass meadow, but this may also partly apply to the herb meadow. The intensively managed and grazed hayfield at Mývatn has, as one would expect, a qualitatively (and most certainly also quantitatively) poor spider fauna. The richest spider fauna, in terms of species, was found in the birch wood, despite the fact that none of the species is typical for the canopy strata. The birch wood in Vogahraun has not much ground vegetation or litter

compared with many other woods in Iceland. However, within 900 m², no less than 21 out of 88 species (i.e. 24%) recorded in Iceland have been found. In the survey of the invertebrates of Skaftafell in southeastern Iceland (approx. 64°N, 16°W), 40 species of spiders were found within an area of 27 km² including woods with luxuriant field vegetation and many other biotopes (Lindroth 1965).

Annotated list of species

The following list includes only species for which our data contribute to the data presented by Brændegård (1958), Lindroth (1965), and Lindroth et al. (1973). One species new to Iceland is included. Date of collecting is often given as e.g. '22–30 June 1974', which means that the specimen(s) was obtained in a pitfall trap. Exact dates invariably mean that the specimens were collected by hand.

Pardosa hyperborea (Thorell). Found in two localities (both birch woods) in N Iceland: Vaglaskógur, 40 km W Mývatn, 2–6 July 1974 2 ♂♂ 1 ♀; Vogahraun, Mývatn, 4 June–2 July 1975 2 ♂♂ 1 ♀, 2 July–28 August 1975 2 ♂♂. Previously recorded in one locality in SW.

Pardosa sphagnicola (Dahl). Found in nine localities in N, E, SE, and S Iceland; common at Vík in Mýrdal. Altogether about 500 specimens were collected. Previously recorded only in nine localities (not at Vík) and considered rather rare.

Ceratinella brevipipes (Westring). Found in two localities: Vík in Mýrdal 22–30 July 1974 1 ♂; Vogahraun, Mývatn, 4–28 June 1975 4 ♀♀. Previously recorded in several localities in S and a few in N and NW.

Walckenaeria nodosa (O. P. – Cambridge). Found in one locality: Vík in Mýrdal 22–30 June 1974 1 ♀. Previously recorded in two localities in S.

Parawideria melanocephala (O. P. – Cambridge). Found in one locality: Vogahraun, Mývatn, 4 June–27 August 1975 8 ♂♂ 9 ♀♀. Previously only found at Skaftafell in S.

Heterocornicularia cuspidata (Blackwall). Found in one locality: Reykjahlið, Mývatn, 28 June–2 July 1975 1 ♀. Previously only recorded in one locality in E.

Dismodicus bifrons (Blackwall). Found in three localities: Vaglaskógur 2–6 July 1974 1 ♀; Vogahraun, Mývatn, June–August 1973–1975 9 ♂♂ (only in June) 11 ♀♀; near Reykja-

hlið, Mývatn, 29 June 1975 1 ♀. Previously only recorded in two localities; S and N.

Diplocentria bidentata (Emerton). Found in two localities (both birch woods): Vaglaskógur 9 July 1973 3 ♀♀, 2–6 July 1974 1 ♀; Vogahraun, Mývatn, 4–28 June 1975 1 ♂. Previously recorded in two localities; NW and SE (Skaftafell).

Latithorax faustus (O. P. – Cambridge). Found in two localities: Höfði, Mývatn, 24–27 July 1974 1 ♀; Vík in Mýrdal 12 June–4 July 1975 1 ♀. Previously recorded in two localities in S (incl. Skaftafell).

Agyneta subtilis (O. P. – Cambridge). Found in one locality: Vogahraun, Mývatn, 2 July–17 August 1975 1 ♀. Previously recorded in three localities; two in N and one in S.

Agyneta decora (O. P. – Cambridge). Found in three localities in N: Vaglaskógur 9 June 1973 1 ♂; Vogahraun, Mývatn, 4 July 1974 1 ♂, 28 June–2 July 1975 1 ♂ 1 ♀; Geitafell, 25 km NW Mývatn, 12 July 1973 1 ♀. Previously recorded in four localities in S and on Vestman Islands.

Meioneta rurestris (C. L. Koch). Found in one locality: Reykjahlið, Mývatn, 28 June–2 July 1975 3 ♂♂. Previously recorded in six localities; one in N and five in S and SE.

Centromerita bicolor (Blackwall). Found in one locality: Vík in Mýrdal 30 October–4 November 1974 12 ♂♂ 2 ♀♀ and 28–31 October 1975 3 ♂♂ 7 ♀♀. Previously only recorded in one locality on the Vestman Islands.

Bathyphantes gracilis (Blackwall). Found in one locality: Slúttnes, Mývatn 3 August 1974 1 ♂. Not previously recorded in Iceland but a well-known aeronaut (Duffey 1956).

Lepthyphantes leprosus (Ohlert). Found in one locality: in a house at Vík in Mýrdal 29 June 1974 1 ♀. Not previously found in this district but widely scattered records from other parts of Iceland.

Lepthyphantes complicatus (Emerton). Found in three localities in N: Vaglaskógur 2–6 June 1974 1 ♀; 2 km N Bakkasel in Öxnadalur, 2 July 1974 1 subad. ♀; Höfði, Mývatn, 27 August 1975 1 ♀. Previously recorded in five localities; one of which in N.

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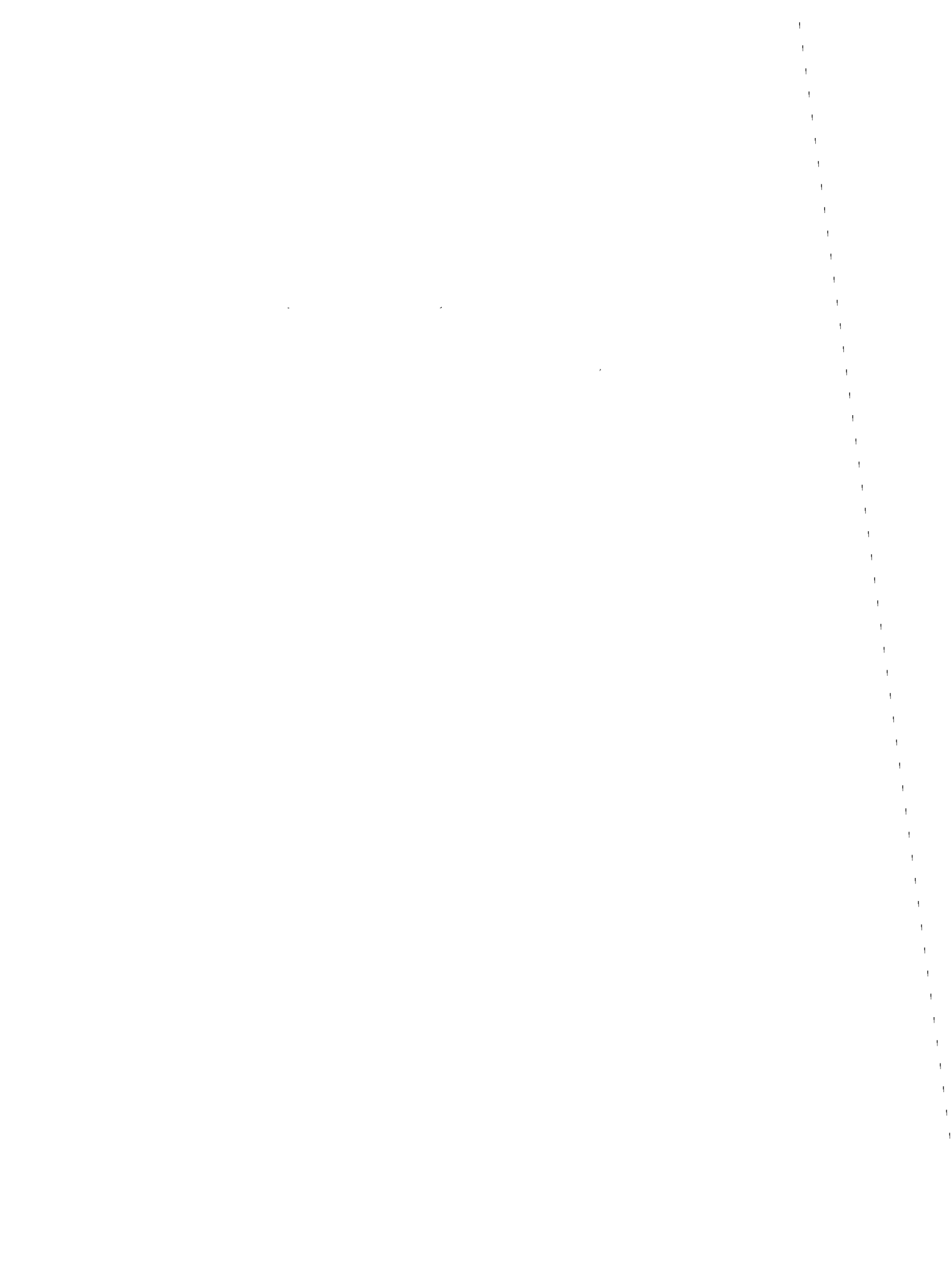
The data were collected during the course of a research project on the dispersal and population ecology of certain terrestrial inverte-

brates and rodents in Iceland. The project is supported by the Norwegian Research Council for Science and the Humanities, Swedish Natural Science Research Council, and Nordic Council for Terrestrial Ecology. We are most grateful to Professor Hans Kauri, Bergen, who kindly read and criticized the manuscript.

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Density and composition of crane fly larvae (Diptera, Tipulidae) from an alpine wet meadow at Stigstuv, Hardangervidda, South Norway

TROND HOFVANG & SIGMUND HÅGVAR

Hofsvang, T. & Hågvar, S. 1976. Density and composition of crane fly larvae (Diptera, Tipulidae) from an alpine wet meadow at Stigstuv, Hardangervidda, South Norway. *Norw. J. Ent.* 23, 41–43.

Larvae of Tipulidae were collected in July, August and September 1971 from soil in an alpine wet meadow, situated 1320 m a.s.l., near Stigstuv, Hardangervidda, South Norway. The dominating species was *Tipula subnodicornis* Zett., which appeared to have an annual life cycle. In September, the mean larval density of this species was 59 larvae per m², representing 97 per cent of all tipulid larvae.

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The invertebrate fauna of an alpine wet meadow habitat, situated 1320 m a.s.l. near Stigstuv, Hardangervidda (60°18'N–7°40'E), has earlier been described from soil samples and quick-trap samples (Solhøy 1972). None of the methods used were suitable for collecting larvae of Tipulidae, an important group of insects in alpine ecosystems. To estimate the density of these larvae, a more efficient method was used.

Description of the habitat is given by Solhøy (1972), Brown & Veum (1974), French (1974), and Wielgolaski (1975).

MATERIAL AND METHODS

The tipulid larvae were extracted from the soil by a hot water process (Hofsvang 1972), modified after Milne et al. (1958).

16 soil samples, 30 × 30 cm large and 10 cm deep, were taken in each of the months July, August, and September 1971. The

sampling dates were: 2–3 July, 10–11 August, and 16–17 September.

The soil samples were in most cases taken at sites where quick-trap samples had been taken previously. According to Solhøy (pers. comm.), the number of tipulid larvae in these quick-trap samples was quite insignificant.

Trying to separate the different larval instars, the diameters of the spiracular discs of the larvae were measured. Several authors have demonstrated that this character is satisfactory for determination of the larval instars (Hemmingsen 1965, Hadley 1971, Hofsvang 1972).

RESULTS

Tipula subnodicornis Zett. appeared to be the dominating species during all three sampling periods. Table I gives the larval density of *T. subnodicornis* and the total density of tipulid larvae recorded in the

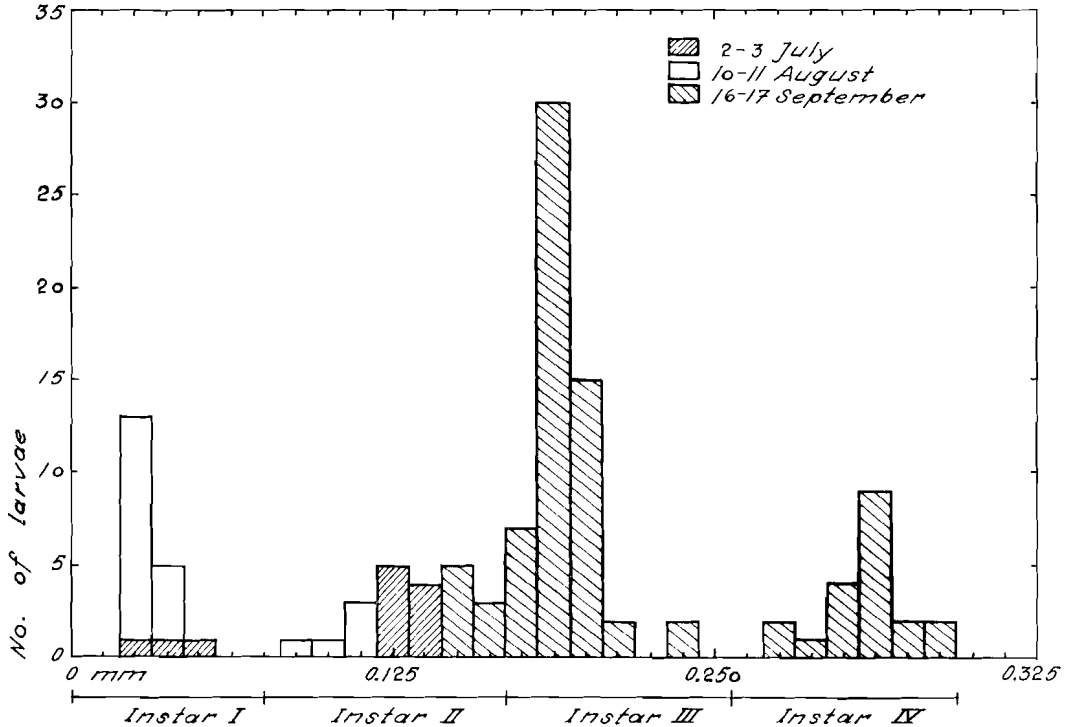


Fig. 1. Diameter of the spiracular discs in larvae of *Tipula subnodicornis* from three sampling periods during the summer 1971. The probable division into larval instars is given.

actual months. The other larvae belonged to *Tipula* sp. except two specimens of *Prinocera turcica* (F.) found in one sample in September.

The diameters of the spiracular discs of *T. subnodicornis* larvae are given in Fig. 1, together with the probable range within each instar. The distribution of larval stages within each sampling period indicates that *T. subnodicornis* passes through the four instars within the short summer period of this mountain area.

Table 1. Density per soil sample covering 30 x 30 cm and the mean density per m² (in brackets) of *Tipula subnodicornis* larvae and of all tipulid larvae found in an alpine wet meadow habitat at Stigstuv, Hardangervidda 1971. n = 16 each month.

Date of sampling	2-3 July	10-11 Aug.	16-17 Sept.
	$\bar{x} \pm$ S.E.	$\bar{x} \pm$ S.E.	$\bar{x} \pm$ S.E.
<i>T. subnodicornis</i>	0.81 [±] 0.28 (9.0)	1.44 [±] 0.36 (16.0)	5.31 [±] 1.01 (59.0)
Tipulidae, total	0.81 [±] 0.28 (9.0)	1.81 [±] 0.50 (20.1)	5.50 [±] 0.98 (61.1)

DISCUSSION

T. subnodicornis has, as common within Tipulidae, four larval instars (Coulson 1962). As shown in Fig. 1, instars I and IV are distinctly limited based on the diameter of the spiracular discs. Few larvae were extracted in July and August. Due to this scarce material, the exact limit between instars II and III is somewhat difficult to assign. However, the large variation of the diameter within this group of medium-sized larvae shown in Fig. 1 clearly indicates that these larvae belong to two different instars.

It is concluded from Fig. 1 that *T. subnodicornis* has an annual life cycle in the high mountain areas at Stigstuv. Imagines collected during the years 1969, 1970, 1972, and 1973 at Finse, 40 kilometres north of Stigstuv, at the same mountain plateau and at similar altitudes, emerged once a year, in late June and in July (Hofsvang 1974). The emergence probably occurs simultaneously at Stigstuv. This assumption agrees with the

present study, which shows that instar I larvae occur in July and August. *T. subnodicornis* seems to spend the winter in larval instar IV.

Coulson (1962) has shown that the species has an annual life cycle in England. The fourth larval instar overwinter, and imagines emerge in May and June.

In alpine and arctic areas insects very often extend their life cycle over two or more years. This has also been demonstrated in some species of Tipulidae (Hofsvang 1972, MacLean 1973). *T. subnodicornis*, however, is evidently able to fulfil its life cycle during the short snow-free period in alpine habitats.

The hot water process is only an effective method for larvae of a certain size, because they have to be picked up by hand after the extraction. This is possibly the explanation of the increasing larval density recorded throughout the summer. The density recorded in September, however, is most certainly representative, since the larvae were very large at this time. This density of about 61 larvae per m² is of a comparable size to other densities of larvae of Tipulidae from high mountain and arctic areas (Hofsvang 1972, MacLean 1973, preliminary IBP-reports). *T. subnodicornis* occurs at densities between 30 and 100 final instar larvae per m² on blanket bogs in high moorland in Britain, where the fauna has a strong arctic affinity (Butterfield & Coulson 1975).

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Notes on eight species of spiders (Araneae) from the Saltfjellet area, Nordland

ERLING HAUGE

Hauge, E. 1976. Notes on eight species of spiders (Araneae) from the Saltfjellet area, Nordland. *Norw. J. Ent.* 23, 45-46.

Three species of spiders are reported for the first time in Norway: *Meioneta saxatilis* (Blw.), *Rhaebothorax sphagnicola* Holm, and *Enteledara media* Kulcz. For five other species new information on their distribution in Norway is given.

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An investigation in the summer of 1974 in Bjøllådalen, an adjacent valley of the Saltfjellet area, Nordland, has resulted in a small collection of spiders, of which eight are presented in this paper. Three species are new to Norway, the remaining five are relatively little known in our country.

Antistea elegans (Blw.)

Fourteen ♂♂ + 3 ♀♀ taken in pitfall traps 1-22 July 1974, in an open sloping mire (intermediate type), UTM references: 33WVP999798. Five ♂♂ + 1 ♀ in pitfall traps 10-22 July 1974, in a sloping mire (rich); UTM references: 33WVP993802. These are the most northern records in Norway. Previously it has been recorded from Sogn (Kauri 1966) and near Kragerø (Waaler 1971).

Meioneta saxatilis (Blw.)

Two ♂♂ in pitfall traps 1-15 July, in an open ombrotrophic, sloping mire, UTM references: 33WVP999798. In the same two pitfall series as mentioned for *A. elegans* 6 ♀♀ were

taken 10-22 July 1974. The species is new to Norway. An additional record from W. Norway: One ♂ + 1 ♀ 8 June 1971 at Hatvik, near Os, south of Bergen, in the moss cover of a mixed forest of deciduous trees and pines, with some junipers in the undergrowth.

Hilaira pervicax Hull.

One ♂ in pitfall traps 12-23 July 1974, in a snow bed with *Salix herbacea*, UTM references: 33WVP998813. The species is previously known from Lyngen (Troms), Tysfjord (Nordland) and Ringsaker (Hedmark).

Gongylidiellum latebricola (Cbr.)

A single ♀ in pitfall traps 10-15 July 1974, in a rich sloping mire, UTM references: 33WVP93802. The first record from N. Norway. Otherwise the species is known from some localities in W. Norway.

Rhaebothorax sphagnicola Holm.

One ♂ in pitfall traps 9-15 July 1974, in an open ombrotrophic sloping mire, UTM references: 33WVP999798. The species is new to Norway.

Entelecara media Kulcz.

One ♀ handcollected in the period of 2–20 July 1974, in an open sloping mire (intermediate), UTM references: 33WVP999798. According to Tullgren (1955) and Wiehle (1960) there has been much confusion between this species and *E. erythropus* (Westr.). However, the comparison of both vulva and epigyne with the corresponding figures from the above cited authors leaves no doubt that I have got a specimen of *E. media*. With the reservation that Strand's record (Strand 1899) of *E. erythropus* (recorded as *Lophocarenum e.* (Westr.)) is correct, this should be the first record of *E. media* in Norway.

Lepthyphantes nigriventris (L. Koch)

Two ♂♂ + 4 ♀♀ in pitfall traps 10–22 July 1974, in a birch forest with high perennials, UTM reference: 33WVP991800. Two ♀♀ were taken in pitfall traps 15–22 July 1974 in a birch forest rich in ling, UTM reference: 33WVP992801. Previously only two records in N.: Hattfjelldal, Nordland (Strand 1902) and Alta, Finnmark (Tambs-Lyche 1955).

Trochosa spinipalpis (Cbr.)

Two ♂♂ + 9 ♀♀ in pitfall traps and 1 ♀ hand-collected, 1–22 July 1974, in the different open humid areas (the sloping mires). One ♀ was taken in pitfall traps 9–15 July 1974, in a birch forest with *Vaccinium myrtillus* and small ferns, UTM reference: 33WVP999798. The specimens have been identified after Holm (1947). Both males have the characteristic spines on the palpal tibiae. All the females, but one, have 3 teeth

at the posterior cheliceral ridge. However, the relations of the epigynal mid-septum do not always seem to be reliable. The species has previously been reported from Møre & Romsdal only, by Tambs Lyche (1942), where he also confirms its presence in Storm's collection from Trondheim.

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Chalcid-flies (Hym., Chalcidoidea) reared from *Ips typographus* L. and *Pityogenes chalcographus* L. at some Norwegian localities

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Pettersen, H. 1976. Chalcid-flies (Hym., Chalcidoidea) reared from *Ips typographus* L. and *Pityogenes chalcographus* L. at some Norwegian localities. *Norw. J. Ent.* 23, 47-50.

A total of twelve species of chalcid-flies were found as parasites or hyperparasites on *Ips typographus* L. and *Pityogenes chalcographus* L. from Norwegian localities. Of these, seven are not previously reported from Norway. The species *Eurytoma blastophagi* Hedqv., *Roptrocerus xylophagorum* Ratz., *R. brevicornis* Thoms., *Dinotiscus eupterus* (Walk.), and *Tomicobia seitneri* (Ruschka) were predominant in the material from the localities examined. The species *Eurytoma arctica* Thoms. and *Heydenia pretiosa* Först. were not frequently found. *Eurytoma arctica* Thoms. and especially *Eurytoma morio* Boh. and *Rhopalicus tutela* (Walk.) are species sporadically found on these spruce bark beetles, but known to be more frequent on pine bark beetles.

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In 1970, when severe outbreaks of *Ips typographus* L. started on Norway spruce (*Picea abies*), little information was available on the parasites and predators connected with this bark beetle in Norway. Of the chalcid-flies, on which this work concentrates, only three species were known (Bakke 1956). Investigations in the neighbouring countries Finland and Sweden indicate that the chalcid-fauna is more complex (Nuorteva 1957, Hedqvist 1963). This paper presents further data concerning the chalcid-fauna of Norway.

MATERIAL AND METHODS

In February and March 0.5 m long log sections were sampled from lying and standing trees attacked by *I. typographus* during the preceding summer. In 1970 to 1972 sections were sampled in Disenå. In 1973 and 1974 the sampling continued in Vestmarka and was supplied with material from Trofors in 1974 (Fig. 1). Each sampling comprised 40 logs, except for the one from Trofors which was made up by 12 sections.

In addition, a limited material was brought in from eight other localities within the outbreak area (Fig. 1). At these localities two sections were cut from a lying, and two from a standing tree.

The sample sizes given as bark-surface areas of the logs may be compared in Table I. The material was stored at the site of origin until rearing started.

Each log section was placed for four weeks at approximately 75% R.H. and a constant temperature of 22°C.

RESULTS AND DISCUSSION

Eurytoma arctica Thomson 1875

Only a single female was found. Descriptions of the biology from Finland and Sweden may indicate that this parasite is more frequently found on pine bark beetles (Nuorteva 1957, Hedqvist 1963). *I. typographus* is recorded as host for *E. arctica* by several authors (Kleine 1944, Ferriere 1950, Sachtleben 1952). In this study the specimen occurred together

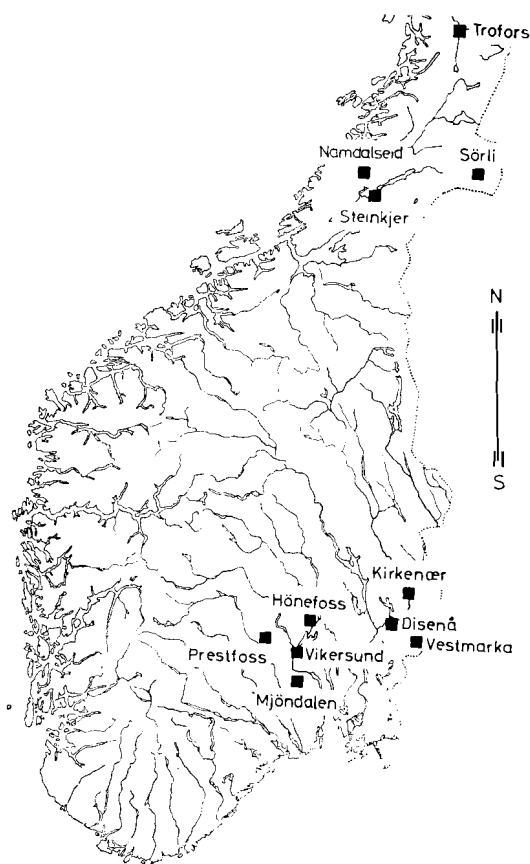


Fig. 1. Map showing the localities of sampling in Southern Norway.

with *Rhopalicus tutela*, which is included as a host by Nuorteva (1967). Whether or not, then, *E. arctica* is a hyperparasite on *I. typographus* is difficult to decide from this material.

Locality: Disenå (1♀).

Eurytoma blastophagi Hedqvist 1963

In Norway, this is the most common *Eurytoma* species found on *I. typographus*. Hedqvist described the species in 1963. He has also identified some of my specimens. Previously *E. blastophagi* was known only as a parasite on *Blastophagus minor* (Hedqvist 1963).

Localities: Disenå and Vestmarka (frequent), Hønefoss (2♀ 3♂), Vikersund (1♀), Prestfoss (1♀ 1♂), Namdalseid (3♀ 4♂), Sørli (1♀).

Eurytoma morio Boheman 1836

This parasite is well known on *Ips* spp. and *Pityogenes* spp. Bakke (1956) recorded it as a parasite on *P. quadridens* and *I. typographus*. This paper includes *P. chalcographus* as a host.

E. morio may live as a superparasite on *Coeleoides bostrychorum* and *C. melanotus* (Sitowski 1930). In this material it appears independent of these Braconidae.

Localities: Disenå and Vestmarka (sporadically).

Heydenia pretiosa Förster 1836

In Russia this species is an important parasite on *I. acuminatus* (Sikanowsky 1936), and in Sweden *B. minor* is a major host (Hedqvist 1963). Hedqvist (1957, 1963) also mentions *I. typographus* as host. Totally, only 5 specimens were reared from the present material. *H. pretiosa* therefore seems to occur more often on pine than on spruce bark beetles.

Locality: Vikersund (2♀ 3♂).

Roptrocerus xylophagorum (Ratzeburg) 1844

This parasite has varying colouration and size depending on the host-size. Ratzeburg was the first to suggest synonymy between the smaller *Pachyceras eccoptogastris* and the larger *Pachyceras xylophagorum* (Sachtleben 1952). This was further discussed by Ruschka (1924) and Nuorteva (1957). Hedqvist (1963) finally transferred the species to the genus *Roptrocerus* and this was accepted by Graham (1969).

Of the chalcid-flies, *R. xylophagorum* is commonly reared from *I. typographus* as well as from *P. chalcographus*. Bakke (1956) also found it to be the dominating species of his material. It is polyphagous, and 43 bark beetles have been recorded as hosts (Hedqvist 1963).

Localities: Disenå and Vestmarka (very frequent), Kirkenær (3♀ 12♂), Hønefoss (2♀ 7♂), Vikersund (48♀ 131♂), Prestfoss (27♀ 9♂), Namdalseid (11♀ 9♂), Steinkjer (2♀ 10♂), Sørli (4♀ 4♂), Trofors (3♀ 7♂).

Roptrocerus brevicornis Thomson 1878

Descriptions from Finland and Sweden indicate that this parasite is associated with bark beetles on pines. The pine bark beetles *Blastophagus pini-perda*, *B. minor*, and *I.*

Table I. Localities and date of sampling of logs from which chalcid-flies were reared. The amount of material is presented as bark area. Geographical notations for Norway are according to Strand (1943).

Locality	Geographical notation	Bark area, dm ²	Rearing started
Vestmarka	HES 1	ca.900	During winter 1973/74
Disenå	HES 5	ca.900	During winter 1970/71
Kirkenær	HES 7	112	Jan. 1973
Hønefoss	BØ 7	122	Feb. 1973
Vikersund	BØ 11	55	Feb. 1973
Mjøndalen	BØ 12	50	March 1973
Prestfoss	BØ 19	108	April 1973
Steinkjer	NTi 34	103	Dec. 1972
Namdalseid	NTi 38	115	Nov. 1972
Sørli	NTi 43	105	Nov. 1972
Trofors	Nsi 24	ca.230	During winter 1974/75

acuminatus are commonly observed as hosts (Nuorteva 1957, Hedqvist 1963), as well as *P. quadridens* and *P. bidentatus*. In my material it was very commonly reared from *P. chalcographus*.

Localities: Disenå and Vestmarka (frequent), Kirkenær (1♀ 1♂), Hønefoss (83♀ 169♂), Vikersund (7♀ 51♂), Mjøndalen (19♀ 41♂), Prestfoss (11♀ 18♂), Steinkjer (1♀), Sørli (3♀ 2♂), Trofors (2♀).

Rhopalicus tutela (Walker) 1836

A widely distributed chalcid-fly in Europe. It is already recorded as a parasite on *I. typographus* in Norway (Bakke 1956), and this study includes *P. chalcographus* as host. In addition to the numerous other Scolytidae, also the genus *Pissodes* (Curculionidae) may be parasitized by *R. tutela* (Sachtleben 1952, Hedqvist 1963). The specimens reared from *I. typographus* were larger (4.5 mm) than the maximum (4.3 mm) given by Nuorteva (1957) and Hedqvist (1963).

Localities: Disenå and Vestmarka (sporadically).

Rhopalicus brevicornis Thomson 1878

According to Graham (1969), the species is most commonly found on pine bark beetles. In the present material it only occurred in

a single locality and there as a parasite on *P. chalcographus*. The specimens fit the description given by Hedqvist (1963).

Locality: Hønefoss (12♀ 24♂).

Dinotusculus eupterus (Walker) 1836

According to several authors, this is a parasite on *P. chalcographus*. It may also be a hyperparasite on the braconid wasp *Dendrosoter middendorffii* Ratz. (Sachtleben 1952). In my material *D. eupterus* parasitized *P. chalcographus*.

Localities: Disenå and Vestmarka (frequent), Kirkenær (4♀ 5♂), Hønefoss (28♀ 48♂), Sørli (2♀), Trofors (1♀).

Tomicobia seitneri (Ruschka) 1924

This imaginal parasite on *Ips* spp. is well known from several European countries (Hedqvist 1963). The biology is described by Sachtleben (1952). In this material I found it common at two localities.

Localities: Disenå and Vestmarka (frequent), Kirkenær (24♀ 16♂), Hønefoss (10♀ 2♂), Vikersund (2♀ 1♂), Prestfoss (6♀ 2♂), Sørli (1♀).

Karpinskiella pityophthori Bouček 1954

This species was reared from *P. chalcographus* at several localities. Bakke (1956) has reared it from *P. quadridens*.

Localities: Disenå and Vestmarka, Kirkenær (6♀ 2♂), Hønefoss (5♀), Vikersund (6♀ 4♂), Sørli (1♀ 4♂).

Mesopolobus typographi (Ruschka) 1924

The biology of *M. typographi* was described by Seitner (1924). The species lives as an ecto-parasite on *Tomicobia seitneri*. As a hyperparasite it has been observed on *I. amitinus*, *I. acuminatus*, *I. typographus* and *I. duplicatus* (Sachtleben 1952). It occurs both in Finland and Sweden (Nuorteva 1957, Hedqvist 1963).

Localities: Disenå and Vestmarka, Kirkenær (3♀ 2♂), Hønefoss (1♀ 4♂), Vikersund (1♀), Prestfoss (1♀ 2♂).

CONCLUSION

Studies at Disenå and Vestmarka confirm that most of the chalcid-flies which parasitize *I. typographus* and *P. chalcographus* in other

Nordic countries and Central Europe are also present in Norway. The species *Eurytoma blastophagi*, *Roptrocerus xylophagorum*, *Roptrocerus brevicornis*, *Dinotiscus eupterus*, and *Tomicobia seitneri* were frequently found at Disenå and Vestmarka. Recorded at several other localities as well, they are probably widely distributed in Norway.

Eurytoma arctica and *Heydenia pretiosa* were sparsely found, even at two field stations where extensive collections were made. In the investigation areas they were found to be of little importance as parasites on spruce fauna.

Previously *Eurytoma morio* and *Rhopalicus tutela*, and especially *Eurytoma arctica*, appeared to be more frequent on pine bark beetles than on bark beetles on spruce (Nuorteva 1957, Hedqvist 1963). This may be the situation also in Norway.

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Energy metabolism in the wolf spider *Pardosa palustris* (L.) (Araneae, Lycosidae) from Hardangervidda, southern Norway

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Steigen, A. L. 1976. Energy metabolism in the wolf spider *Pardosa palustris* (L.) (Araneae, Lycosidae) from Hardangervidda, southern Norway. *Norw. J. Ent.* 23, 51-60.

Field energy metabolism in *P. palustris* was a little higher than previously published data from temperate areas - presumably a response to its environment. Respiratory energy loss varied from 1.21% to 5.28% of total animal energy content, being relatively higher in smaller animals. There was a shift from surface towards weight dependence in metabolism with increasing temperature. Oxygen consumption was reduced by 14% and 21% at 10° and 20°C respectively during night. There was a marked reduction in metabolism during a fasting period. After a longer period of acclimation to constant laboratory conditions, the oxygen consumption/temperature curve moved to the right - presumably a response to the constant conditions. After acclimation, energy metabolism in *P. palustris* followed Arrhenius-Van't Hoff's law.

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The present investigations of energy metabolism in the wolf spider *Pardosa palustris* (L.) (syn.: *Lycosa tarsalis* Thorell) were carried out as part of a study of the energetics of a population of the species during the Norwegian IBP (Steigen 1975b).

A convenient way to measure maintenance energy costs of an organism is to measure oxygen consumption. It is difficult to evaluate the effects on energy metabolism due to stress in the respiratory chamber. In calculating an energy budget of a population, measurements of oxygen consumption must be applied with caution, analyzed, and related to age, weight, feeding, diurnal activity, etc.

The accuracy of the estimates of respiratory energy loss may be checked by calculating the actual energy loss from feeding experiments. In the present study, factors affecting measurements of oxygen consumption are discussed and compared to energy metabolism calculated from feeding experiments on the same animals under the same laboratory conditions. The applicability of measurements of oxygen consumption to productivity studies is also considered.

MATERIALS AND METHODS

Study area

Animals for the experiments were collected by hand at the Norwegian IBP dry meadow site at Stigstuv, Hardangervidda, an atlanto-alpine mountain plateau 1225 m a.s.l. (60° 18'N, 7°40'E). Descriptions of the site are found in Solhøy (1972) and Sonesson et al. (1975).

The collected animals were divided into two groups: a) animals for the measurements of 'field' metabolic rate, and b) animals for feeding experiments carried out in the laboratory. Below they will be referred to as 'field animals' and 'laboratory animals'.

Acclimation

Field animals were acclimated at 10°C for at least 48 hrs before any registrations of oxygen consumption were made. Laboratory animals were acclimated at 10° or 20°C during 2-4 months.

To reduce effects from hunger on oxygen uptake (Zinkler 1966, Miyashita 1969), all field animals were offered food during the

period of acclimation. When measuring oxygen consumption in laboratory animals, only animals that had consumed food during the last 24 hrs were used.

Photoperiod during acclimation was 16 hrs of light (8000 lux) and 8 hrs of dark for all animals.

Apparatus

Scholander volumetric respirometers were used (Scholander & Iversen 1958). As CO₂ absorber a 10% aqueous KOH solution, giving a relative humidity of ca. 91%, was used (Hale 1966). A piece of moistened filter paper on the bottom of the respiratory chamber provided a foothold for the spider and stabilized R. H.

All measurements were carried out in a water-bath with $\pm 0.02^\circ\text{C}$ accuracy.

Experimental temperatures and periods

Oxygen consumption in field animals was measured at 8°, 13°, 18°, and 23°C. Only adult and subadult animals were used to reduce variations in energy metabolism caused by weight differences. Oxygen consumption of eggs/embryos in egg sacs collected in the field was measured at 28°C also. Entire egg sacs were put into the respirometer chamber.

Oxygen consumption in laboratory animals acclimated to 10°C was measured at 10°, 15°, and 20°C. Animals acclimated to 20°C were examined at 20°, 25°, and 30°C. These temperatures were chosen because they correspond to the temperatures during the feeding experiments: 10° and 20°C. Animals from a wide weight range were used.

All measurements were carried out between 0900 hrs and 1500 hrs, which is the period of highest activity in the field population of *P. palustris*. Oxygen consumption at night in laboratory animals was investigated between 2300 hrs and 0300 hrs at 10° and 20°C. All registrations began one hour after closing the respirometer, and each animal was tested at only one temperature each day.

Oxygen consumption during fasting

During feeding experiments some animals were denied food, but were offered water. The experiments were carried out at the

acclimation temperatures. Animals kept at 10°C were denied food for 12 days, and weight and oxygen consumption were measured every 4th day. Animals at 20°C were fasting for 10 days, and registrations were carried out every 2nd day.

Ejecta/oxygen consumption (FUS/R) relationships

Steigen (1975a) has given data on faeces, excreta, and silk production in *P. palustris*. Those are collectively referred to as ejecta (FUS). As a close relationship between production of ejecta and consumption and assimilation may be expected, at a given temperature the FUS/R index will reflect changes in P/R and A/R indices.

Determination of dry weight

Live weights were obtained by weighing animals immediately after the experiments. Field animals were dried at 105°C for 24 hrs and then weighed to obtain dry weight (dw). Laboratory animals were not dried. Their dw was estimated from a regression equation: $y = 0.278x + 0.072$ (x = live weight, y = estimated dw). Egg-sac silk was removed before weighing of eggs/embryos.

Calculations of REL and Q₁₀

An oxycaloric coefficient of 4.75×10^{-3} cal/ μl O₂ consumed has been applied when calculating the respiratory energy loss (REL).

The liberated amount of heat per μl O₂ consumed varies little with the substance oxidized. The error made by using the above-mentioned average value is in most cases negligible (Schmidt-Nielsen 1975). The variations in respiratory quotient (RQ) are mostly due to variations in CO₂ output. By using the average value, the greatest deviation will be about 7%. This is a fairly small inaccuracy compared to the many other sources of error connected with measurements of oxygen consumption. A thorough analysis of CO₂ output consequently does not seem to be necessary (Kamler 1970, 1972).

Respiratory Q₁₀ was calculated according to Prosser (1973).

Table I. Oxygen consumption in *P. palustris*. Field animals.

Animal dw: 4.69 ± 0.21 mg; energy content: 28.35 cal/animal.
 n = number of determinations. REL = respiratory energy loss.

t°C	n	Oxygen consumption		REL cal/animal/24 hrs	REL as % of body energy content
		$\mu\text{l O}_2/\text{mg dw/hr}$ (S.D.)	$\mu\text{l O}_2/\text{mg lw/hr}$		
8	6	0.64 (0.08)	0.17	0.342	1.21
13	7	1.33 (0.24)	0.34	0.713	2.51
18	8	2.30 (0.21)	0.59	1.229	4.33
23	7	2.80 (0.29)	0.72	1.496	5.28

RESULTS

Oxygen consumption in field animals

Table I shows oxygen consumption and REL in *P. palustris* adults and subadults from the field at different temperatures. Respiratory Q_{10} follows the usual pattern and decreases with increasing temperature (Table II). In Table III oxygen uptake in eggs/embryos is shown. Their energy metabolism is about half the rates of adult and subadult animals.

Oxygen consumption in laboratory animals

Day measurements

Energy metabolism during daytime is shown in Fig. 1. Correlations between dw and oxygen consumption were fairly good. The slope of the regression lines decreases as temperature increases. Consequently increase in energy metabolism with temperature is greater in

Table II. Respiratory Q_{10} in *P. palustris*. Field animals

Temperature interval t°C	Q_{10}
8 - 13	4.32
8 - 18	3.59
13 - 18	2.99
13 - 23	2.11
18 - 23	1.48

larger animals. Respiratory Q_{10} values are presented in Table IV. Animals weighing 1 mg dw have a much lower Q_{10} at low temperature intervals than animals of 10 mg dw, and Q_{10} in smaller animals reveals smaller variations.

In Table V an estimate of REL is presented. It has been calculated from oxygen consumption in daytime, and is therefore a maximum value.

The logarithmic equation $y = ax^b$ shows the relations between energy metabolism (y) and body dw (x). Their reciprocal relationship is expressed by the regression coefficient b (Table VI).

Night measurements

Measurements of energy metabolism during night are presented in Table VII. At 10°C it is 14% lower than in daytime, at 20°C the reduction is 21%. This gives lower REL and an 8% lower Q_{10} than during the day.

Table III. Oxygen consumption per mg live weight in eggs/embryos of *P. palustris*. Field animals.

t°C	n	$\mu\text{l O}_2/\text{mg lw/hr}$ (S.D.)
8	4	0.095 (0.008)
13	5	0.166 (0.015)
18	4	0.249 (0.010)
23	4	0.343 (0.056)
28	3	0.469 (0.013)

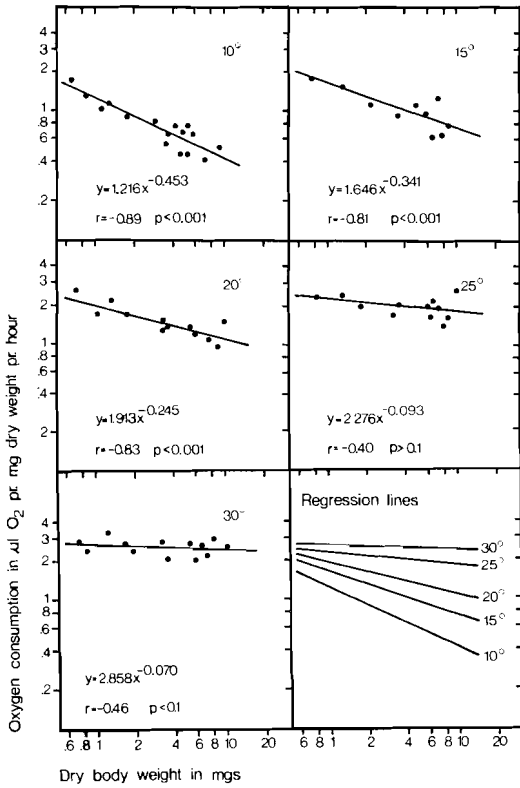


Fig. 1. Oxygen consumption in *P. palustris*. Laboratory animals.

Oxygen consumption during fasting

Oxygen consumption during fasting conditions in *P. palustris* is shown in Fig. 2. At 10°C the curve falls gently during the ex-

Table IV. Respiratory Q_{10} in *P. palustris*. Laboratory animals.

Temperature interval $t^{\circ}C$	Q_{10}	
	1 mg dw	10 mg dw
10 - 15	1.84	3.07
15 - 20	1.35	2.10
20 - 25	1.42	2.86
25 - 30	1.58	1.76
10 - 20	1.57	2.54
20 - 30	1.49	2.24

periment. At 20°C it falls abruptly during the first days, and stabilizes at a level half of the initial rate after 6-8 days. There is a reduction in Q_{10} during the experiment.

Ejecta/oxygen consumption relationship

Fig. 3 shows variations at 10° and 20°C in FUS/R index dependent on the dw of the spider. FUS has been estimated from exponential regression equations obtained by Steigen (1975a) for *P. palustris* from Hardangervidda.

Effects of temperature on oxygen consumption

In Fig. 5 the oxygen consumption/temperature relationships are shown on a semilogarithmic graph. Animals from the feeding experiments weighing 1 and 10 mg dw yields straight

Table V. Respiratory energy loss in *P. palustris*. Laboratory animals. Calculated for animals of 1 and 10 mg dw. Average calorific content of spiders: 6096 cal/g dw.

$t^{\circ}C$	REL		REL	
	cal/animal/24 hrs		as % of body energy content	
	1 mg dw	10 mg dw	1 mg dw	10 mg dw
10	0.139	0.489	2.28	0.80
15	0.188	0.856	3.08	1.41
20	0.218	1.239	3.58	2.03
25	0.259	2.094	4.25	3.43
30	0.326	2.775	5.35	4.54

Table VI. Oxygen consumption in *P. palustris* calculated from regression equations. Laboratory animals. b = regression coefficient. See text for further explanations.

t°C	mg dw	Oxygen consumption	
		$\mu\text{l O}_2/\text{animal/hr}$	b
10	1	1.216	0.55
	10	4.282	
15	1	1.646	0.66
	10	7.506	
20	1	1.913	0.75
	10	10.872	
25	1	2.276	0.91
	10	18.371	
30	1	2.858	0.93
	10	24.338	

lines, whereas this relationship in animals from the field shows a pattern deviating from a straight line.

DISCUSSION

Field animals

A compilation of data from literature is presented in Table VIII. The rate of oxygen consumption in *P. palustris* from Hardangervidda seems to be higher than in other species of hunting spiders, with the exception of *Pardosa rabida* (Walkenaer). An increased energy metabolism may be a result of temperature adaptation in *P. palustris*. The high values in *P. rabida* cannot be evaluated from the data presented by Van Hook (1971). Q₁₀ values and percentage REL are in good agreement with values from Table VIII.

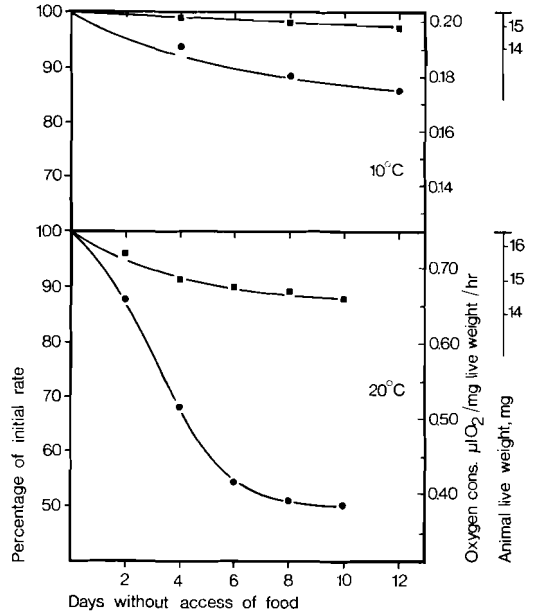


Fig. 2. Variations in body weight (■) and oxygen consumption (●) in *P. palustris* during fasting at 10°C and 20°C.

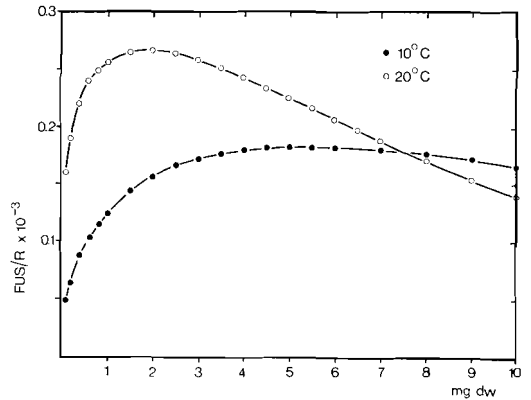


Fig. 3. FUS/R index in *P. palustris*.

Table VII. Oxygen consumption during day and night measurements in *P. palustris*. Laboratory animals. n = number of determinations.

t°C	n	mg dw (S.D.)	Oxygen consumption		REL		Night reduction in %
			$\mu\text{l O}_2/\text{mg dw/hr}$ (S.D.)		cal/animal/24 hrs		
			Day	Night	Day	Night	
10	6	4.68 (0.36)	0.610 (0.09)	0.525 (0.06)	0.328	0.281	14.3
20	6	4.97 (0.40)	1.327 (0.11)	1.050 (0.90)	0.750	0.596	20.5

Table VIII. Compilation of measurements of oxygen in hunting spiders carried out by various authors.

Species	Acclimation t°C	Experimental t°C	$\mu\text{l O}_2/\text{mg lw}/\text{hr}$	Q_{10} (temp. int., t°C)	REL/ mg dw/ 24 hrs	REL in % of energy content	Author
<i>Pardosa lenta</i> (Hentz)	10	10	0.031 ^a				Anderson 1970
" " "	ad.10	20	0.117 ^a	3.77 (10-20)			" "
<i>Phidippus regius</i> (C.L.K.)	♀♀ 10	10	0.028 ^a				" "
" " "	10	20	0.099 ^a	3.54 (10-20)			" "
Lycosidae, 3 species		15-30	0.1-1.5		0.028-0.40	0.48-6.85	Breymeyer 1967
<i>Pardosa pseudoannulata</i>	10-25	29			0.15 ^d	2.6	Ito 1964
<i>Pardosa T-insignita</i> (Bos & Str.)		15-25		2.85 (15-25) ^b			Miyashita 1969
				1.59 (") ^c			
				2.22 average			
<i>Pardosa rubida</i> (Walk.)	15	15	0.72				Van Hook 1971
" " "	20	20	0.96	2.07 (15-25)	0.11		" " "
" " "	25	25	1.49				" " "
<i>Tarentula kochi</i> Keyserling		20	0.25	2.3 (15-25)			Hagstrum 1970

a) measurements done in periods of low activity; b) animals at rest; c) active animals; d) fasting animals

Low oxygen uptake in eggs (cf. Table III) has been shown in the orthopteran *Chorthippus parallelus* (Zett.) (Gyllenberg 1969).

Laboratory animals

Day measurements

The laboratory population was exposed to artificial light, temperature, and feeding conditions for a long period. Consequently energy metabolism in those animals cannot be compared directly to values obtained from the field animals. It is, however, of interest to investigate the effects of a long acclimation period on the animals. In Fig. 4 oxygen consumption during daytime of field and laboratory animals of the same weight are shown at different temperatures. The curve has shifted towards the right in laboratory animals. This can be interpreted as a reduction in compensation ability to low temperatures (Scholander et al. 1953). It may also be an effect from acclimation to a constant laboratory temperature and a thereby reduced amplitude of diurnal activity.

Larger spiders have higher Q_{10} than smaller ones. Animals having low Q_{10} will show a smaller metabolic response to temperature fluctuations in their environments than animals with a relatively higher Q_{10} . This may

be interpreted as a wider temperature range of optimal physiological activity in the smaller instars of *P. palustris*, and may increase their possibilities to complete development in this harsh environment. Rao & Bullock (1954) claim that adaptation in respiratory Q_{10} occurs, and present data showing that within physiologically normal temperature ranges it usually increases with age. Tribe & Bowler (1968) have shown that Q_{10} is also dependent on acclimation temperature. Scholander et al. (1953) concluded that one should always look for responses to different environmental temperatures in the position of the temperature/oxygen consumption curve. They doubted whether Q_{10} is subject to acclimation or adaptation. Adaptations to low temperatures consequently always will move the curve towards the left. This view may be correct in environments where diurnal amplitude in temperature is small, e.g. in arctic regions (Remmert & Wisniewski 1970, Remmert & Wunderling 1970). In alpine regions with great diurnal temperature fluctuations, a low respiratory Q_{10} may be advantageous in addition to increased metabolism at low temperatures. It is important to consider the differences between arctic and alpine climates, each of them demanding different powers of adaptation in animals.

There are no literature data to indicate that low Q_{10} in juvenile spiders is a common phenomenon, or that an adaptation to diurnal temperature fluctuations occurs.

Bertalanffy (1957) has described three species-specific types of dependence between metabolic rate and body weight expressed by different b . 1. Metabolic rate follows the surface rule: $b = 2/3$. 2. Metabolic rate is proportional to body weight: $b = 1$. 3. Intermediate to 1. and 2.

Hemmingsen (1960) stated that at 20°C there is a universal $b = 0.75$ in most organisms, ectotherms, endotherms, and even beech trees (*Fagus* sp. L.). This corresponds to the intermediate metabolic type of Bertalanffy. This generalization seems a little wide and data compiled by Prosser (1973) seem to support Bertalanffy's model.

At 20°C $b = 0.75$ in *P. palustris* (Table VI), showing that the metabolic rate is of Bertalanffy's 3. type. b also increases with increasing temperature in *P. palustris*, indicating a shift in metabolism from surface to weight dependence. Variations in b , increasing or decreasing with increasing temperature, have been demonstrated in other species (Prosser 1973). Miyashita (1969) found $b = 0.97$ in *Pardosa T-insignita* (Boes. et Str.) at 25°C. This corresponds to the value in *P. palustris* : $b = 0.91$. Van Hook (1971) ob-

tained a regression coefficient of 1.24 in *P. rabida*. This value is rather high and is beyond the range of most known data. Zeuthen (1953) claims that the total amount of enzymes, metabolites, and inhibitors controlling the metabolic processes will increase less than the total protoplasm. As a general

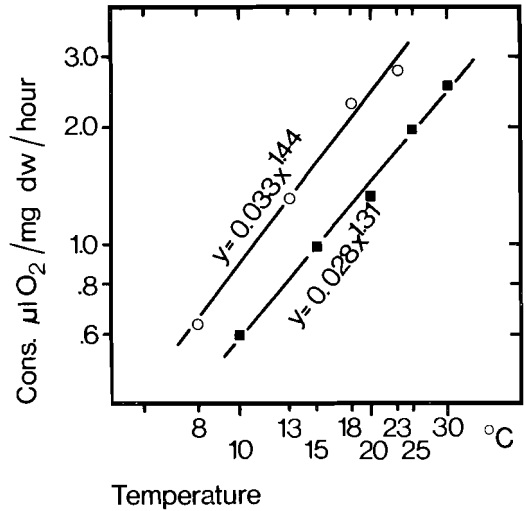


Fig. 4. Graph showing the shift in the oxygen consumption/temperature curve in *P. palustris* after acclimation to constant laboratory temperature. \circ : field rate, \blacksquare : laboratory rate. Animal dw 4.69 mg.

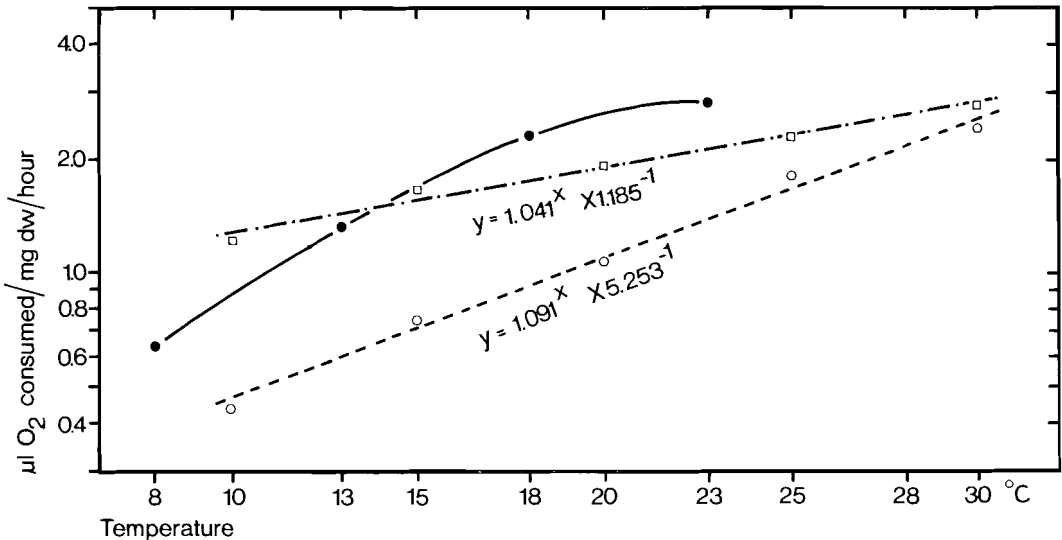


Fig. 5. Temperature/oxygen consumption relationship in *P. palustris*. \square - - - - \square : acclimated animals weighing 1 mg dw; \circ - - - - \circ : acclimated animals weighing 10 mg dw; \bullet - - - \bullet : non-acclimated animals weighing 4.7 mg dw, curve fitted by eye.

rule the regression coefficient never exceeds 1, and when this happens it is within narrow size ranges, and caused by other factors than size as such. A b higher than 1 means in fact that the animal metabolizes to self-destruction.

The presented data of night energy metabolism in *P. palustris* does not allow an estimation of REL where diurnal variations are incorporated (Table IV). Smaller animals lose more energy through metabolism according to total energy content than greater animals, but the difference is reduced with increasing temperature.

Night measurements

Diurnal variations in energy metabolism confirm field observations of the restricted daytime activity of *P. palustris* at Hardangervidda, and show that the animals have maintained the same pattern in the laboratory.

Anderson (1970) found a 40% reduction in diurnal oxygen consumption during periods of reduced activity in *Phidippus regius* (C. L. Koch). Hagstrum (1970) measured a reduction in night energy metabolism of ca. 8% in *Tarentula kochi* Keyserling.

Oxygen consumption during fasting

Variations in energy metabolism during fasting conditions in *P. palustris* resemble the patterns in *P. T-insignita* (Miyashita 1969) and the collembole *Onychiurus fimatus* (Gisin) (Zinkler 1966). Miyashita made his experiments at 25°C, and registered a little higher reduction in oxygen consumption than observed in *P. palustris*. In both species energy metabolism stabilized at a reduced level after 6–7 days.

The respiratory coefficient (RQ) was not measured during the experiment, and may have altered during the fasting period. Richman (1958) showed that in *Daphnia pulex* (De Geer) RQ fell from 1.13 to 0.75 during six days fasting. This indicates a shift from carbohydrate to fat/protein metabolism (Florey 1966). The spiders' diet, consisting mainly of proteins and fats, should not cause any great changes in RQ during fasting. In his experiment Richman (1958) did not find any significant variations in oxygen consumption during one week of fasting conditions in *D. pulex*.

Differences in energy metabolism calculated from feeding experiments and measured by respirometer

Steigen (1975b) calculated energy metabolism of individual spiders from feeding experiments at 20°C carried out on all instars of *P. palustris*, and obtained the equations:

$$\text{Females: } y = 1.18 x^{0.75} \quad r = 0.99p < 0.001$$

$$\text{Males: } y = 1.16 x^{0.75} \quad r = 0.99p < 0.001$$

$y = \mu\text{l O}_2$ consumed/spider/hour, $x =$ animal dw.

The energy metabolism calculated from feeding experiments is approx. 40% lower than that obtained by respiratory measurements during daytime on the same animals (Fig. 1). These differences can be explained by diurnal variations in oxygen consumption and variations in feeding rate during the feeding experiments. The regression coefficient b is nearly identical in the two cases, showing that the discrepancy is identical at all instars of *P. palustris*. During the feeding experiments, the production in the laboratory population was close to the production in the field population at Hardangervidda (Steigen 1975b). This shows that the energy metabolism calculated from the feeding experiments may be applicable to the field population.

Ejecta/oxygen consumption relationships

At 10°C the FUS/R index increases with weight and stabilizes in animals greater than 3–4 mg dw (Fig. 3). This is caused by the fact that oxygen consumption has a higher increase in small animals than ejecta production.

At 20°C the index has a maximum in animals weighing approx. 2 mg dw. This is the weight group having the highest growth rate (Steigen 1975b) during the life cycle in *P. palustris*. At this weight too, morphological differentiation of the two sexes occurs. If the assumption that ejecta production reflects consumption and assimilation rates is correct, the curves in Fig. 3 indicate that the relationship between production and energy metabolism with increasing/decreasing temperature is not linear.

Effects of temperature on oxygen consumption

Various mathematical expressions have been suggested to give the best fit to the temperature/oxygen consumption relationship. Krogh

(1914, 1916) presented an empirical expression and the current view is that his formula gives the best estimate of energy metabolism at various temperatures. Ivleva (1973), however, points out that Arrhenius – Van't Hoff's law shows the best fit to measurements of oxygen consumption in an ectothermous animal at different temperatures. She asserts that a deviation from this formula is an effect from insufficient acclimation of animals to experimental conditions. She also showed that especially with transference to low temperatures, acclimation is a slow process, taking a minimum of 6–8 days. Most measurements of oxygen consumption have been carried out without a proper period of acclimation, e.g. the experiments from which Krogh derived his empirical formula. Sometimes the investigators even impose different temperatures upon the animal during the same experiment, only offering the experimental apparatus a short period of acclimation. Ivleva (1973) worked with marine ectotherms, but her conclusions may also be valid in animals from terrestrial environments. On the other hand, Wieser & Kanwisher (1960), working on the marine nematode *Enoplus communis* Bastian, found no differences in energy metabolism immediately after extraction or after a period of acclimation.

If the temperature/oxygen consumption curve follows Arrhenius–Van't Hoff's law, an exponential graph with temperature on the linear abscissa will yield a straight line.

The curves in Fig. 5 show that the deviations from the straight line in animals acclimated to constant temperature conditions for 2–3 months are small. The increase in energy metabolism with increasing temperature seems to follow Arrhenius–Van't Hoff's law. Animals acclimated for two days to laboratory conditions show a more deflected pattern, indicating a too short period of acclimation.

Hence the data for *P. palustris* seem to support the conclusion of Ivleva (1973) that oxygen consumption in ectotherms follows Arrhenius–Van't Hoff's law with increasing/decreasing temperature as any chemical process.

All animals are to a certain degree genetically adapted to their particular environment, and also a substantial acclimation occurs. Ivleva (1973) showed that after a period

of laboratory acclimation the animals obtained a 'steady state' in energy metabolism at those constant conditions.

Most animals are, however, adapted and acclimated to a diurnally and seasonally fluctuating environment. Ethological patterns may play a significant part in reducing the effects from environmental variations imposed on the animal. Under laboratory conditions those fluctuations are reduced to almost nil, and so is nearly every environmental stimulus, abiotic or biotic. This may render a significant stress to the animal, very difficult to evaluate. If the *change* in temperature is the main factor causing pre-acclimation effects, one might presume that animals from arctic climates will require a longer acclimation period than animals from alpine areas. The latter are more or less adapted to abrupt changes in temperature. On the other hand, if it is the transference from a *fluctuating* to a *constant temperature* which is the main stress factor, animals from the arctic should need a shorter period of acclimation. One must assume, however, that the animals are acclimated to experimental temperatures that are ecologically relevant and not beyond the temperature range which the animals may be subject to in the field.

There are great variations in oxygen consumption according to weight, diurnal activity, hunger, respirometer stress, etc. Consequently one must be very cautious when using respirometer techniques in investigations of animal productivity. Feeding experiments, although laborious, seem to be a better method if they can be proved to reflect field conditions in an acceptable way. The main problem during feeding experiments in the laboratory is 'overweight', a situation probably not often found in the field. Respiratory techniques seem to have their best applicability in acclimation/adaptation investigations in animals from different environments, or when investigating responses to environmental stress in closely related organisms.

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Altitudinal zonation of the invertebrate fauna on branches of birch (*Betula pubescens* Ehrh.)

SIGMUND HAGVAR

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

The invertebrate fauna on branches of birch (*Betula pubescens* Ehrh.) was investigated during 1967 at Sogndal, western Norway, by sweep-netting at the following altitudes: 10-40 m, 250-300 m, 450-500 m, 650-700 m, and 850-900 m. From the lowest to the highest station, the following numbers of Heteroptera species were recorded: 12, 5, 4, 3, 0; of Cicadidae: 11, 10, 7, 3, 2; of Coleoptera: 21, 16, 18, 13, 8; and of Araneida: 9, 5, 8, 2, 1. The generally low number of species above 500 m accompanies a change from mixed forest to an almost purely birch forest. The density of Araneida, Heteroptera, and *Anthocoris nemorum* (L.) (Het.) decreased greatly with increasing altitude. Cicadidae showed similar densities up to 500 m, but markedly lower densities above. Psocoptera was most numerous in the middle of the gradient. Predators and parasites collectively decreased greatly in density with increasing altitude. Total invertebrate densities were lowest above 500 m. The material that year was dominated by larvae of Geometridae (Lep.), which had a mass occurrence during 1966-67. Trophic relationships at different altitudes are discussed.

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Some invertebrate groups have been investigated with respect to the altitudinal zonation of their species composition. Among these investigations are Lindberg's (1945) study of the Heteroptera-fauna in the mountains of Bulgaria, Lindroth's (1949) study of Carabidae (Col.) in Scandinavia, a study of the same group by Ponomarchuk (1963) in the Carpathes, a study of the zonation of Lamellicornia (Col.) species by Pek (1961) in the Kirgisia Mountains north of the Himalayas, and Kopaneva's (1962) work on Orthoptera in the Caucasian Mountains. The general trend seems to be that, within a given taxonomic group, the number of species decreases with increasing altitude. This is, however, not always the case. In a study of Araneida in Chile, Zapfe (1961) found the highest number of species in the middle ranges of the gradient.

Most species seem to have a vertical occurrence which includes the lowlands and is limited upwards. A few species may be endemic for high altitudes. Species endemic to certain sections of the altitudinal gradient

have been identified in Orthoptera by Pravdin (1965) and in Lepidoptera by Kuznetsov (1958). The vertical occurrence of a given species is usually continuous, but the density may vary much over the range of occurrence.

In most such studies, the intention has been to record the total number of species at different altitudes. The altitudinal zonation of the total number of species depends on many factors, among which the altitudinal zonation of vegetation communities is of high importance. However, if the habitat could be kept relatively constant, the changes in species composition would mainly be a response to changing climate. Of course, biotic factors such as predators, parasites, or competing species may still be relevant. However, maintaining constant habitat greatly standardizes the situation.

In this study, branches of birch (*Betula pubescens* Ehrh.) were chosen as the habitat. The field work was performed during 1967 on a rather steep mountain slope near Sogndal, Sogn og Fjordane County, in the western part of South Norway. That year, the density



Fig. 1. Part of the forest at the lowest station, 10–40 m a.s.l. The most common tree species besides birch are *Prunus padus* L., *Sorbus aucuparia* L., and *Tilia cordata* Mill.

of geometrid larvae (Lep.) on birch was especially high. The data achieved on the altitudinal zonation of geometrid larvae has been published earlier (Hågvar 1972). The present paper deals with the altitudinal zonation of the species composition within Araneida, Heteroptera, Cicadidae, and Coleoptera. An analysis of the altitudinal zonation of the density is also presented, which covers all invertebrate groups recorded. Some information is given on the trophic structure of the invertebrate fauna at the respective altitudes.

MATERIAL AND METHODS

Five stations were chosen, one at each of the following altitudes: 10–40 m, 250–300 m, 450–500 m, 650–700 m and 850–900 m. The timber line is at 900 m. The photos in Figs.

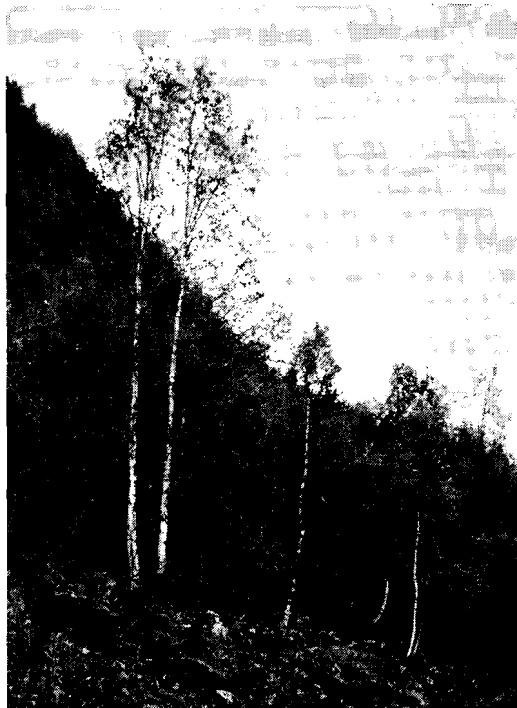


Fig. 2. Part of the forest at the second station, 250–300 m a.s.l. Epiphytic lichens on birch are more common than at sea level. Other tree species are *Sorbus aucuparia*, *Populus tremula* L., *Alnus incana* (L.), *Pinus silvestris* L., and *Juniperus communis* L.

1–5 show representative views of each station. The actual 'habitat' is not quite constant throughout the gradient. At the upper part of the slope, the trees grow more slowly, are smaller, are more covered with epiphytic lichens, and often have crooked stems because of larger seasonal accumulation of snow.

Invertebrates were collected from branches on the lowest three metres of the trees by a sweep-net, as described by Zubareva (1930). For each sampling at a given station, a new group of trees was chosen. The net was used on all sides of each tree. The effectiveness of the sweep-net may be somewhat different for different taxonomic groups, but the method gives a picture of the composition of the total invertebrate fauna. Within a given species or group, the method is less selective. At each collection, from 100 to 400 sweeps were made. The density of animals is given as number per 100 sweeps. Acarina and Collembola were not collected.



Fig. 3. Part of the forest at the third station, 450–500 m a.s.l. Among the birches are some *Sorbus aucuparia*, *Prunus padus*, *Alnus incana*, *Pinus silvestris*, and *Juniperus communis*.

The weather conditions were favourable (without wind or rain) during all collections. Collection dates were: 10–40 m a.s.l.: 14 May, 15 June, 13 July, 27 July and 1 September; 250–300 m a.s.l.: 15 May, 16 June, 14 July, 28 July and 2 September; 450–500 m a.s.l.: 19 May, 17 June, 15 July, 29 July and 4 September; 650–700 m a.s.l.: 24 June, 16 July, 1 August and 5 September; 850–900 m a.s.l.: 17 July, 5 August and 6 September.

A total of 9384 invertebrates were collected.

RESULTS

Altitudinal zonation in number of species

Tables I–III show at which altitudes the different species from the four groups mentioned were recorded. A few species not naturally occurring on birch are excluded in the tables. The data is based on the 68 adult Heteroptera collected, and some of the larvae, on the 377 adult Cicadidae, the 497 adult Coleoptera, and 183 of the Araneida, in-

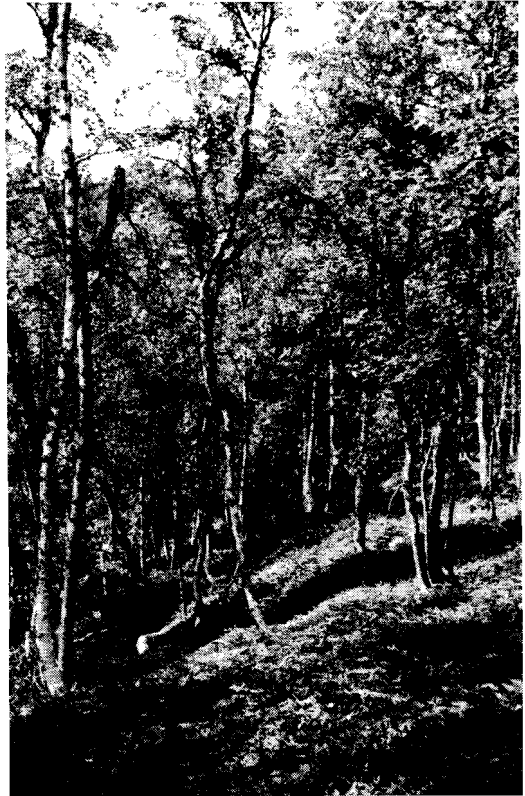


Fig. 4. Part of the forest at the fourth station, which at this altitude, 650–700 m a.s.l., is an almost pure birch forest. A few specimens of *Sorbus aucuparia*, *Populus tremula*, *Pinus silvestris* and *Juniperus communis* occur. The birch stems are often more or less crooked due to rather large amounts of snow.

cluding all adults and some of the juveniles.

No species of Heteroptera and only a few species of the other groups were recorded at the timber line. In all groups, the greatest number of species was found at the lowest station, and the lowest number at the highest station.

The number of Heteroptera species recorded dropped rapidly with increasing altitude. Among Cicadidae, the number of species decreased more gradually, but most slowly in the beginning. As for Coleoptera and Araneida, the number of species recorded at the second lowest station was somewhat lower than at the two neighbouring stations. In Coleoptera, the number dropped evenly from the middle to the uppermost station. In Araneida, the two uppermost stations showed



Fig. 5. Part of the forest at the fifth and upper station, 850–900 m a.s.l., just below the timber line. The branches and stems may be rather densely covered by lichens. Large amounts of snow at this altitude have resulted in markedly crooked stems. Scattered *Juniperus communis* and *Betula nana* L. occur.

low numbers of species compared with the three lowest stations.

Probably the picture of zonation becomes more correct if we assume that the vertical distribution of each species is continuous. By filling such empty holes in Tables I–III, the number of Coleoptera species from the lowest to the highest station becomes: 21, 21, 20, 14, 8 and of Araneida species: 9, 8, 8, 2, 1. If we furthermore assume that all species listed may occur down to sea level, the number of species is as follows: Heteroptera: 13, 6, 4, 3, 0; Cicadidae: 12, 10, 7, 3, 2; Coleoptera: 31, 27, 24, 14, 8 and Araneida: 15, 11, 9, 3, 1.

These corrections do not change the zonation pattern in Heteroptera and Cicadidae. They do, however, indicate that the number of Coleoptera and Araneida species is not markedly changed in the lower half of the gradient, but clearly lower in the two uppermost stations.

According to Ossiannilsson (pers. comm.),

Table I. The occurrence of different species of Hemiptera (Heteroptera and Homoptera Cicadidae) on branches of birch (*Betula pubescens*) at different altitudes (m a.s.l.). "sp." denotes that the genus has been recorded.

	10-40	250-300	450-500	650-700	850-900
Heteroptera					
<i>Anthocoris nemorum</i> (L.)	x	x	x	x	
<i>Psallus betuleti</i> (Fall.)			x		
<i>Psallus falleni</i> Reuter	x	x	x		
<i>Temnostethus gracilis</i> Horvath	x	x	x		
<i>Stenodema holzatum</i> (Fabr.)	x	x			
<i>Loricula pselaphiformis</i> Curtis	x				
<i>Lygocoris contaminatus</i> (Fall.)	x				
<i>Blepharidopterus angulatus</i> (Fall.)	x				
<i>Psallus ambiguus</i> (Fall.)	x				
<i>Acalypta carinata</i> (Panzer)	x				
<i>Elasmucha grisea</i> (L.)	x				
<i>Elasmostethus interstinctus</i> (L.)	x				
Additional species (Larvae)	1	1		2	
Total number of species	12	5	4	3	0
Homoptera, Cicadidae					
<i>Oncopsis flavicollis</i> (L.)	x	x	x	x	x
<i>Oncopsis tristis</i> (Zett.)	x	x	x	x	x
<i>Speudotettix subfuscus</i> (Fall.)	x	x	x	x	
<i>Oncopsis subangulatus</i> J. Sahlb.	x	x	x		
<i>Lirnavuoriana decempunctata</i> (Fall.)	x	x	x		
<i>Kybos betulicola</i> W. Wagner	sp.	x	x		
<i>Typhlocyba bergmani</i> Tullgren	x	sp.	x		
<i>Alnetoidia alneti</i> (Dahlbom)	x	x			
<i>Oncopsis planiscuta</i> (Thomson)		x			
<i>Empoasca flavescens</i> (F.)	x	sp.			
<i>Cixius cunicularius</i> (L.)	x				
<i>Cixius distinguendus</i> (Kbm.)	x				
Total number of species	11	10	7	3	2

Kybos betulicola and *Oncopsis subangulatus* (Cicadidae) are new to Norway.

In addition to the four groups mentioned, small numbers of Psyllidae were also identified. *Psylla nigrita* (Zett.) and *P. sorbi* (L.) were recorded at the three lowest stations. *P. corcontum* Sulc was found at the medium station and *P. alni* (L.) at the uppermost station. The material indicates that the Psyllidae species are limited mainly to the three lowest stations.

Altitudinal zonation of density

Figs. 6–10 show how the density of some major groups changes from May to September at different altitudes (Araneida, Heteroptera, *Anthocoris nemorum* (L.) (Heteroptera), Cicadidae and Psocoptera). The figures

Table II. The occurrence of different species of Coleoptera on branches of birch (*Betula pubescens*) at different altitudes (m a.s.l.).

	10 - 40	250 - 300	450 - 500	650 - 700	850 - 900
<i>Polydrosus undatus</i> Fabr.	x	x	x	x	x
<i>Podistra pilosa</i> Payk.	x	x	x	x	x
<i>Anthophagus omalinus</i> Zett.	x	x	x	x	x
<i>Anoplus plantaris</i> Naezen	x	x	x	x	
<i>Otiorrhynchus salicis</i> Ström	x	x	x		x
<i>Anthophagus alpinus</i> Fabr.			x	x	x
<i>Malthodes fuscus</i> Wärtl.				x	x
<i>Rabocerus foveolatus</i> Ljungh				x	x
<i>Acrotrichis rugulosa</i> Rosk.	x	x	x	x	
<i>Athous subfuscus</i> Müll.		x	x	x	
<i>Malthodes guttifer</i> Kies.	x			x	
<i>Malthodes brevicollis</i> Payk.	x			x	
<i>Malthinus frontalis</i> Mrsh.				x	
<i>Anaspis rufilabris</i> Gyll.				x	
<i>Coccinella 14-guttata</i> L.	x	x	x		
<i>Malthodes marginatus</i> Latr.	x	x	x		
<i>Anthophagus caraboides</i> L.	x	x	x		
<i>Apion simile</i> Kirby	x	x	x		
<i>Polydrosus pilosus</i> Gredl.	x	x	x		
<i>Rhagonycha limbata</i> Th.		x	x		
<i>Corymbites affinis</i> Payk.	x		x		
<i>Malthodes mysticus</i> Kies.	x		x		
<i>Podistra rufotestacea</i> Letzn.	x		x		
<i>Malthodes spathifer</i> Kies.			x		
<i>Deporaus betulae</i> L.	x	x			
<i>Dolopius marginatus</i> L.	x	x			
<i>Coeliodes rubicandus</i> Hbst.		x			
<i>Schizotus pectinicornis</i> L.	x				
<i>Rhinosimus planirostris</i> Fabr.	x				
<i>Cis alni</i> Gyll.	x				
<i>Phytodecta intermedius</i> Hellies.	x				
Total number of species	21	16	18	13	8

include larval or juvenile stages. For simplicity, the altitudes are denoted as 0, 300, 500, 700 and 900 m a.s.l.

Characteristic for Figs. 6-8 is a decreasing density with increasing altitude. In no case was the maximum density found to be higher at a given altitude than at any lower station. There is a great difference in maximum density between the lowest and the uppermost station at which a group was recorded. The maximum density of imagines in Heteroptera (Fig. 7, vertical lines) and in *A. nemorum* (Fig. 8, vertical lines) also decreases with increasing altitude.

In Cicadidae, both the total density and the

Table III. The occurrence of different species of Araneida on branches of birch (*Betula pubescens*) at different altitudes (m a.s.l.).

	10 - 40	250 - 300	450 - 500	650 - 700	850 - 900
<i>Araneus patagiatus</i> Cl.					x
<i>Lepthyphantes expunctus</i> (Cambr)		x	x	x	
<i>Araneus cucurbitinus</i> Cl.	x	x	x	x	
<i>Linyphia peltata</i> Wider.			x		
<i>Pityohyphantes phrygianus</i> (Koch)			x		
<i>Lepthyphantes obscurus</i> (Blw.)	x		x		
<i>Helophora insignis</i> (Blw.)	x		x		
<i>Dictyna pusilla</i> Thorell	x		x		
<i>Theridion pallens</i> Blw.	x	x	x		
<i>Philodromus aureolus</i> (Cl.)		x			
<i>Meta segmentata</i> (Cl.)		x			
<i>Anyphaena accentuata</i> (Walck.)	x				
<i>Theridion varians</i> Hahn	x				
<i>Bathypantes nigrinus</i> (Westr.)	x				
<i>Lepthyphantes alacris</i> (Blw.)	x				
Total number of species	9	5	8	2	1

density of imagines were similar for all three of the lowest stations, but clearly lower at the two uppermost stations (Fig. 9). Psocoptera (Fig. 10) showed a very high maximum density at the second and third station relative to the density at sea level and in the highest part of the gradient.

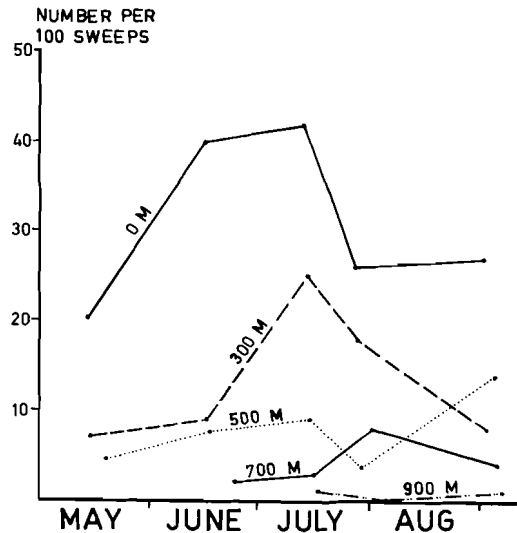


Fig. 6. Density of Araneida, given as number per 100 sweeps, during summer at different altitudes.

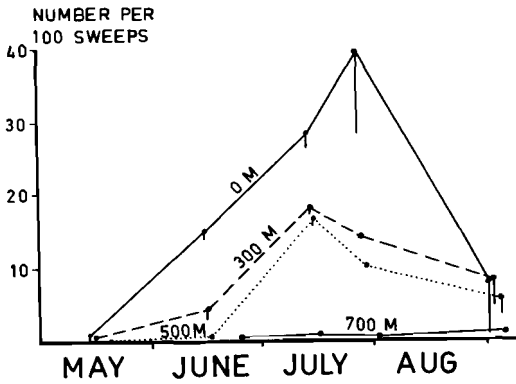


Fig. 7. Density of Heteroptera, given as number per 100 sweeps, during summer at different altitudes. Heteroptera were not recorded at 900 m a.s.l. Length of vertical lines denotes the density of imagines.

The seasonal variations in density at different altitudes of the other groups recorded are shown in Table IV, together with the total catches of invertebrates. Some groups are so sparsely represented in the actual habitat that the material gives no good picture of their altitudinal zonation, but merely their presence at certain altitudes (viz. Opiliones, Ephemeroptera, Plecoptera, Thysanoptera,

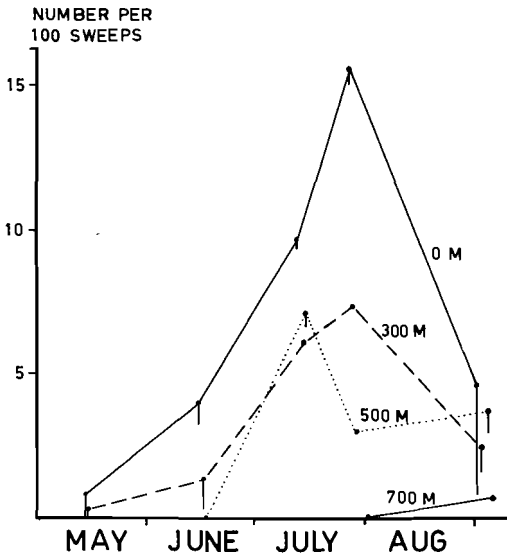


Fig. 8. Density of *Anthocoris nemorum* (Heteroptera), given as number per 100 sweeps, during summer at different altitudes. The species was not recorded at 900 m. Length of vertical lines denote the density of imagines.

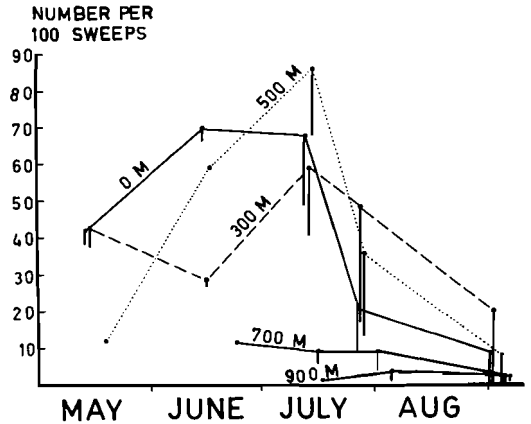


Fig. 9. Density of Cicadidae (Homoptera), given as number per 100 sweeps, during summer at different altitudes. Length of vertical lines denote the density of imagines.

Neuroptera, Trichoptera, Hymenoptera symphyta, insect larvae and pupae).

The maximum density of Aphidae recorded at the four lowest stations is very similar (11–16 animals per 100 sweeps), but a much higher density (112) was recorded at the uppermost station in July. This may have been a local phenomenon. Some three weeks later the density was again low, but the density of Formicidae was then high (48), probably as a response to the peak in aphid density.

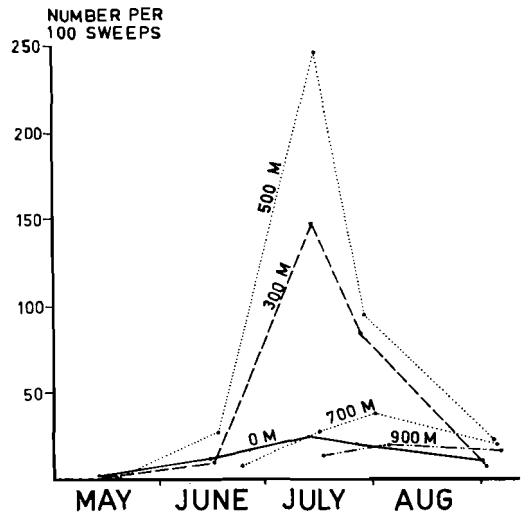


Fig. 10. Density of Psocoptera, given as number per 100 sweeps, during summer at different altitudes.

Table IV. Number of invertebrates collected per 100 sweeps with a sweep-net on birch (*Betula pubescens*) during different months (from May to September) and at different altitudes. The actual collecting dates are given in "Material and methods". The following groups have been excluded in the table, as their densities are presented elsewhere: Araneida (Fig. 6), Heteroptera (Fig. 7), Cicadidae (Fig. 9) and Psocoptera (Fig. 10). These groups are, however, included in "TOTAL CATCHES". All figures are calculated to the nearest whole number.

Altitude	10 - 40 m					250 - 300 m					450 - 500 m					650 - 700m				850 - 900 m							
	Month	M	J	J	J/A	S	M	J	J	J/A	S	M	J	J	J/A	S	J	J	J/A	S	J	J/A	S				
Opiliones					1	4					4	1	2			4	2	3			1	2	2			1	
Ephemeroptera				1	1																					1	
Plecoptera							1	1		1				<1	2	2	1	1							20	5	2
Thysanoptera								1						1	2	7					<1						
Homoptera:																											
Aphididae		2	16	8	12	15	<1	4	5	14	6			3	8		14			<1	4	11	2		112	8	1
Psyllidae				118	7				1	2				1		1	1	1									1
Hemiptera, total		45	102	222	81	32	43	37	83	80	34	13	62	112	48	28	12	13	20	5				113	12	3	
Neuroptera					1	2				1	3			1		1											1
Trichoptera					3																						
Microlepidoptera		1	1	6	19	1		1	2	15	4			1		1						1	1				
Coleoptera:																											
Cantharidae				19	4	4			1	4				1	6	2					2	4					1
Staphylinidae				19	4	13				17	12	3			49	30	2				4	14			7	14	
Curculionidae		1	12	6	10	2	1	5	12	8			2	7	6	2	1	3	2	4				5	3		
Other Coleoptera			4		1	3	<1	5	1	1	1		1	2		1	<1	1	1	1						1	
Coleoptera, total		1	16	44	19	23	2	10	34	21	3	3	64	38	4	1	10	21	5					12	18		
Diptera:																											
Brachycera			7	26	8	5		8	24	14	6		13	28	15	5	6	7	14	3				14	10		
Cyclorrhapha		1	30	14	15	10	1	9	14	22	9		10	12	14	19	10	6	7	2				3	7	1	
Nematocera		53	109	78	32	9	11	33	60	55	12	2	185	47	10	21	46	8	14	7				8	3	5	
Diptera, total		54	146	118	55	24	12	49	98	91	27	2	207	86	38	45	62	21	35	12				25	19	6	
Hymenoptera:																											
Formicidae								2												<1	2					48	3
Hym. parasitica		9	18	19	9	21	2	11	6	10	21	<1	6	1	10	8	6	3	2	4				5	5	1	
Hym. symphyta				1				1													<1				1		
Hymenoptera, total		9	19	19	9	21	2	13	6	10	21	<1	6	1	10	8	7	5	2	4				6	53	4	
Larvae, Geometridae (Lep.)		30	636	3		5	49	1792	45	2		10	1188	217	11		123	32	6					384	11		
Insect larvae (not Lep.)		<1	7	5	1	6		1	11	1			1	1	2	1					1					1	2
Insect pupae			1	5	3	3		1	5	5	5		1		3	2					2	5	3		1	3	2
TOTAL CATCHES		161	979	493	235	158	115	1921	463	329	115	32	1505	752	251	128	216	118	138	46				575	140	36	
Total catches except																											
larvae of Geometridae		131	343	490	235	153	66	129	418	327	115	22	317	535	240	128	93	86	132	46				191	129	36	

Psyllidae, generally sparsely represented throughout the gradient, showed a high density at sea level in July. This was due to a mass occurrence of *P. sorbi*, probably repre-

senting a local and temporary aggregation. The data on Microlepidoptera may indicate that this group occurs mainly in the lower part of the gradient. Hymenoptera parasitica

were recorded in all collections, with the densities being highest at the lower stations.

Brachycera and Cyclorrhapha, from among the Diptera, showed very similar maximum densities at each given altitude. The maximum density within each group varied between 19 and 30 animals per 100 sweeps at the three lowest stations and was somewhat lower (7–14) at the two uppermost stations. Nematocera appears to be well represented in the defined habitat. The density of this group varied greatly at the first, third and fourth station throughout the season, probably depending upon varying swarming activity. Only very low densities were, however, recorded at the upper station. Total Diptera density was greatest at the three lowest stations.

Cantharidae, Staphylinidae, and Curculionidae were the dominant coleopterous groups. While the catches of Cantharidae and Curculionidae indicate a slightly higher density in the lower part than in the upper part of the gradient, Staphylinidae were most numerous at the middle station. The material of this last group consisted of three *Anthophagus* species, which are typical inhabitants of birch (Strand; pers. comm.). *A. omalinus* preferred the medium range of the gradient, with the following maximum densities per 100 sweeps from the lowest to the highest station: 7, 16, 48, 13, 14. Corresponding numbers for *A. caraboides* were 16, 3, 2, 0, 0, indicating a preference for the lower part, and for *A. alpinus*: 0, 0, 1, 1, 6, indicating a preference for the upper part of the gradient. As shown in Table IV, the total density of Coleoptera did not change greatly throughout the gradient. The two upper stations had the lowest maximum densities, and the highest density was recorded at the middle station.

Hemiptera collectively showed rather high maximum densities at all altitudes except 650–700 m.

The maximum total density of invertebrates recorded at each altitude depended wholly upon the occurrence of geometrid larvae. At their maximum density, the latter group made up the major part of the invertebrate material throughout the gradient. For both geometrid larvae and invertebrates as a whole, the sequence of stations with decreasing maximum total density was: 250–300 m, 450–500 m, 10–40 m, 850–900 m and 650–700 m.

If we exclude the geometrid larvae, the plot of total invertebrate densities across the season at the three lower stations is much the same (Table IV). The values at the two uppermost stations are clearly lower, however, and rather similar. At the time of maximum invertebrate density at each level, different groups dominated when geometrid larvae were disregarded, as follows: Psyllidae, 24% at 10–40 m; Psocoptera, 35% at 250–300 m; Psocoptera, 46% at 450–500 m; Psocoptera, 29% at 650–700 m; and Aphidae, 59% at 850–900 m.

The main conclusion that can be made concerning altitudinal zonation in total density is that the two uppermost stations showed clearly lower densities than any of the three lowest stations, both when geometrid larvae are included and when they are not.

A short description of the invertebrate fauna characteristic to each altitude

The fauna collected at each altitude can be characterized as follows:

10–40 m: Highest recorded number of species among Heteroptera, Cicadidae, Coleoptera, and Araneida. Highest maximum density of Heteroptera in general, of the species *Anthocoris nemorum*, and of Araneida. Probably preferred altitude of *Anthophagus caraboides* (Col., Staphylinidae).

250–300 m: Highest maximum density of invertebrates and highest degree of defoliation in the gradient, mainly caused by larvae of *Operophtera* sp. (Lep., Geometridae), which prefer this altitude. Relatively high maximum density of Psocoptera.

450–500 m: Highest maximum density of Psocoptera and of *Anthophagus omalinus* (Col., Staphylinidae). Lowest station at which populations of *Oporinia autumnata* Bkh. (Lep., Geometridae) were recorded.

650–700 m: Overlapping zone between geometrid larvae of *O. autumnata* and *Operophtera* sp. Lowest maximum density of invertebrates and of geometrid larvae. Lowest degree of defoliation. Few species of Araneida, Heteroptera, and Cicadidae.

850–900 m: Absence of Heteroptera. Lowest number of species from among Cicadidae, Coleoptera, and Araneida. Low maximum density of invertebrates. Preferred altitude for larvae of *O. autumnata*, and probably of *Anthophagus alpinus* (Col., Staphylinidae).

Trophic relationships at different altitudes

Although the effectiveness of the method may be somewhat different for different groups, it is of interest to analyze roughly the catches in view of the trophic position of the invertebrates. The recorded fauna can be divided into three trophic groups:

1. *Birch leaf or sap feeders*: Thysanoptera, Homoptera, Heteroptera except the predatory species mentioned below, the coleopterous families Curculionidae, Elateridae and Chrysomelidae, Lepidoptera larvae, larvae of Hymenoptera symphyta and probably a few other insect larvae recorded. 2. *Feeders on fungi, lichen, excrements or detritus and non-feeders on birch*: Diptera adults; Psocoptera; Trichoptera; Ephemeroptera; Plecoptera; the coleopterous families Cisitidae, Ptiliidae, probably the actual Staphylinidae, Cantharidae and Heteromera; imagines of Lepidoptera and of Hymenoptera symphyta; Formicidae (probably eating excrements of aphids); larvae of Dermoptera and insect pupae. 3. *Predators and parasites*: Araneida, Opiliones, Hymenoptera parasitica, probably the few Neuroptera imagines and larvae collected, and the following Heteroptera species: *Anthracoris nemorum*, *Temnostethus gracilis*, *Loricula pselaphiformis* and *Blepharidopterus angulatus*.

The highest density of birch leaf or sap feeders, 1836 animals per 100 sweeps, was recorded in June at the second lowest station, where the density of geometrid larvae was highest. In the actual sample, geometrid larvae made up 97.6% of this trophic category.

Psocoptera and Nematocera dominated the second trophic group (Table IV). The highest density of this category, 393 animals per 100 sweeps, was found at the middle station in July. In this sample, Psocoptera represented 63% of the group.

The density of predators and parasites was always highest at the lowest level and decreased with increasing altitude (Fig. 11). At all stations, the density changes from July to September were rather small. Araneida dominated this trophic group.

Fig. 12 shows the relative dominance of each trophic group in the different catches. Because of the dominance of geometrid larvae in early summer over the whole gradient, there is a distinction made between this group

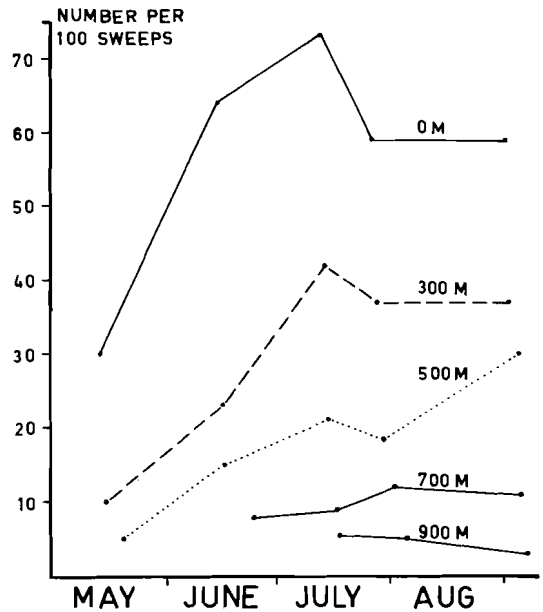


Fig. 11. Density of invertebrate predators and parasites, given as number per 100 sweeps, during summer at different altitudes.

and the rest of the first trophic category. This remainder always constituted less than 50% of the total catches. When the geometrid larvae had disappeared or was only found incidentally, this percentage remained fairly constant throughout the gradient, varying between 17 and 29.

It is a general feature of all altitudes that the second trophic group becomes dominant when the density of geometrid larvae has dropped.

Due to a rather stable density of predators and parasites at each altitude from July to September (Fig. 11) and to a general decline in total invertebrate density at all stations during the last half of the summer (Table IV), the relative dominance of predators and parasites increased at all stations during the latter period (Fig. 12). The highest percentage achieved by this trophic group, 37%, was recorded at the lowest station in September.

Of the total season's catches at each altitude, the first trophic group was represented by the following percentages, listed from the lowest to the highest station: 56, 74, 64, 43, and 72%. Corresponding values for geometrid larvae alone were 33, 64, 53, 31, and 53%, and for the rest of this trophic group 23, 10,

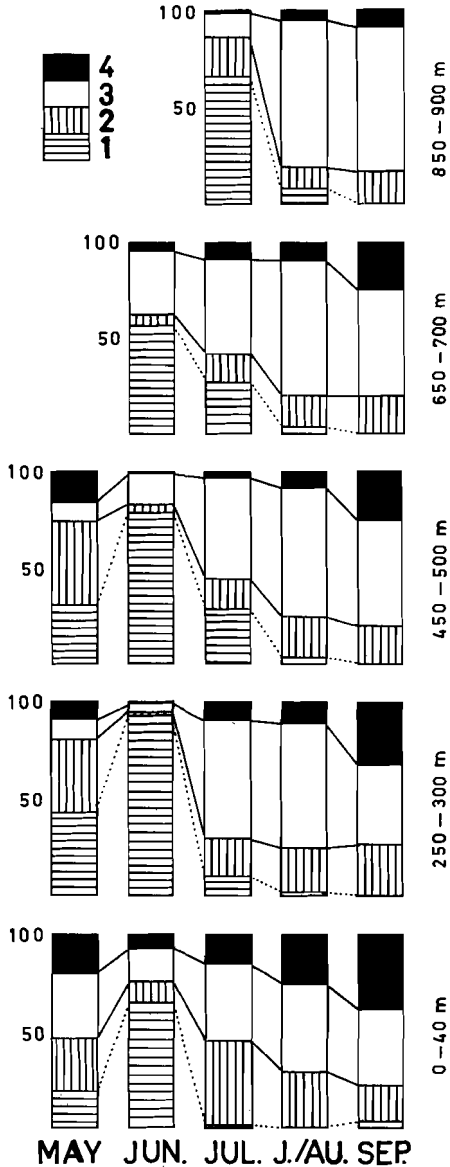


Fig. 12. Relative composition (in % of total number) of the invertebrate fauna on branches of birch during summer at different altitudes. 1: Larvae of Geometridae. 2: Other leaf or sap feeders. 3: Feeders on fungi, lichen, excrements or detritus and non-feeders on birch. 4: Predators and parasites. Further explanation in text.

11, 12, and 19%. For the second trophic group, these mean values were 29, 21, 33, 49, and 27%. For the third trophic group, they were 14, 5, 3, 8, and 2%.

If we pool all catches over the whole

gradient during the season, the mean value for the first trophic group was 65% (geometrid larvae 51% and other 14%), for the second group 29%, and for the third group 6%.

Altitudinal zonation of development

In spring, the birch leaves developed about four days later for every 100 m increase in altitude. It is reasonable to infer that this delay also retards the start of development of the invertebrate species at different altitudes. In addition, the lower mean temperatures occurring at higher altitudes will slow down the developmental rate.

Anthocoris nemorum (Heteroptera) may serve to illustrate the altitudinal zonation of development. The species overwinters as imago and lays eggs in young leaves. As shown in Fig. 13, the development of the species is delayed one larval stage between

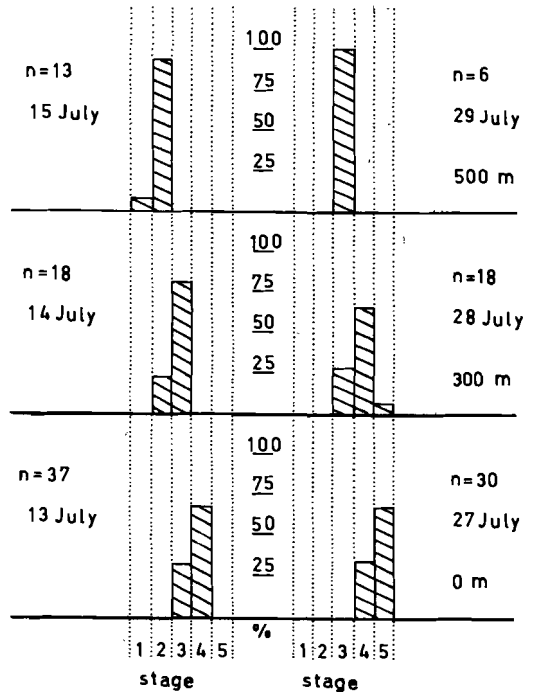


Fig. 13. Percentage distribution of larval stages in *Anthocoris nemorum* (Heteroptera) at different altitudes. Data from two samplings in July, 14 days apart, at each station. n = number of larvae.

the first and second station and between the second and third station. This is evident both when stage four dominates at sea level, and when stage five dominates fourteen days later.

DISCUSSION

The results clearly demonstrate that the invertebrate fauna on branches of birch changes with altitude. The change can be characterized by the species number and species composition; the presence, density or absence of certain groups; the preferred altitude of groups or single species; the relative dominance of groups at different altitudes; and by the total density of invertebrates.

No invertebrate orders clearly preferred the upper part of the gradient, neither by their level of highest density nor by their level of highest number of species when these were identified. Among single species, *O. autumnata* occurred mainly in the upper half of the gradient and had its highest density at the uppermost station. The preference for the timber line level is typical for the species (Tenow 1972). No other species identified, with the possible exception of *A. alpinus*, showed any clear preference for the upper two stations.

Psocoptera are characterized by mainly inhabiting the middle part of the gradient. Being to a high degree dependent on lichens as food (Landin 1967), the group would favour the higher altitudes where there is greater lichen growth on the trees. As climate, however, probably becomes less favourable with increasing altitude, it seems reasonable that a central range of the gradient may offer Psocoptera the most optimal environmental conditions.

A. omalinus, occurring at all altitudes, also prefers the centre of the range. This may, at least partly, be a result of competition with *A. alpinus* on the upper half, and with *A. caraboides* on the lower half of the mountain slope.

That the maximum observed density level of *Operophtera* sp. was in the lower half of the birch wood gradient confirms earlier observations (Tenow 1972).

All groups in which the species were iden-

tified, except the geometrid larvae (Hågvar 1972), showed a higher number of species in the lower part of the gradient than in the upper part. The groups respond differently, however, to the gradient, the number of species being reduced most rapidly among Heteroptera. Lindberg (1945) also found a strong decline in the total number of Heteroptera species over the altitudinal gradient from the deciduous forests (*silva frondosa*) in the Bulgarian mountains, through the coniferous forest belt (*silva acerosa*) to the areas above the timber line (*regio alpina*). Among 180 species recorded by him, only one species was endemic for *regio alpina*.

The number of Cicadidae species decreased rather evenly over the gradient, whereas with Coleoptera and Araneida the most marked difference occurred between the three lowest and the two uppermost stations. A general decline in the number of Carabidae species (Col.) with increasing altitude has been previously demonstrated in Scandinavia by Lindroth (1949). The relative low number of Coleoptera species in alpine habitats has also been demonstrated by Brundin (1934), Fridén (1968 and 1971), Østbye (1969), and Fjellberg (1972).

The drop in the number of species occurring from the three lowest to the two highest stations is correlated with a change in the composition of the forest. While the forest in the lower part of the gradient contains a mixture of many tree species, it becomes an almost purely birch forest above 500–600 m. This change may exclude species that prefer a more varied habitat than found in the purely birch forests.

Just as the number of species within a given animal group generally decreases with increasing altitude, the species number also usually decreases with increasing latitude, i.e., increasing distance from equator (Fisher 1960). Usually, there is a correlation between altitudinal and latitudinal distribution of single invertebrate species. Examples of such studies are those of Lindberg (1945) and Lindroth (1949). The altitudinal distribution of the present material has been compared with the known latitudinal distribution of the relevant species of Heteroptera, Cicadidae, Curculionidae, and Staphylinidae. The correlation is, however, not good. This may be explained by the fact that the direction

of the isotherms in western Scandinavia is NE to SW, probably due to the Gulf Stream.

Brinck & Wingstrand (1949) found that the subarctic Scandinavian birch forests just below the timber line have few endemic invertebrate species and should be regarded as a transition zone between the lower forests and the treeless mountain areas. The present material confirms this view.

At the three uppermost stations, no collections were made just after the birch leaves were developed in 1967. However, samplings during that same phase the next spring at 450–500 m and 650–700 m did not reveal additional species, indicating that the species composition recorded in the upper part of the gradient is representative.

It is difficult to estimate the effect of the high densities of geometrid larvae on the other part of the invertebrate fauna. It is, however, reasonable to assume that the species composition has been little if at all affected. The population density of certain leaf-eating species or groups may have been seriously affected in the zones of most heavy defoliation (Hågvar 1972). Predators and parasites of geometrid larvae may have been positively affected.

Koponen (1973) studied the density and composition of the invertebrate fauna of the mountain birch *B. tortuosa* Led. (synonymous with *B. pubescens* in the present study) at Kevo, Finnish Lapland. Birch leaf or sap feeders represented 78.7% of the total material; fungi, lichen, detritus or non-feeders 16.0%, and predators and parasites 5.4%. In the present material, there was generally a somewhat lower percentage of the first trophic group and a higher percentage of the second group. The differences are partly due to a relatively low occurrence of Psocoptera in Koponen's (1973) material (averaging 1.8% during 1971–1972). In the present material, Psocoptera were well represented even on the 'mountain birch' at the two upper stations, viz. 16% of the total catches at 650–700 m and 6% at 850–900 m. The mean percentage of parasites and predators is roughly the same in the two investigations, both over the gradient as a whole, and when the two upper 'mountain' stations are concerned.

The unusual high density of geometrid larvae in the present material makes it diffi-

cult to compare directly the composition of the herbivorous trophic group with Koponen's (1973) data. However, a pronounced difference exists because of the fact that Psyllidae and larvae of Hymenoptera symphyta totally dominated this trophic group on birch at Kevo, while the groups were almost absent over the altitudinal gradient at Sogndal. The rather high catch of Psyllidae at sea level in July probably reflects swarming activity. In this investigation, Cicadidae was generally the dominant herbivore group next to geometrid larvae. If geometrid larvae were disregarded, Cicadidae would represent 63–98% of the herbivores recorded at the four lowest stations in May and June. At the uppermost station, however, the density of Cicadidae was always very low. In this last respect, the present results correspond with the conditions at Kevo, where the occurrence of Cicadidae was also quite insignificant.

It is interesting to note that the changes in relative dominance of the three trophic groups followed a very similar pattern throughout the summer at all altitudes, although the absolute densities were different. It is also a remarkable feature of the fauna of this habitat that a major part of it belonged to the second trophic group, i.e. either non-feeders on birch, or species which obtained their food from other sources than from birch leaves or by predation/parasitizing. This trophic group became dominant at all stations when the geometrid larvae left the habitat. The main reason for this dominance is the consistently rather high densities of lichen-feeding Psocoptera and non-feeding Diptera.

The very clear decrease in density of predators/parasites with increasing altitude, shown in Fig. 11, may partly be a response to lower density of prey or host specimens, although this cannot be ascertained from this material.

As the vertical range covered by each species is anticipated to be quite constant from year to year, even during heavy outbreaks of geometrid larvae, the picture achieved regarding the altitudinal zonation in species number is most probably representative.

However, the altitudinal zonation in total invertebrate density, and in the relative dominance of different taxonomic groups,

should be regarded as quite flexible from year to year. This is due to the occurrence of several 'unstable' groups in the habitat, which during special years, or during shorter periods (and sometimes rather locally) may occur in great numbers. Typical examples of this are geometrid larvae, Psyllidae, Aphidae and probably Psocoptera, or species which may migrate from other habitats, such as swarming Diptera. Koponen (1973) found marked differences in the relative composition of the invertebrate fauna on birch in two successive years. Due to the mass occurrence of geometrid larvae during the present study, the total invertebrate densities were most certainly higher than in 'normal' years.

It may, however, be suggested that the total invertebrate density in most years will be lower at altitudes above 500–600 m than in the lower part of the mountain slope. This highest part of the gradient, being an almost purely birch forest, does not seem to be preferred by any of the typical 'eruptive' taxonomic groups.

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Parasites (Hym., Chalcidoidea) associated with bark beetles in Norway

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Pettersen H. 1976. Parasites (Hym., Chalcidoidea) associated with bark beetles in Norway. *Norw. J. Ent.* 23, 75-78.

Seven chalcid-parasites are presented as new to Norway: *Dinotiscus aponius* (Walk.), *Cheirapachys quadrum* (Fabr.), *Tomicobia acuminati* Hedqv., *Nasonia vitripennis* (Walk.), *Calosota vernalis* Curt., *Entedon leucogramma* (Ratz.), and *Eupelmus urozonus* Dalm. Furthermore, six new bark beetles are presented as new hosts to some already known chalcid-parasites. The bark beetles are: *Scolytus laevis* Chap., *S. ratzeburgi* Jans., *S. intricatus* Ratz., *Hylesinus fraxini* Panz., and *Ips duplicatus* Sahlb.

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The parasite fauna associated with bark beetles has been studied in Fennoscandia by Nuorteva (1956, 1957) and Hedqvist (1963). These studies present approximately 40 species of bark beetles and the same number of chalcid-parasites. In Norway, analogous studies by Bakke (1956) and Pettersen (1976) have resulted in registration of 15 chalcid flies from five bark-beetle species.

MATERIAL AND METHOD

Chalcid-parasites from bark beetles, or insects living together with bark beetles, have been reared at the Norwegian Forest Research Institute for several years.

Bark-beetle infested branches and stems from *Betula*, *Fraxinus*, *Ulmus*, *Picea*, and *Pinus* were collected at different localities in southern Norway and the material was placed in rearing boxes. The emerging parasites were labelled according to locality and host insect. In this paper the locality is recorded by the name of the nearest post-office and listed according to the geographical notations of

Strand (1943). In addition, the month of emergence is given. Where only year is given, information about the month is unavailable.

The material has been collected mainly by Dr. A. Bakke, but Mr. Ø. Austarå, Mr. S Tvermyr, and the author have also contributed with recordings. Finally, in the record list the names of the collectors are abbreviated A.B., Ø.A., S.T., and H.P. respectively.

Identification is based on the identification keys worked out by Hedqvist (1963) and Graham (1969).

RESULTS AND DISCUSSION

Chalcid-species new to Norway

Dinotiscus aponius (Walker) 1846

The species was reared from *Scolytus ratzeburgi*. Hedqvist (1963) mentions other *Scolytus* spp. as well as possible hosts, and *D. aponius* parasitizes obviously on bark beetles on hardwood.

Recordings: Vestby (AK 1) February 1960 (S.T.), Ås (AK 6) March 1973 (H.P.).

Cheirophachys quadrum (Fabricius) 1787

This parasite was identified both from *S. laevis* and *Hylesinus fraxini*. Hedqvist (1963) mentions *C. quadrum* to be both a frequent and an important parasite on *H. fraxinus*.

Recordings: Tjølling (VE 19) October 1964 (Ø.A.), Ås (AK 6) May 1971 (A.B.).

Tomicobia acuminati Hedqvist 1959

The species was found on *Ips acuminatus*. No other host is known to the parasite, and it is monophagous in Sweden from where it is described (Hedqvist 1959).

Recordings: Meheia (Bø 15) February 1967 (A.B.), Kongsberg (Bø 15) February 1967 (A.B.).

Nasonia vitripennis (Walker) 1836

N. vitripennis is not known as a parasite on bark beetles, but on the predaceous Diptera *Medetera* living on bark beetle larvae (Hedqvist 1963). In this material it is reared from material infested with *I. acuminatus* or *I. typographus*. It is widely distributed and a parasite known from different groups of insects. A complete list of hosts is given by Peck (1963).

Recordings: Meheia (Bø 15) February 1966 (A.B.), Disenå (HEs 5) February 1972 (H.P.), Vestmarka (HEs 1) March 1974 (H.P.).

Calosota vernalis Curtis 1836

The species was reared from *Blastophagus minor*. *C. vernalis* is described as a hyperparasite on several families, such as *Scolytidae*, *Anobiidae* and *Curculionidae*, but at the same time Hedqvist (1963) considers the species unimportant because of its sporadic appearance.

Recording: Vestmarka (HEs 1) August 1973 (H.P.).

Entedon leucogramma (Ratzeburg) 1844

This species was recorded from one sample of *S. ratzeburgi* and three samples of *S. intricatus*. It is a well known parasite on *Scolytus* spp. (Hedqvist 1963).

Recordings: Greipstad (VAy 7) February 1960 (A.B.), Vestre Moland (AAy 24) February 1960 (A.B.), Mandal (VAy 10) February 1960 (A.B.), Ås (AK 6) May 1974 (H.P.).

Eupelmus urozonus Dalman 1820

The species was found together with *I. acuminatus*. Hedqvist (1963) assumes *E. urozonus* to be a hyperparasite on other chalcid-flies, and has obtained the species from material infested by *B. minor*.

Recording: Drøbak (AK 8) July 1956 (A.B.).

*New bark beetle hosts**Eurytoma morio* Boheman 1836

E. morio was found on both *B. minor* and *I. acuminatus*. Hedqvist (1963) considers the species to be living on the thin-barked parts of the pine stems. These rearings may confirm his observations, but Bakke (1956) and Pettersen (1976) have reared it from spruce as well.

Recordings: Drøbak (AK 8) June 1956 (A.B.), Bø (TEi 22) July 1959 (A.B.), Andebu (VE 14) July 1959 (A.B.), Halse (VAy 9) July 1959 (A.B.), Kongsberg (Bø 15) December 1965 (A.B.).

Heydenia pretiosa Förster 1856

The species emerged from pine infested with *B. minor*. Even if Pettersen (1976) obtained a few specimens from spruce material, its main host is *B. minor* (Hedqvist 1963).

Recording: Bø (TEi 22) July 1959 (A.B.).

Roctrocerus xylophagorum (Ratzeburg) 1844

On two occasions *R. xylophagorum* was obtained in great numbers from *I. duplicatus*. Recordings: Hønefoss (Bø 7) February 1973 (H.P.), Vestmarka (HEs 1) March 1974 (H.P.).

Rhopalicus brevicornis Thomson 1878

The species was reared from *I. acuminatus*. Hedqvist (1963) states that thin-barked pine areas are its main habitat.

Recordings: Meheia (Bø 15) 1966 (A.B.), Kongsberg (Bø 15) 1967 (A.B.).

Dinotiscus colon (Linnaeus) 1758

The species emerged from *B. minor*. Bakke (1956) reported *D. colon* (syn. *D. calcaratus*) from *I. acuminatus*. Nuorteva (1957) and Hedqvist (1963) recorded the same two hosts. Recordings: Siljan (TEy 1) May 1959 (A.B.), Hornnes (AAi 29) July 1959 (A.B.).

Metacolus unifasciatus Förster 1856

In one sample *M. unifasciatus* was reared from *B. minor*, and three recordings

Table I. Chalcid-parasites and the bark beetles from which they are reared. Records published by Bakke (1956) and Pettersen (1976) are marked B and P, respectively. New records are marked X.

	<i>Scolytus laevis</i>	<i>" ratzeburgi</i>	<i>" intricatus</i>	<i>Hylesinus fractini</i>	<i>Blastophagus minor</i>	<i>Pityogenes bidentatus</i>	<i>" quadridens</i>	<i>" chalcographus</i>	<i>Ips acuminatus</i>	<i>" typographus</i>	<i>" duplicatus</i>
<i>Eurytoma arctica</i>											F
<i>E. morio</i>					X				P	X	B
<i>E. blastophagi</i>											P
<i>Heydenia pretiosa</i>				X							P
<i>Roptrocercus xylophagorum</i>									B		B X
<i>R. brevicornis</i>										P	
<i>Rhopalicus tutela</i>											B
<i>R. brevicornis</i>									P	X	P
<i>Dinetiscus aponius</i>	X										
<i>D. colon</i>				X							B
<i>D. eupterus</i>										P	
<i>Metacolus unifasciatus</i>				X		B				X	
<i>M. azureus</i>						B	B			X	
<i>Cheilropachys quadrum</i>	X		X								
<i>Tomicobia seitneri</i>										P	X
<i>T. acuminati</i>										X	
<i>Karpinskiella pityophlori</i>								B	P		
<i>Mesopolobus typographi</i>									B	X	P
<i>Nasenia vitripennis</i>										X	X
<i>Calosota vernalis</i>				X							
<i>Entedon leucogramma</i>		X	X								
<i>Eupelmus urozonus</i>										X	

from *I. acuminatus* show that the species also lives on pine in Norway, as in Finland and Sweden (Nuorteva 1957, Hedqvist 1963). Recordings: Bø (TEi 22) July 1959 (A. B.), Tinn (TEi 32) 1959 (A.B.), Buen (Bø 15) 1965 (A.B.), Meheia (Bø 15) 1966 (A.B.), Kongsberg (Bø 15) 1967 (A.B.).

Metacolus azureus (Ratzeburg) 1844

The species emerged from pine branches infested by *I. acuminatus*. Bakke (1956) reported it (syn. *M. aulloi*) from *Pityogenes bidentatus* and *P. quadridens*. Nuorteva (1957) and Hedqvist (1963) consider the mentioned bark beetles as usual hosts, not including *I. acuminatus*, which is given as host name on the specimens I have identified. Recording: Meheia (Bø 15) 1966 (A.B.).

Tomicobia seitneri (Ruschka) 1924

In the same two samples in which *R. xylophagorum* was reared from *I. duplicatus*, also *T. seitneri* occurred.

Recordings: Hønefoss (Bø 7) February 1973 (H.P.), Vestmarka (HEs 1) March 1974 (H.P.).

Mesopolobus typographi (Ruschka) 1924

This study includes *I. acuminatus* as host in Norway. *M. typographi* is an ectoparasite on *T. seitneri*, and a hyperparasite on *Ips* spp. (Sachtleben 1952).

Recording: Meheia (Bø 15) 1966 (A.B.).

CONCLUSIONS

The results of the present study are summarized in Table I, which shows that twenty-two species of chalcid-flies are known from bark-beetle habitats in Norway. Some of the species registered from Sweden by Hedqvist (1963) and from Finland by Nuorteva (1957) have not yet been recorded in Norway. It seems probable that a study including even more differentiated bark beetle habitats from Norway would result in additional species to those listed in this study.

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Simuliidae (Diptera) of Rendalen, Norway. II. Adult females attacking cows and humans

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Golini, V. I., Davies, D. M. & Raastad, J. E. 1976. Simuliidae (Diptera) of Rendalen, Norway. II. Adult females attacking cows and humans. *Norw. J. Ent.* 23, 79-86.

Catches of adult female simuliids comprising 13 species from cows and humans in the Rendalen region of Norway at an altitude of 640 m and 61°43'N latitude indicated that at least some species fed on both cow or humans. *Prosimulium hirtipes* (Fries) was captured feeding exclusively on cows, and *Schoenbaueria pusilla* (Fries) primarily on humans and to a lesser degree on cows. *Simulium rostratum* (Lundström) was attracted equally to both cows and humans, but it fed primarily on cows and although it occasionally landed on humans, it seldom fed on them. From 28 June to 7 August 1967 *P. hirtipes*, *S. pusilla*, and *S. rostratum* comprised 27%, 40%, and 22% respectively of seven species captured from cows, while the latter two species comprised 66% and 27% respectively of seven species captured from humans. From 12 July to 20 August 1968 *S. pusilla*, *S. rostratum* and *Simulium curvistylum* Rubzov comprised 5%, 75% and 9% respectively of 11 species captured from cows.

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During the summers of 1967 and 1968 we had an opportunity to study simuliids (and other biting flies) of the Rendalen region in Norway (Davies et al. 1971, Golini 1970, Raastad 1974a). The feeding behaviour of simuliids of Norway had been little studied prior to 1967, although the general distribution of various species in Norway was inferred from previous publications (Petersen 1924, Carlsson 1962, Rubzov 1959-64, Rubzov & Carlsson 1965, Davies 1966). This opportunity to study the feeding behaviour of some simuliid species, to assess their attraction to various stimuli, and to ascertain their role as vectors of avian haematozoa (Eide et al. 1969, Eide & Fallis 1972, Golini & Davies 1975, Golini 1975), resulted from a cooperative programme supported by NATO and directed by Prof. A. M. Fallis. Some simuliid species are attracted to ducks (Golini 1975), others to passeriform birds (Golini 1970), and still others as reported herein are attracted to and feed on cows and/or humans. The seasonal distribution of females of the latter species is also reported.

MATERIALS AND METHODS

The study was conducted near Renådalen seter (61°43'N, 11°24'E) Y. Rendal, Hedmark, at an altitude of about 640 m a.s.l. and just below the treeline. The region is low mountainous, with plateaus interspersed with a few deep valleys. At altitudes of about 600 m the ground is covered with taiga-type vegetation which consists primarily of grasses (Gramineae), sedges (*Carex limosa* L. and *C. rostrata* L.), cloudberry (*Rubus chamaemorus* L.) and shrubs, mainly dwarf birch (*Betula nana* L.), *Salix* spp., and those of the family Ericaceae, of which *Vaccinium* spp. and *Callunia vulgaris* (L.) are dominant. At elevations below 550 m the vegetation consists of a heterogeneous growth of coniferous and deciduous trees of which white birch (*Betula pubescens* Ehrh.) and Scot's pine (*Pinus silvestris* L.) are dominant. At altitudes of about 640 m, Scot's pine becomes dominant but less dense. Gradually a transition of ground cover occurs where shrubs replace trees, and lichen, primarily *Cladina*

Table I. Relative abundance of female Simuliidae captured from cows and humans in Rendalen, Norway from 28 June to 7 August 1967 and 12 July to 20 August 1968.

Species	Cows				Humans	
	1967		1968		1967	
	No.	%	No.	%	No.	%
<i>Prosimulium hirtipes</i> (Fries)	375	26.6	23	1.4	4	0.4
<i>Metacnephia pallipes</i> (Fries) [▼]	-	-	9	0.5	-	-
<i>Schoenbaueria pusilla</i> (Fries)	567	40.3	89	5.3	832	66.2
<i>Eusimulium vernum</i> (Macquart)	-	-	-	-	4	0.4
<i>Simulium rostratum</i> (Lundström)	308	21.8	1234	74.0	333	26.5
<i>S. ornatum</i> Meigen	69	4.9	6	0.4	20	1.6
<i>S. monticola</i> Friederichs	10	0.7	4	0.2	4	0.4
<i>S. curvistylum</i> Rubzov	32	2.3	147	8.8	11	0.9
<i>S. reptans</i> (Linné)	-	-	75	4.5	-	-
<i>S. sublacustre</i> Davies	6	0.4	78	4.7	-	-
<i>S. truncatum</i> (Lundström)*	45	3.2	4	0.2	45	3.6
<i>S. tumulosum</i> Rubzov	-	-	4	0.2	-	-
Totals	1412		1673		1253	

* Includes also *S. morsitans* Edwards

[▼] Similar to *M. fuscipes* (Fries) #1 (Raastad, 1974)

spp., becomes dominant as thick spongy mats covering the rocky ground. This region forms a typical watershed with numerous shallow streams with average widths of 50 cm which drain into the Renåa river. This river has an average width of about 5 m and flows in a northerly direction towards the Mistra river, which drains into Storsjøen, a lake at an elevation of about 251 m. These streams and rivers are natural habitats for the immature stages of several species of Simuliidae of this region.

Female simuliids were captured periodically from two black and two reddish-brown dairy cows which are brought regularly each summer to graze on the mountain pasture of Renådalen seter. Simuliids hovering about both cows and humans were captured by sweeping with a standard insect net, and occasionally an aspirator was employed to capture females that were actually engorging on their hosts. Collections over 20–30 minute periods were made almost daily from 26 June

to 8 Aug. 1967 from cows and humans, and from cows only in 1968, from 12 July to 20 Aug. Simuliids captured during each collection were preserved in 70% ethanol for later identification.

OBSERVATIONS

Thirteen species of simuliids were captured from both cows and humans in the Rendalen region (Table I). Only the most numerous of those species captured showed various degrees of host preference, as certain simuliid species were attracted to and fed more commonly on cows than on humans.

The two black cows were invariably attacked by a larger number of simuliids and tabanids than the two reddish-brown cows. These animals frequently licked flies off their front legs and shoulders, and often stampeded across the pasture and sought shelter in their barn, presumably to escape from flies biting and hovering constantly as

a dense swarm around their heads and shoulders. Simuliids swarming around cows were not attracted to the collector, and those which were engorging on cows could not be removed easily unless they had fully fed. Engorged flies often flew with difficulty and landed on the grass in the vicinity of their host. Presumably, a proportion of these engorged simuliids fell prey to various birds which fed avidly on the ground while following closely the cows in pasture. It is estimated that these cows spent about half their grazing time attempting to relieve themselves of flies. They stopped grazing completely when flies were very abundant. The cows learned to associate the sweeping net with relief from flies, and they were quiet as long as flies were being swept from them. However, they would often charge towards the collector when he stopped sweeping flies or when he attempted to leave the pasture at the end of each collection. They did not show this aggressive behaviour when flies were absent.

During the 1967 season, *Prosimulium hirtipes* (Fries) was almost exclusively feeding on cows and comprised 26.6% of the total simuliid population taken from cows and only 0.4% of the total from humans. The apparent scarcity of this species from cows in 1968 presumably resulted from a later start in collecting in that season, coupled with a more advanced fly season (Davies et al. 1971).

Schoenbaueria pusilla (Fries) comprised 66.2% and 40.2% of the population captured from humans and cows respectively in 1967. Although many females of this species were found feeding on both cows and humans, it was the major pest species of humans. However, in 1968 the population of *S. pusilla* comprised only 5.3% of the simuliids collected from cows. *Simulium rostratum* (Lundström) was captured in about equal proportions from both cows and humans, forming 21.8% and 26.5% respectively of the population from these hosts in 1967. However, females of this species were attracted to humans in the form of tightly knit swarms around the shoulders and head, but they seldom landed and rarely fed. On the other hand, this was the major species feeding on cows in 1968, comprising 74% of the total simuliid population captured from them.

Although *S. rostratum* and *S. pusilla* were invariably the predominant species found biting, only *S. pusilla* bit humans on the exposed neck and head, while *S. rostratum* was only attracted to humans and rarely bit. However, both these species and *P. hirtipes* severely attacked cows on the head, neck, shoulders, front legs and breast, venter and udder; sometimes they were so numerous that they appeared as a compact layer on the skin of these animals.

Simulium ornatum Meigen was captured primarily from cows, but *Simulium curvistylus*

Table II. Period of occurrence of various species of female Simuliidae captured from cows in Rendalen, Norway, during the 1967 and 1968 seasons (with dates of abundance peak(s) in parentheses).

Species	1967	1968
<i>Prosimulium hirtipes</i>	28 June - 21 July (28 June)	12 July - 26 July
<i>Metacnephia pallipes</i>	-	12 July - 21 July (15 July)
<i>Schoenbaueria pusilla</i>	7 July - 7 Aug. ⁺ (15 July, 25 July)	12 July - 17 Aug. (17 July, 26 July)
<i>Simulium rostratum</i>	3 July - 7 Aug. ⁺ (10 July, 20 July, 7 Aug.)	12 July - 20 Aug. ⁺ (16 July, 29 July)
<i>S. ornatum</i>	28 June - 17 July (10 July)	15 July - 20 Aug.
<i>S. monticola</i>	1 July - 21 July	12 July - 15 July
<i>S. curvistylum</i>	21 July - 7 Aug. ⁺ (7 Aug.)	26 July - 20 Aug. ⁺ (11 Aug.)
<i>S. reptans</i>	-	29 July - 20 Aug. ⁺ (6 Aug.)
<i>S. sublacustre</i>	17 July - 5 Aug. (29 July)	17 July - 20 Aug. ⁺ (20 Aug.)
<i>S. truncatum</i>	1 July - 17 July (6 July)	16 July - 29 July
<i>S. tumulosum</i>	-	15 July - 26 July

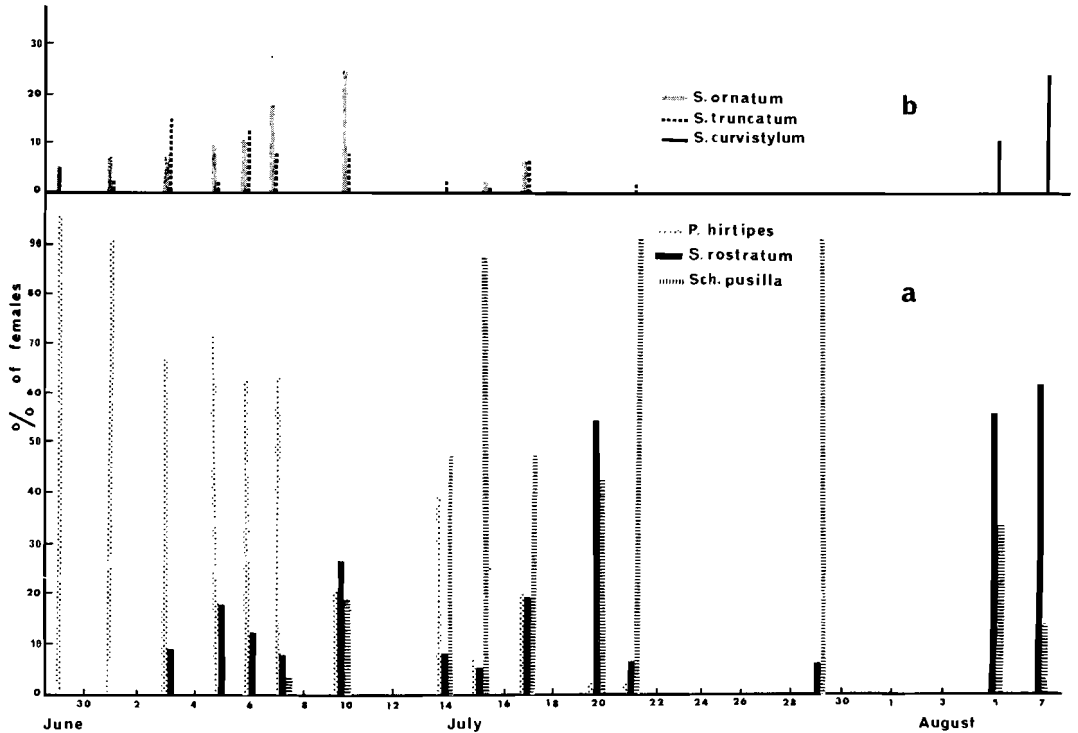


Fig. 1a, b. Relative abundance and seasonal distribution of simuliids captured from cows during the summer, 1967.

lum Rubzov and *Simulium monticola* Friedrichs apparently showed no preference (Table I). *Metacnephia pallipes* (Fries) was captured from cows in 1968 and *Eusimulium vernum* (Macquart) (until recently this species was named *E. latipes* (Meigen)) from humans in 1967, but comprised only 0.5% and 0.4% respectively of the total population from these mammalian hosts; as these are considered mainly ornithophilic species, it is doubtful that they were feeding on these hosts. It is difficult to deduce meaningfully any host preference for the remaining species because of their scarcity. *Simulium reptans* (Linné) and *Simulium sublacustre* Davies were captured only from cows, and in 1968 they comprised 4.5% and 4.7% respectively of the biting population (Table I). In 1967 *S. sublacustre* comprised about 0.4% of the population biting cows, and *Simulium truncatum* (Lundström) was captured in about equal numbers from cows and humans. *S. curvistylum*, *S. morsitans* Edwards, and *S. truncatum*

were captured in relatively low numbers in 1967 (Table I), but in 1968 *S. curvistylum* comprised nearly 9% of the population biting cows. *Simulium tumulosum* Rubzov was captured also in relatively low numbers from cows only in 1968.

The biting activity of simuliids in Rendalen was observed to be restricted mainly to the period from late morning to sunset on days when the air temperature was above 7°C. Most species encountered in larger numbers showed biting-activity peaks at different times of the season (Table II). *P. hirtipes* was the earliest species encountered and in 1967 it showed a biting peak at the end of June with diminishing numbers being encountered until the latter half of July (Fig. 1a). As the biting population of *P. hirtipes* declined, that of *S. rostratum* increased to its first peak around 10 July, with a second peak around 20 July and a third around 7 Aug. (Figs. 1a, 2a). *S. pusilla* bit during the same period as *S. rostratum*, but their biting peaks were asynchron-

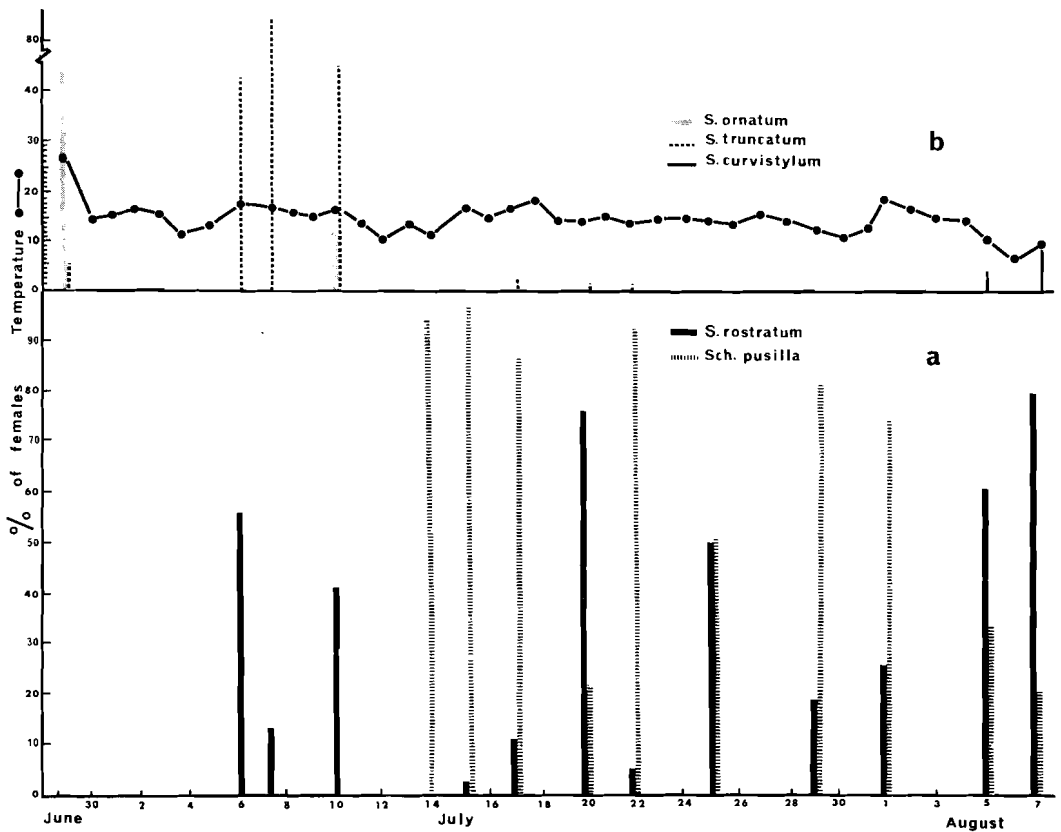


Fig. 2a, b. Relative abundance and seasonal distribution of simuliids captured from humans during the summer, 1967. Maximum air temperature in °C.

ous (Figs. 1a, 2a); as the biting population of *S. rostratum* increased, that of *S. pusilla* decreased and vice versa. However, *S. pusilla* showed only two biting peaks, the first around 15 July and the second around 28 July (Figs. 1a, 2a, 3a). The relative abundance of these two species in both years was significantly different.

The larger population of *S. rostratum* in 1968 made differentiation of its biting peaks more difficult (Fig. 3a). *S. ornatum* captured from cows showed one biting peak around 10 July, coinciding with the first peak of *S. rostratum* and with the declining phase of *P. hirtipes*. The population of *S. ornatum* from humans, however, reached its peak 12 days earlier, on 28 June, and declined to zero around 20 July (Fig. 1b). *S. curvistylum* showed a biting period extending from 21 July to beyond 20 August with a peak occurring around 10 August. *S. truncatum* and

S. morsitans were biting from 1 July to 17 July with a peak on 6 July (Figs. 1b, 2b, 3b). *S. reptans* was found from the end of July through most of August, with one biting peak around 6 August. *S. sublacustre* was found biting from the latter half of July through most of August, with an apparent first peak around 27 July and a second around 20 Aug. (Fig. 3b), but in 1967 its smaller population extended over a shorter period (Table II). *S. monticola* was captured in relatively low numbers from 14 July to 22 July. Records of *S. tumulosum* in 1968 comprised two females on 15 July and two on 26 July from cows.

DISCUSSION

Of 29 species of simuliids now found in Rendalen (Golini 1970, 1975, Raastad 1974a) only 13 species were captured on cows and humans. Although differences were found in

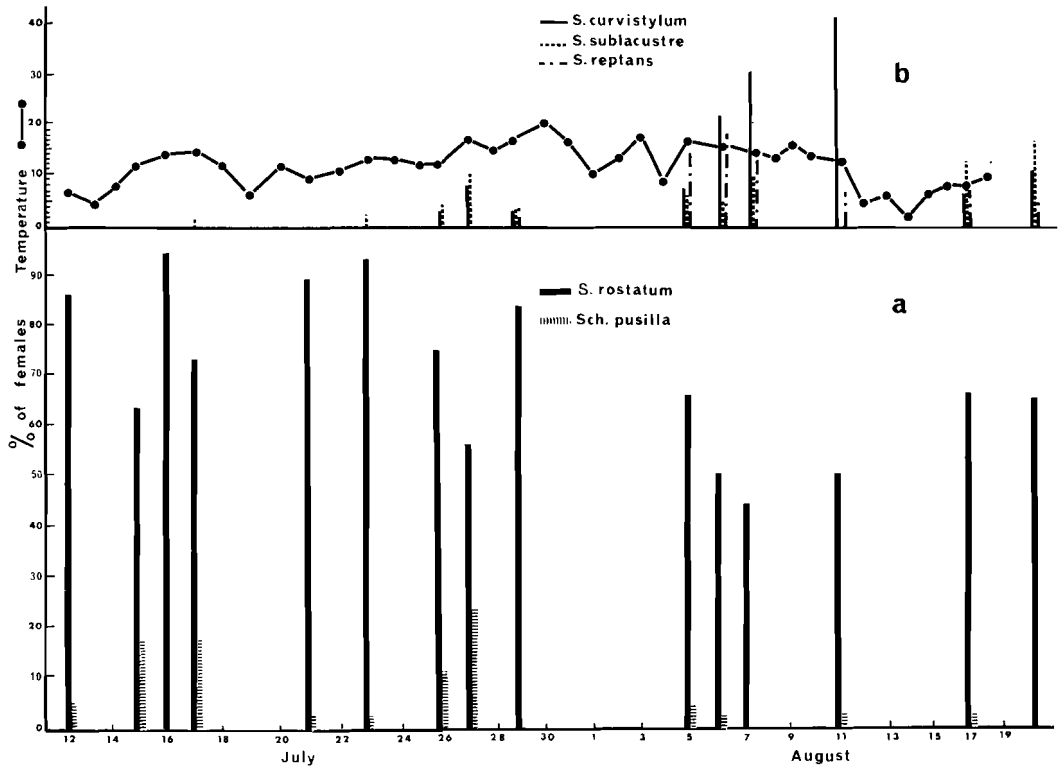


Fig. 3a, b. Relative abundance and seasonal distribution of simuliids captured from cows during the summer, 1968. Maximum air temperature in °C.

their seasonal distribution and biting activity periods, host preference between man and cows was found only for the most abundant species. Of the three most abundant species, *P. hirtipes* and *S. rostratum* fed almost exclusively on cows, while *S. pusilla* fed readily on both cows and humans. In certain parts of Europe *P. hirtipes* is considered a vicious bloodsucker of mammals, including man (Usova 1961). In Rendalen *P. hirtipes* was the only species biting cows early in the season, and its biting activity indicated that this species bites only once and is univoltine. As for most of the species considered here, *P. hirtipes* had a flight period related to its period of adult emergence (Raastad 1974a). As the population of *P. hirtipes* was declining at the beginning of July, *S. pusilla* and *S. rostratum* began biting. Although *S. rostratum* in Rendalen rarely bit humans, in other parts of Norway it is reported to attack humans, horses, and cattle (Raastad, unpubl.). Three

biting peaks were distinguished for *S. rostratum* in 1967, but in 1968 these were less distinct, possibly due to the larger population and a warmer summer which shortened the life span of the adult flies.

The biting period of *S. rostratum* extended beyond mid-August and coincided with that of *S. pusilla*, although their respective biting peaks were somewhat asynchronous. This was noticeable especially in 1967 when their populations were almost equal; however, in 1968 when *S. pusilla* appeared in smaller numbers, its biting peaks were more easily distinguished. Both *S. pusilla* and *S. rostratum* fed in different degree on cows, probably on the same areas of the body; this competitive interference may have effected the significant reduction in the population of *S. pusilla* in 1968. Normally humans protect themselves more readily from biting simuliids, and the availability of smaller mammals, on which *S. pusilla* may also feed, could vary in

different years. Unsheared sheep were also present in the pasture during the summer, but simuliids were never observed on these animals.

Usova (1961) reports *S. pusilla* attacking humans and animals in July in northern Karelia, and Berzina (1953) showed this species to form up to 70% of the total number of biting simuliids in the Archangel region. Alychev (1952, in Usova 1961) reports animals in Belorussia severely intoxicated by bites of this species which normally appeared in large swarms. In Rendalen *S. pusilla* was univoltine (Raastad 1974a), and it was found to be autogenous for its first ovarian cycle (D. M. Davies, unpubl.), indicating that females of this species do not begin searching for a blood host until the beginning of their second ovarian cycle. According to Fredeen (1963), this may influence the mass appearance of certain pest species of simuliids.

The remaining ten simuliid species comprised 12–19% of the population captured from cows and about 5% of that from humans. *S. curvistylum* was scarce in 1967 but comprised nearly 9% of the population biting cows in 1968. Biting records of this species are scarce; however, in England, females of the closely related *S. morsitans* were found to bite humans (Edwards 1915), and in Eastern Europe flies of this species complex attack horses, cattle, and humans (Usova 1961). *S. morsitans* was also found in Rendalen, but this species was not captured on either cows or humans. Females of *S. ornatum* and *S. truncatum* were more abundant in 1967, but they were scarce in 1968 when *S. sublacustre* appeared in larger numbers. The scarcity of *S. ornatum* biting cows in 1968 may also account for the lower population of this species ovipositing during that season (Golini & Davies 1975). This species is considered a major pest of cattle in England (Davies 1957) and a vector of *Onchocerca gutturosa* to them (Steward 1937), while *S. monticola* and *S. sublacustre* are not known as blood-suckers of any importance (Davies 1966). *S. truncatum* is considered a major pest of man and cattle in parts of Sweden and Norway (Carlsson 1962, Raastad 1974b). The low number of *S. tumulosum* captured from cows in Rendalen supports the hypothesis that this species feeds normally on burrow-dwelling mammals (Golini 1970). Hence,

considering that certain species may be habitat and host specific, females of these secondary species may have been more abundant than indicated by the collecting method used in this study. *M. pallipes* and *S. tumulosum*, which were captured in low numbers from humans and cows, were captured in larger numbers with CO₂ traps in 1968 (Golini 1970). Furthermore, *M. pallipes* and *E. vernum* have been reported to feed on mammals in Europe (Petersen 1924, Rubzov 1956 (in Usova, 1961), Carlsson 1962), but our studies indicate that they may feed normally on some species of birds in Rendalen.

This study has shown that although certain simuliid species of Rendalen feed in various degrees on either cows or humans, a wider spectrum of hosts should be used in future studies in order to acquire additional knowledge of the host preferences of these simuliid species.

ACKNOWLEDGEMENTS

This study was part of a cooperative research project in 1967 and 1968 between the Zoological Laboratory, University of Bergen, and the Department of Parasitology, University of Toronto, made possible by a NATO grant to Professor A. M. Fallis of the latter department. We appreciate being invited to share in the project. We are grateful to Drs. L. Davies, A. Eide, and A. Kjaer for helping in 1967 to select the research site in Rendalen; Mr. O. Kvaernes, Managar, Renåvænget Motel, for providing facilities in the field; and Mrs. H. Györkös for assisting in the laboratory. Dr. Fallis kindly reviewed the manuscript.

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Short communications

New localities for three species of spiders (Aranea) from Norway

ERLING HAUGE & KJELL ARNE FURUNES

New localities are given for three relatively rare spider species in Norway, *Lepthyphantes suffusus* Strand, *L. kochiellus* (Strand) and *Moebelia penicillata* (Westr.).

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Kjell Arne Furunes, Zoological Institute, University of Trondheim, N-7000 Trondheim, Norway.

During an investigation of the winter fauna on conifers near Målsjøen, Klæbu, Sør-Trøndelag, three species of spiders were found, whose distribution in Norway is very poorly known.

The animals were found on the distal, needle-coated parts of the boughs of spruces and pines. The forest is situated in a south-facing slope approximately 250 m a.s.l. Spruces predominate, but there are also pines (approximately 10%) and some alders (*Alnus incana*) and birches.

Lepthyphantes suffusus Strand

Two ♀♀ 9 December 1974, 1 ♂ + 2 ♀♀ 11 January 1975, and 1 ♂ + 4 ♀♀ 6 March 1975. All specimens on spruces. Additionally 1 ♂ was found 14 February 1975 on a pine. The species was described from specimens from Hattfjelldal, Northern Norway (Strand 1901), and since then recorded only once in Norway at Ringsaker (Waalder 1972). Recently one ♀ has also been found at Skrukkelia, AK: Hurdal, 25 March 1975 (S. Hågvar coll.). The species seems to be rare also in Sweden (Holm 1944). Palmgren (1975) suggests a synonymy between *L. suffusus* and *L. mughi* (Fickert). Our specimens are all in accordance with Palmgren's Figure 10, 6-7 (Palmgren 1975).

L. kochiellus (Strand)

One ♂ and 1 ♀ on pines 16 December 1974. In Norway the species is previously known only from Hattfjelldal and Ringsaker.

Moebelia penicillata (Vestr.)

One ♂ 14 September 1974. According to Bristowe (1939) the species is previously known in Norway, but he does not give any further localization. Bonnet (1958), also citing Bristowe (1939), does not include Norway in his list.

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Trioza chrysanthemii Löw (Hom., Psyllidae) ny for Norge

KJELL ARNE FURUNES & FREJ OSSIANILLSSON

One imago specimen of *Trioza chrysanthemii* Löw was found at Målsjøen, Klæbu, Sør-Trøndelag 28 October 1974. The specimen was found in a collection of Psyllids taken at spruce branches.

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Under en undersøkelse av evertebratfaunaen på bartrær om vinteren ved Målsjøen, Klæbu, Sør-Trøndelag, UTM NR 32V 7213, ble en ny art av Psyllidae funnet. I perioden fra oktober 1974 til april 1975 ble det gjort systematisk innsamling av evertebrater fra den ytterste, nålekledte delen av greiner av gran (*Picea abies*). Gjennom denne perioden ble det bare funnet en imago ♀ av *Trioza chrysanthemii* – den 28. oktober 1974. Det totale antall psyllider funnet i perioden var 308 fordelt på 19 arter. *T. chrysanthemii* ble funnet 8 meter over bakken, på vestsida av treet.

Arten er beskrevet av Löw (1878). Klimaszewski (1973) angir arten utbredt i Østerrike, Tsjekkoslovakia, Finland, Tyskland, Sverige, Sveits og USSR: Moldavia. I Sverige er den hittil bare funnet i Västergötland, Södermanland og Uppland, men dette skyldes trolig

Mottatt 20. september 1975

Notes on *Limnephilus hirsutus* Pict. (Trichoptera, Limnephilidae)

TROND ANDERSEN

Limnephilus hirsutus Pict. is recorded for the second time in Norway. In August 1972 one male was caught in a light-trap on Ostøya, an island at the bottom of the Oslofjord.

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

One male of *Limnephilus hirsutus* (Pictet, 1834) was caught in a light-trap on Ostøya (UTM: 32VNM887380), Bærum, in Akershus county on 17 August 1972 by Arild Fjeldså. The trap was placed on the east shore of the island. The island is only about 2 km² large without any freshwater systems except for some small ponds, the nearest situated some

manglende undersøkelser (Ossianillsson, upubl.).

T. chrysanthemii legger sine egg på undersida av bladene hos prestekrage (*Chrysanthemum leucanthemum*). Larvene utvikles i små grønne groper i bladene. Som ytterligere vertsplante angis *Chrysanthemum japonicum*. (Klimaszewski 1973) Arten overvintret som imago.

Eksemplaret er oppbevart på DKNVS – museet, Zoologisk avdeling, Trondheim.

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150 m from the trapping site. But the distance to watercourses on the mainland is not great.

L. hirsutus was reported as new to the Norwegian fauna from Mostrand, Tjøme, in Vestfold county by Andersen (1975). Elsewhere in Fennoscandia the species is recorded from Gotland and Skåne (Forsslund & Tjeder 1942, Ulfstrand 1969).

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Camisia foveolata Hamar 1955 (Acari, Oribatei) found in Norway and on Svalbard

TORSTEIN SOLHØY

The oribatid mite *Camisia foveolata* Hammer is for the first time reported from Norway and Svalbard.

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The oribatid mite *Camisia foveolata* was described from material collected near Point arrow, Alaska (Hammer 1955). Several specimens were obtained from debris of lemming runways on grass/sedge tundra close to the coast. Hammer (1955) mentioned that the species had also been found at Klaushavn, western Greenland, though previously identified as *Camisia lapponica* (Träg.). In 1956 *C. foveolata* was found near Abisko in Swedish Lapland, in moss immersed in cold water (Hammer 1960). The late Prof. K.-H. Forsslund found 2 specimens near lake Hornsvatn (1286 m a.s.l.), SFi: Aurland, western Norway in Aug. 1965 (M. Hammer pers. comm.). They were found in wet moss among stones and *Salix herbacea*.

On Hardangervidda, Hoi: Ullensvang, Stigstuv, 1220 m a.s.l., I collected 5 specimens on 9 August 1972. The samples from which they were obtained were taken in mosses in a stand of *S. herbacea* on a slope facing north. This habitat is usually snow-covered from the end of September to mid-June, but cannot be considered as especially wet during the summer.

In the surroundings of Ny Ålesund, Svalbard, *C. foveolata* was found to be a dominant oribatid species on the wet moss tundra at Kjørstranda and common on the relatively moist lichen tundra site at Knudsenheia (site descriptions in Bengtson et al. 1974). No

previous records of *C. foveolata* are published from Svalbard. The oribatid fauna of Svalbard is comparatively well known and since *C. foveolata* turned out to be common in wetter areas at Ny Ålesund, it probably occurs in similar habitats elsewhere on Svalbard. It is possible that earlier workers may have confused *C. foveolata* with *C. lapponica* which has been recorded on Svalbard. *C. foveolata* is similar to *C. lapponica* in colour, body form, and size, but can be identified by its three tarsal claws (one in *C. lapponica*), and interlamellar and notogastral setae which have bristles and are broadest at their base (sword-like, nude, and broadest in the middle in *C. lapponica*).

ACKNOWLEDGEMENT

I am indebted to Dr. Marie Hammer, Fredensborg, Denmark, for confirming my identification of the species and informing me of the record of the late Prof. K.-H. Forsslund.

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Maro minutus (Cbr.) (Araneae) new to Norway

ERLING HAUGE, BJARNE MEIDELL & TORSTEIN SOLHØY

The linyphiid spider *Maro minutus* (Cbr.) is reported for the first time in Norway. Erling Hauge, Bjarne Meidell & Torstein Solhøy, Zoological Museum and Dept. of Morphology, Systematics and Animal Ecology, University of Bergen, N-5014 Bergen-Univ., Norway.

A hilly woodland area on Hetlebakksåta, Åsane (HOy: Bergen, western Norway) was destroyed by a heavy fire in spring 1974. The burned area was about 800 acres. In a sample taken 12 June 1975, one of the sample units contained one male of the linyphiid spider *Maro minutus* (Cbr.). This species has not previously been reported from Norway.

The sampling plot is situated on a rather steep west-facing slope about 270 m a.s.l. Prior to the fire the forest consisted mainly of *Pinus* with a few scattered specimens of *Betula* and *Sorbus*. The understory vegetation consisted of *Juniperus*, *Mollinia*, *Calluna*,

and mosses. Except for some partly undamaged spots of *Sphagnum* and some *Mollinia* tussocks, the ground vegetation and much of the raw humus layer were burned out.

Maro minutus was found in a sample unit consisting almost completely of *Sphagnum*. In Finland moist places with or without *Sphagnum* have been indicated as habitat preference of the species (Saaristo 1971).

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Received 9 December 1975

Syrphus torvus Osten-Sacken (Dipt., Syrphidae). Records from Spitsbergen, Svalbard

ERLING SENDSTAD

Five specimens of *Syrphus torvus* are recorded from the northwestern coast of Spitsbergen, during the summer season 1975. A survey of the known distribution of this species is given.

Erling Sendstad, University of Trondheim, Royal Norwegian Society of Sciences and Letters, the Museum, N-7000 Trondheim, Norway.

The Syrphidae belong to the exotic element of the invertebrate fauna of Svalbard. They are particularly found in the vegetation-rich slopes beneath bird cliffs. From Svalbard only two species are recorded (Kanervo 1968).

During the summer season 1975 five speci-

mens, all females, of *Syrphus torvus* were collected. Three of them were caught ultimo July, at Stuphallet, a bird cliff with a relatively rich flora, near to Ny Ålesund. Another specimen was, however, caught 8 Aug. 1975 at Gazertfjellet by one of the geological

teams of Norsk Polarinstitut. The last report of *S. torvus* from Spitsbergen this summer is from the southern slopes of Karl Schmidts fjellet (leg. Dag T. Elgvin). This specimen was caught 10 Aug. 1975.

S. torvus has earlier been recorded from the British Isles, Canada, Greenland, Iceland, and Novalja Zemlya (Nielsen et al. 1954). It was therefore not unexpected that this species should appear on the archipelago.

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Plusia interrogationis L. (Lep., Noctuidae) found at Svalbard

E. SENDSTAD, T. BERGVIK & A. HEGSTAD

Plusia interrogationis, a new species to the fauna of Svalbard, is recorded from the Ny Ålesund area. A survey of its known distribution is given. It is discussed whether the species is a stable element in the fauna of Svalbard or not.

E. Sendstad, T. Bergvik, & A. Hegstad, University of Trondheim, Royal Norwegian Society of Sciences and Letters, the Museum, N-7000 Trondheim, Norway.

One female of *Plusia interrogationis* L. was caught flying on a sunny day, 16 Aug. 1975, near Gåsebu, a hut east of Ny Ålesund, Spitsbergen. The vegetation in the area was dominated by *Saxifraga oppositifolia* and *Cetraria delisei*. Nordstrøm et al. (1941) give a list of normally preferred plant hosts for the larva in the temperate region: *Vaccinium uliginosum*, *V. myrtillus* and *Calluna*. Among these plants only *V. uliginosum* belongs to the flora of Svalbard (Rønning 1964). *P. interrogationis* is nevertheless known to be a species which can utilize different plants as hosts.

The invertebrate fauna of a high arctic habitat like Svalbard is restricted because of a short summer season with low and relatively stable temperature. This fact permits only small species of invertebrates to colonize the archipelago (Remmert 1972). For geographical reasons too, the invertebrates have problems with regard to colonization. Consequently, the lepidopterous fauna of Svalbard is very scarce. Only seven species have been recorded (Kaisila 1973, Aagaard et al. 1975).

ACKNOWLEDGEMENTS

I wish to thank Cand. real. T. R. Nielsen for kindly identifying the specimens of *S. torvus*, and also those who have contributed with specimens and information about *S. torvus*.

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P. interrogationis is known from the mountainous areas in Scandinavia and on the continent. It is further known from Scotland and the northern parts of England, the Apennines, the Pyrenees, the Carpathians, the Urals, and east Siberia (Seitz 1914). It is also recorded as far north as the Cola peninsula (Nordstrøm et al. 1969). Further, it is known to be a species with a tendency to migrate (Hoffmeyer 1974). Such information may indicate that the specimen could have been an accidental visitor. On the other hand, it may also have developed on Svalbard. Anyway, the specimen, a female, had no spermatophores in bursa copulatrix. If therefore the species is a stable element in the fauna of Svalbard, the population density must be extremely low.

ACKNOWLEDGEMENT

Our thanks to Cand. mag. J. Gulbrandsen for kindly determining the specimen of *P. interrogationis*.

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Hemerobius fenestratus Tjeder, 1932 (Neuroptera, Planipennia) new to Norway

LITA GREVE

Hemerobius fenestratus Tjeder is reported new to Norway. One male was caught at Langvann during the period of 6-10 Aug. 1974, and four males were caught at Gjennestadvann 12-25 Sept. 1974, both localities in Vestfold county.

Lita Greve, Zoological Museum, University of Bergen, N-5014 Bergen-Univ., Norway.

Five males of *Hemerobius fenestratus* were caught in two light-traps both in Vestfold county. One male was caught during the period of 6-10 Aug. 1974 at Langvann (UTM: 32 VNL 715668), Ramnes, and 4 males 12-25 Sept. 1974 at Gjennestadvann (UTM: 32 VNL 683805), Stokke. The light-traps used were Robinson Traps fitted with mercury vapour bulbs (Philips HPL 125 W).

Hemerobius fenestratus has hitherto not been recorded from Norway, although Meinander (1962) mentioned distribution in Norway (no localities given). This was, however, an error (Meinander, personal communication). The species has been recorded from southern Finland (Meinander 1962) and southern Sweden (Tjeder 1940, 1953), but it cannot be considered common. It is found scattered in Europe (Aspöck & Aspöck 1964, Kis, Nagler & Mandru 1970).

Received 16 December 1975

ACKNOWLEDGEMENTS

I wish to express my gratitude to Dr. Bo Tjeder for identifying the material, and to cand. mag. Trond Andersen for giving me the material.

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Bokanmeldelser

A. Bakke 1975. *Dagsommerfugler*. 145 pp. J. W. Cappelen, Oslo. Pris kr. 46.-.

Til tross for at vi i senere år også har fått andre norske håndbøker om sommerfugler, dekker denne nye boken et stort behov. Med sitt hensiktsmessige format, fargeplansjene, og den gode redigering av teksten er den en ypperlig og lett anvendelig felt-håndbok. Dertil vil den være til stor nytte ved den senere bearbeidelse og identifikasjon av innsamlet materiale. Den er laget i den nå så velkjente «Dyrene i farger»-stil, som har vist seg å være en populær form for bestemmelseslitteratur.

Boken bygger på en dansk bok, «Sommerfugle i farver I», med tekst av Leif Lyneborg og med fargeplansjer av Niels Jønsson. Den omhandler dagsommerfugler med utbredelse i de nordiske land og vestlige deler av Europa. Med unntagelse av fire arter, er alle norske dagsommerfugler gjengitt på fargeplansjene som omfatter noe over 200 arter. Det er en stor fordel at de arter som fins i Norge, er avmerket med en asterisk i teksten til hver plansje.

Teksten i den norske utgaven er sterkt omskrevet og bearbeidet av Alf Bakke, som har gjort et utmerket arbeid ved å tilrettelegge boken for norske forhold. Innledningsvis gir han en oversikt over insektenes bygning og utvikling, og et kapittel om hvorledes man kan lage en sommerfuglsamling. Særlig for nybegynnere er slike opplysninger verdifulle. Kapitlet om dagsommerfuglenes utbredelse i Norge, som forteller om hva som er kjent fra forskjellige deler av landet, er interessant og nyttig, men kunne gjerne vært mer omfattende.

Bokens viktigste tekstdel følger etter fargeplansjene. Hver art er beskrevet med hensyn til utseende, flygetid og tilholdssted. I den grad man kjenner forholdene, er også larvenes utseende, valg av vertsplanter og levevis forøvrig beskrevet. Alle nordiske arter har fått en bred omtale, mens omtalen av de arter som ikke hører til den norske fauna er relativt kort. For de nordiske arters vedkommende er det spesielt verdifullt at forfatteren gir en ajourført oversikt over utbredelsen i Norge og våre naboland. Slike opplysninger, som ikke alltid er like lett tilgjengelige, vil være av stor interesse for en som har sommerfugler som hobby. Det vil også boken i sin helhet, og den kan trygt anbefales for alle som er interessert i sommerfugler.

Lauritz Sømme

V. J. A. Novák 1975. *Insect Hormones*. 2nd. English edition. 600 pp. Chapman & Hall, London.

Insekt-endokrinologien har utviklet seg raskt i de senere år, og har fra å være et spesialfelt for relativt få, fått en meget større interesse, spesielt av to grunner. For det første fordi det har gitt oss nye kunnskaper om hvordan hormoner generelt kan virke på celler, og for det annet fordi bruken av insekthormoner eller deres analoger er et av de mulige fremtidsaspekter for insektbekjempelse.

Novák har selv i mange år arbeidet aktivt som forsker på området og har utviklet sin egen gradient-hypotese om den endokrine regulering av insektenes metamorfose. Den første utgave av hans bok kom på tysk i 1959, og utviklingen innen feltet illustreres bl. a. av at bokens omfang er økt med over 300 sider fra den første til den foreliggende utgave. Slik den nå foreligger, er den den største samlede oversikt over feltet. Den behandler både de klassiske hormoner (fra neurosekretoriske celler, juvenilt hormon og ecdyson) og også hva vi nå kjenner til av naturlige og syntetiske stoffer med hormonal aktivitet. I et eget kapittel behandles den endokrine regulering av morfogenesen og i et annet hormoner og diapause. De siste resultater om hvordan hormoner virker på det subcellulære plan er med, og boken avsluttes med å behandle vekselvirkningen mellom hormoner fra insekter og andre dyregrupper, og de potensielle muligheter som insekthormoner representerer som insektmidler. Av spesiell interesse er et eget kapittel om metoder og teknikk, noe som sikkert vil kunne spare både tid og ergrelser hvis man leter etter en spesiell teknikk.

Referansene er ordnet slik at monografier og oversiktsartikler er med, mens tidsskriftartikler fra før 1965 er utelatt. Allikevel dekker referatlisten over 100 sider. I tillegg fins en indeks over emner og en over siterte forfattere.

Boken er klar og velskrevet og rikt illustrert. Den kan sterkt anbefales, og burde bli en selvfølgelighet i bibliotekene i alle entomologiske og zoologiske institusjoner.

Arne Semb-Johansson

R. N. B. Prior. 1974. *Key for the Field Identification of Apterous and Alate Cereal Aphids with Photographic Illustrations*. 22 pp. Ministry of Agriculture, Fisheries and Food, Middlesex. Pris £ 2.10.

Bladlus hører med til de viktigste skadeinsekter på korn. Foruten den direkte skade ved å suge saft fra plantene, er de også potensielle spredere av virusmitte i kornåkrene. Bl. a. for å begrense bruken av kjemiske skadedyrmedler, er det nødvendig med observasjoner over forekomster av de ulike arter. Det er derfor nødvendig å kjenne artene.

Nøkkelen omfatter 7 arter, deriblant de viktigste arter også hos oss, nemlig havrebladlus, kornbladlus og grasbladlus. Av hver art er det både fargefoto og en strektegning som fremhever de viktigste kjennetegn. Både fotos og tegninger er av meget god kvalitet. En vanlig håndlupe vil være tilstrekkelig for å identifisere artene. Nøkkelen inneholder 11 blad (22 sider) innlagt i solid plast – og således beskyttet mot fuktighet. Formatet er 21 x 13 cm, altså en hendig sak å ta med seg i åkeren.

Nøkkelen har vel størst verdi for folk i landbruket, men den burde også være av interesse for naturfaglærere både i ungdomsskolen og i videregående skoler, og for alle som ellers måtte være interessert i bladlus på korn.

Trygve Rygg

G. Seifert. 1975. *Entomologisches Praktikum. 2. Auflage*. 430 pp. G. Thieme, Stuttgart. Pris DM 24.80.

Selv om økologien har en sentral posisjon i våre dagers biologiske forskning og undervisning, skal man ikke glemme betydningen av morfologiske kunnskaper. Insektenes adferd og forholdet til deres omgivelser er dypt forankret i bygning og funksjon av kroppens forskjellige organer.

Gjennom en utførlig morfologisk beskrivelse gir «Entomologisches Praktikum» grunnlag for å forstå hvorledes insektenes ytre og indre organer fungerer. Boken er både en konsentrert lærebok og en veileder for kursvirksomhet. I de forskjellige kapitler blir organ for organ gjennomgått, både med hensyn til ytre morfologi og indre histologisk struktur. Den detaljerte beskrivelse etterfølges av arbeidsoppgaver til nærmere studier av de forskjellige organer. Til dette hører opplysninger om hvilke insekter som er best egnet til de enkelte oppgaver, og de beste fikserings- og fargemetoder for fremstilling av histologiske preparater av de forskjellige organene.

Seifert er en dyktig forfatter, og har skrevet en usedvanlig klar og presis tekst. Boken har 265 illustrasjoner hvorav de fleste er meget oversiktlige strektegninger. Dessuten fins en del mikro- og elektromikroskopiske fotografier. Den andre utgaven skiller seg tilsynelatende lite fra den første, som kom i 1970. Forskjellen ligger i en ajourføring av stoffet som har forårsaket om-

skrivning av en rekke detaljer, og at mange av illustrasjonene er tegnet på nytt.

Med sin utførlige behandling av stoffet kan boken tjene både som håndbok og lærebok. Den kan anbefales for alle som underviser om insekter, og trenger en kilde til ideer om oppgaver studentene selv kan utføre.

Lauritz Somme

W. Jacobs & F. Seidel. 1975. *Wörterbücher der Biologie. Systematische Zoologie: Insekten*. 377 pp. 638 ill. VEB Gustav Fischer, Jena. Pris 16.50 M

Denne boken er et bind i en serie på 12 ordbøker, som tilsammen behandler alle biologiske disipliner. Det foreliggende bind omfatter systematisk entomologi, samt insektenes embryologi og morfologi; emner som er nær knyttet sammen. På norsk vil det være mer betegnende å kalle boken et leksikon enn en ordbok. Innholdet er en samling kortfattede, men allikevel innholdsrike artikler. Med sin kompakte og presise stil, er det nesten utrolig hva hver enkel liten artikkel kan romme. Trykningsmessig er boken satt med tett skrift, men stoffet er allikevel oversiktig ved at det er ordnet i to spalter. Boken har et relativt lite format, og er bundet i myke permer.

Artiklene, som er alfabetisk ordnet, tar i første rekke for seg de største taksonomiske enhetene innen entomologien. Men foruten ordner, familier og viktige slekter, blir også en del viktige insektarter behandlet. Hver artikkel gir en kortfattet oversikt over gruppens eller artens biologi, økologi og taksonomiske stilling. Stikkordene er både de latinske betegnelser og de tyske trivialnavn.

Et stort antall morfologiske og embryologiske begreper er behandlet i egne artikler. Disse er til dels ganske omfattende oversikter over bygning og funksjon av forskjellige organer, vev og celled typer. Stikkordene for disse artiklene er på tysk, og hvis man ikke er kjent med tysk terminologi på området, kan det kanskje by på visse vanskeligheter å finne frem.

Bokens 638 illustrasjoner er hentet fra en rekke forskjellige lærebøker og andre kilder, og er tegnet om for å passe bokens format og spalter. De er klare og tydelige strektegninger, og et viktig supplement til teksten.

Dette er utvilsomt en velskrevet oppslagsbok, som med sin kompakte utforming også er meget praktisk. For alle som arbeider med eller interesserer seg for insekter vil den være en nyttig tilvekst til håndbiblioteket.

Lauritz Somme

DET XVII NORDISKE ENTOMOLOGMØTE vil bli holdt i Bergen 2.–4. august 1977, med etterfølgende ekskursjon 5.–8. august. Nærmere opplysninger om påmelding etc. vil bli sendt ut høsten 1976.

Hans Kauri 70 år



Den 30. mai 1976 fyller professor fil.dr. Hans Kauri 70 år. Det er livets lov at vi blir eldre med årene, men i faglige samtaler og diskusjoner rundt Kauri milepelen uten å virke en dag eldre enn da han kom til Bergen i 1963. For oss som har fått være hans elever har aktelse og respekt for hans faglige dybde og bredde bare kunnet stige.

Hans Kauri er født i Estland hvor han studerte ved Universitetet i Tartu. Under siste verdenskrig måtte han forlate sitt fedreland og kom til Sverige i 1944. Etter en tid som «arkivarbetare» ble han etterhvert amanuens, forskningsassistent, docent, tf. professor ved Zoologiska Institutionen i Lund. I 1963 ble han utnevnt til professor i spesiell zoologi ved Universitetet i Bergen med plikt til å styre Zoologisk Museum.

Kauri's første publikasjon gjaldt Lepidoptera. Magistergraden tok han på Odonata. En doktoravhandling på Ösels arachnoider,

mange års arbeide, ble flammens rov da han flyktet fra Estland. Han ble spesialist på Tabanidae da han i Lund ble satt til å bestemme entomologisk avdeling samlinger av denne gruppen. Så tok han fatt på en ny doktoravhandling og disputerte på frosk i 1959. Tallrike publikasjoner om reptiler, amfibier, opilioner, aranea og insekter vitner om hans kapasitet som forsker. De populariserende evner kommer bl. a. tilsyne i bidragene til Djurens Värld og Norges Dyr.

Da Kauri kom til Bergen, overtok han en institusjon som måtte få de fleste med tilsvarende kvalifikasjoner til å fortvile. Her finner vi en av hans sterkeste sider. Med pågangsmot og arbeidsinnsats, som få kan vise til, bygget han på kort tid opp et livskraftig institutt med systematikk og økologi som bærende elementer. Studenter med forkjærlighet for moderne forskning strømmet til. I løpet av et par år ble Zoologisk Museum et av de største biologiske institutter ved Universitetet i Bergen. En så rask fremvekst går dessverre ikke upåaktet hen - særlig når det alltid er hard kamp om bevilgninger og stillinger. Kauri har nok mange ganger fått merke dette. Av og til følte vi at han presset seg for hardt. Vi trodde ikke det kunne være mulig å arbeide så intenst fra tidlig morgen til seint på kveld, ørk som helg. Vår angst i så måte ble heldigvis gjort til skamme. Hans helse har også holdt til å knytte en rekke prosjekter til museet, bl. a. var han leder for IBP's prosjekt på Stigstuv, Hardangervidda 1969-74. I 1969 kom Laboratorium for ferskvannsoøkologi. Med sine evner til å trekke opp de store linjer - gi problemene perspektiv - har Kauri skapt et aktivt, faglig miljø, en uvurderlig stimulans for såvel yngre som eldre forskere.

Kauri's posisjon og faglige bredde gjen-speiler seg både i nasjonale og internasjonale aktiviteter og han er ettertraktet som gjesteforeleser, opponent i disputaser, medlem av ekspertgrupper og ulike bedømmelseskomiteer. Blandt utallige tillitsverv kan nevnes at han var formann i Norsk Entomologisk Fore-

ning 1968-1970, medlem av foreningens redaksjonskomité 1968-1970, styremedlem i Norges Naturvernforbund 1967-1972. Han er medlem av Det Norske Videnskapsakademi og korresponderende medlem i en rekke svenske og finske vitenskapelige selskaper.

Det er en markant personlighet som nå faller for aldersgrensen, og foruten tidligere

og nåværende elever har særlig Nordens entomologer og arachnologer meget å takke ham for. Vi unner ham å få tid til å fordype seg i egen forskning, og vi ønsker ham lykke til med åremålsdagen i håp om at han fortsatt vil arbeide ved Zoologisk Museum - om enn i et noe roligere tempo.

Roald Larsen

Instructions to Authors

The *Norwegian Journal of Entomology* publishes papers in English, occasionally in Norwegian and German. When preparing manuscripts for publication, authors should consult current copies of the journal and follow the style as closely as possible.

MANUSCRIPTS

Manuscripts must be typewritten on one side of the paper only, with double spacing throughout, and with a wide margin. Authors should submit the original manuscript (preferably with two copies) to the Editor whose address is on page 2 of the cover.

Separate sheets should be used for the following: (1) Title page, with the author's name; (2) Abstract not exceeding 11 lines (770 letters and spaces) with the name and full postal address of the author underneath; (3) References; (4) Tables with their headings; (5) Legends to Figures.

In the case of articles submitted in a language other than English, the Abstract, Table headings and Figure legends must be accompanied with an English translation.

Brief *Acknowledgements* of grants and other assistance, if any, will be printed at the end of the text.

FIGURES AND TABLES

All illustrations will be considered as Figures. Each graph, drawing or photograph should be numbered in sequence with arabic numerals, and should be identified lightly on the back with the name of the journal, the author's name, and the Figure number. The top should be indicated.

The Figures should be the original drawings and should be constructed in proportion to either the entire width of the type area (14 cm) or to the column width (6.7 cm). Lines must be thick enough to allow for reduction. Letters and numbers must not be less than 2 mm in the printed illustration. Photographs should be submitted as unmounted glossy enlargements showing good detail.

Tables should be numbered in Roman numerals, each having a descriptive heading and typed on a separate sheet. Since Tables, as well as Figures, are reproduced photographically, they should be constructed in the same proportion as for Figures. Very large Tables should be typewritten on separate sheets to be printed on facing pages. They must be typewritten on good quality paper with all rules drawn in with a fine pen.

All Figures and Tables should be referred to in the text by their number, and their approximate position indicated in the margin of the manuscript.

All drawings and microphotographs should have a scale giving the appropriate metric unit (m, cm, mm, μm , or nm).

REFERENCES TO LITERATURE

In the text. Brown (1957), Brown & White (1961). If more than two authors, Brown et al. (1963). Multiple references: 'As several authors have reported (Brown 1957, Brown & White 1961, Green et al. 1963)', i.e. chronological order, no commas between names and year.

The list of *References* should be in alphabetical order and not numbered. The international alphabetical order of Scandinavian and German vowels should be observed: Å = AA, Æ and Å = AE, Ø and Ö = OE, Ü = UE. Indicate 1st, 2nd, 3rd, etc. works by the same author in the same year by a, b, c, etc. e.g. (White 1966a). *Ditto marks, et al. and ibid.* should not be used. Generally, titles of journals should be abbreviated according to the *World List of Scientific Periodicals*.

Examples:

Løken, A. 1964. Social wasps in Norway (Hymenoptera, Vespidae). *Norsk ent. Tidsskr.* 12, 191-218.

Schwartz, R. J. 1955. *The Complete Dictionary of Abbreviations*. 211 pp., T. Y. Cromwell Co., New York.

Whitman, L. 1951. The arthropod vectors of yellow fever. pp. 229-298 in Strode, K. (ed.) *Yellow Fever*. McGraw-Hill, New York and London.

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