

## Springtail (Collembola) populations in hayfields and pastures in northern Iceland

BJARNI E. GUDLEIFSSON<sup>1</sup>

AND

BRYNHILDUR BJARNADOTTIR<sup>2</sup>

<sup>1</sup>*Agricultural University of Iceland, Modruvellir, 601 Akureyri, Iceland  
E-mail: beg@lbhi.is*

<sup>2</sup>*Icelandic Forest Research, Mogilsa, 116 Reykjavik, Iceland  
E-mail: brynhildur@skogur.is*

### ABSTRACT

Surface-living invertebrates in grassland habitats were collected in pitfall traps for one year in three hayfields and three pastures in northern Iceland. Hayfields and pastures were on three different soil types; sand, silt and peat. Traps were renewed at weekly intervals during summer (six replicates) but at longer and variable intervals during winter (two replicates). Collembolans were counted and grouped to families or subclasses. During the summer season Collembola were most abundant in late summer and early autumn (second part of July to end of August) and Isotomidae and Symphypleona dominated. Onychiuridae and Entomobryidae culminated in spring, Hypogastruridae and Symphypleona in late summer and Istomidae in early autumn. During summer Collembolans dominated by Onychiuridae, Isotomidae and Entomobryidae were significantly more abundant in pastures than hayfields, indicating that hayfield cultivation (fertilization and mowing) disturbs the natural pasture habitat. Hypogastruridae and Symphypleona were not significantly more abundant in hayfields. Isotomidae and Symphypleona thrived significantly best in peat soil and Onychiuridae in silt soil. The number of collected Collembolans was about nine times higher during the summer than in the winter. During winter Entomobryidae were also more abundant in pastures than in hayfields and also more abundant than Hypogastruridae in hayfields. In soil samples collected in September four species dominated: the Hypogastruridae species *Ceratophysella denticulata* in hayfields on peat soil, the Onychiuridae species *Protaphorura bicampata* on silt soil and mainly in pastures, and the Isotomidae species *Isotoma caerulea* on peat soil. The fourth species, the Isotomidae *Parisotoma notabilis*, was not attracted by a specific environment.

**Keywords:** Collembola, hayfields, Iceland, pastures, seasonal activity, soil types

### YFIRLIT

*Mordýr (Collembola) í túnnum og úthaga á norðanverðu Íslandi*

Hryggleysingjum sem lifa á jarðvegisyfirborði var safnað í eitt ár í fallgildrum í þremur túnnum og þremur sambærilegum úthagaspildum á Norðurlandi. Túnin og beitolöndin voru á þrenns konar jarðvegi; sandi, mólendi og mýri. Fallgildir voru tæmdar vikulega að sumri (sex endurtekningar) en með breytilegu og lengra millibili að vetri (tvær endurtekningar). Mordýr voru talin og flokkuð í ættir eða undirflokk. Heildarfjöldi

mordýra varð mestur síðla sumars og að hausti (síðari hluti júlí til ágústloka) og mordýr af undirflokknum kúlumor (*Symphyleona*) og af ættinni stökkmor (*Isotomidae*) voru ríkjandi. Mordýr af pottamorsættinni (*Onychiuridae*) ásamt kengmori (*Entomobryidae*) náðu hámarki að vori en blámor (*Hypogastruridae*) og kúlumor síðla sumars og stökkmor snemma að hausti. Yfir sumartímann voru pottamor, stökkmor og kengmor marktækt algengari í úthaga en túnum, sem bendir til þess að ræktun (áburður og sláttur) trufla náttúrulegt búsvæði þessara mordýraætta. Blámor og kúlumor voru heldur algengari í túnum en úthaga. Stökkmor og kúlumor döfnuðu best í mýrlendi en pottamor í mólendi. Fjöldi stökkmora var um það bil níu sinnum meiri að sumri en vetri. Kengmor var einnig að vetri algengara í úthaga en túnum en blámor hins vegar í túnum. Í jarðvegssýnum sem safnað var í september voru fjórar mordýrategundir ríkjandi, *Ceratophysella denticulata* (blámor), *Protaphorura bicampata* (pottamor) í úthaga á mólendi og *Isotoma caerulea* (stökkmor) á mýrlendi. Fjórdá algengasta tegundin, *Parisetoma notabilis* (stökkmor) virðist ekki laðast að neinum sérstökum jarðvegi eða meðferð.

## INTRODUCTION

Establishing hayfields in Iceland includes draining if needed, followed by tillering and sowing with a mixture of grass species. From then on the hayfields are fertilized annually, sometimes also with manure, harvested once or twice a year, and occasionally also grazed by cattle or sheep in spring and autumn. The introduced grass species in these permanent hayfields, mainly *Phleum pratense* L. and *Alopecurus pratensis* L., gradually disappear and more tolerant native grasses and weeds become predominant (Thorvaldsson 1996). Grazed pastures on the other hand are not subject to tillering, sowing and fertilization and keep their natural vegetation, dominated by *Deschampsia caespitosa* (L.) Beauvois.

Collembola are both soil-inhabiting and surface-living invertebrates. However, some species move diurnally between soil and vegetation, dependent on external conditions such as temperature, water and food supply (Curry 1994, Hopkin 1997). Collembola are tolerant of a wide range of environmental conditions, including agricultural and industrial pollution, but species differ strongly in their sensitivity to environmental stress. Management of grassland, including fertilization, grazing and cutting, creates a major disturbance to the sward structure and therefore to the microarthropods living there. Manure, which generally increases invertebrate activity, has in some cases reduced the number of invertebrates in grasslands (Curry et al. 1980). In a study of soil-living microarthropods, collected by a Berlese Tullgren funnel, Siepel and van de Bund (1988)

found that nitrogen fertilization had a major influence on the species composition of Acari and Collembola populations, while mowing and grazing had only a minor influence. Petersen et al. (2004), on the other hand, found that grazing significantly reduced the abundance of total Collembola. Tillage reduces the Collembola population (Miyazawa et al. 2002) and soil compaction decreases the proportion of large soil pores and reduces the number of soil-inhabiting microarthropods (Schrader & Lingnau 1997). This effect is more pronounced in the Onychiuridae species than in Isotomidae (Niwranski et al. 2002, Larsen et al. 2004).

Böðvarsson (1957), in an extensive study of Icelandic Collembola, recorded 76 species. A species list by Ólafsson (1991) contains 77 species and later studies of the Icelandic Collembola fauna have increased the number to 140 (Fjellberg 2006, 2007). This is still considerably less than in the Scandinavian countries which have 200–300 species of Collembola each (Fjellberg 2006). The low species number in Iceland is partly because of insufficient studies but is certainly also related to the geographical isolation of the country.

Microarthropods belonging to Acari and Collembola are the two dominating groups of surface-living invertebrates collected in pitfall traps in Icelandic grasslands (Gudleifsson & Bjarnadóttir 2002) and moderate fertilization in general increases their abundance (Gudleifsson 2002). The composition and abundance of microarthropods in Icelandic grasslands is not well known and the impact of human management on Collembola has not been investigated.

Davíðsson (1996) found that grass burn decreased the number of most Collembola families and species except for *Folsomia quadrioculata* (Tullberg 1781). Sigurðardóttir (1991) established that land reclamation with grass seeds and fertilizer and protection from grazing increased the number of Collembola, especially Isotomidae. Oddsdóttir (2002) studied the impact of afforestation and land reclamation on soil biology and found that reclamation, especially with lupin, increased the total number of Collembola, mainly the number of Isotomidae.

The aim of the present study was to investigate the activity of Collembola in grassland swards in Iceland and to establish the impact of hayfield management on the family composition of these invertebrates.

#### MATERIALS AND METHODS

Invertebrates were collected from 20 May 1996 to 27 May 1997 at 6 locations on the Modruvellir Experimental Farm, Eyjafjörður, Iceland. The study included three pairs of man-

aged hayfields and unimproved pastures, both on three different soil types. The pastures are supposed to represent the condition of the grassland ecosystem before cultivation. One hayfield was cut once, the other two were cut twice. One pasture was grazed every year, the other two only in some years. Information on the experimental sites is presented in Table 1. Detailed information on location of traps, management of hayfields, analyses of soil and vegetation, as well as soil and air temperature and species of identified invertebrates, has been presented elsewhere (Gudleifsson & Bjarnadóttir 2002).

On 20 May 1996 six pitfall traps (Barber traps) were placed centrally and in a direct line at 1 m intervals in each of the six sites. The traps were 200 ml plastic beakers with a 38.5 cm<sup>2</sup> opening placed at the soil surface, filled with 25 ml of water with a drop of detergent. A wider lid was placed about 5 cm above the surface of the beakers to hinder rain from entering. The traps were usually emptied at weekly intervals during the summer season, but at

**Table 1.** Management practices, mean soil temperature at a depth of 2.5 cm, soil analysis down to 5 cm, and dominating vegetation on the six experimental sites.

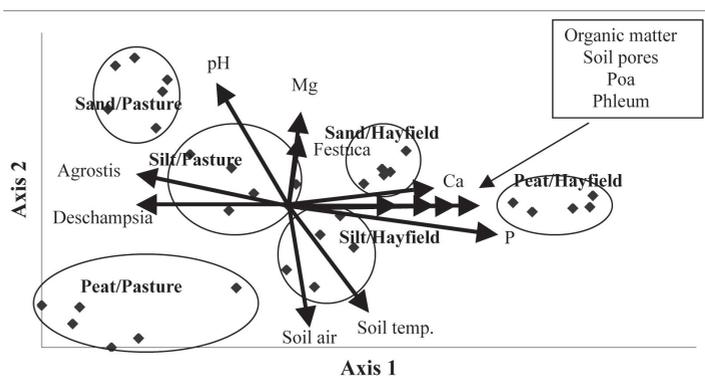
Soil type Soil classification	Sand		Silt		Peat	
	Vitrosol	Vitrosol	Brown andosol	Brown andosol	Histic andosol	Histic andosol
Utilization	Hayfield	Pasture	Hayfield	Pasture	Hayfield	Pasture
Fertilizing	Annually	Never	Annually	Rarely	Annually	Never
Manure	Never	Never	Very often	Rarely	Often	Never
Grazing	Occasionally	Occasionally	Occasionally	Always	Frequently	Frequently
Date of hay cutting	9 July		20 June, 8 August		21 June, 6 August	
Size of site, hectares	8	20	6	20	4	2
Summer soil temperature at 2.5 cm depth °C	10.5	9.4	11.4	10.9	10.9	10.5
Organic matter, %	24	32	40	50	70	30
pH	5.5	5.7	5.4	5.6	5.5	5.5
<i>Deschampsia caespitosa</i> (L.) Beauvois, %	79	73	27	77	13	90
<i>Poa pratensis</i> L., %	3	3	10	10	64	5
<i>Festuca rubra</i> L., %	10	10	10		3	
<i>Agrostis</i> spp., %	3	8		8		5
<i>Alopecurus pratensis</i> L., %	5		42	5		
<i>Phleum pratense</i> L., %			3		20	
Other, %		6	8			

longer and variable intervals during the winter season. Winter season collection was only performed in 2 out of 6 replicates on each field and then 5% formalin was put into the traps to prevent the liquid from freezing. On some occasions during winter the traps were covered with snow. In January water had entered some traps during periods of thawing, especially on the hayfields, though arthropods seemed to remain at the bottom of the traps. Trapped specimens were stored in 50% isopropanol at 4°C for later sorting, counting and identification under a stereoscope. Collembola were grouped into the families Hypogastruridae, Onychiuridae, Isotomidae and Entomobryidae and the subclass Symphyleona according to Fjellberg (1997). A few specimens of the families Neanuridae (*Neanura*, *Friesea*, *Micranurida*) and Odontellidae (*Xenyllodes*) may have been counted and included in Hypogastruridae.

Summer collections lasted from 20 May to 7 October 1996 and winter collection from 8 October to 27 May 1997. For calculation the summer collections were divided into five periods: spring (20 May – 19 June), early summer (20 June – 15 July), late summer (16 July – 6 August), early autumn (7 August – 28 August) and late autumn (29 August – 7 October). Winter collections were divided into 3 periods: early winter (8 October – 10 November), mid-winter (11 November – 28 April) and late winter (29 April – 27 May). Pitfall trapping does not allow calculation on an area basis but expresses the abundance of the invertebrates, which is dependent on number and activity. Therefore the abundance of surface-living Collembola is presented as collected specimens trap<sup>-1</sup> day<sup>-1</sup>. Hay cutting disturbed summer sampling in the hayfields and the number of sampling days therefore differed between sites. For statistical calculations, summer and

winter collections were analysed separately, the summer collections in six replicates and winter collections in two replicates for each site. General linear additive regression models were designed to estimate the effects of soil types, periods within each collection and management versus no management on the number of specimens trap<sup>-1</sup> day<sup>-1</sup> (Y), hence:  $Y = \text{constant} + \text{three soil types (sand, silt, peat)} + \text{periods (five in summer, three in winter)} + \text{two management practices (hayfields, pastures)} + \text{error}$ . This model allows calculations of F-values with an F-test for each treatment factor, i.e. soil type, periods or management (Pyne et al. 1993). To analyse the connection between species and environmental factors Detrended Component Analysis (DECORANA) was used, where species and samples are ordinated simultaneously on two axes (McCune & Mefford 1999). Because of missing values in hayfields only 5 replicates were used there in contrast to 6 for the pastures.

On 18 September 2004 soil samples were taken from the six experimental sites in four replicates. Samples were taken from a depth of 0-2 cm with a 47.5 cm<sup>3</sup> metal cylinder 5.5 cm in diameter. Collembola were extracted in Berlese traps. Samples of invertebrates were stored at 4°C for later sorting, counting and identification to species level by Arne Fjellberg.



**Figure 1.** Results of DECORANA analysis where samples from the six experimental sites are ordinated on the basis of all surface invertebrates identified in the study.

## RESULTS

Out of 166,580 specimens of surface arthropods collected in pitfall traps during summer in the present study 80,351 (48.2%) were Collembola and 67,136 (40.3%) were Acari. These two groups of invertebrates therefore comprised 88.5% of the specimens collected. The daily means throughout the year were 11.0 specimens of Collembola, 9.1 of Acari and only 0.7 of Araneae and Coleoptera and 0.6 of Diptera.

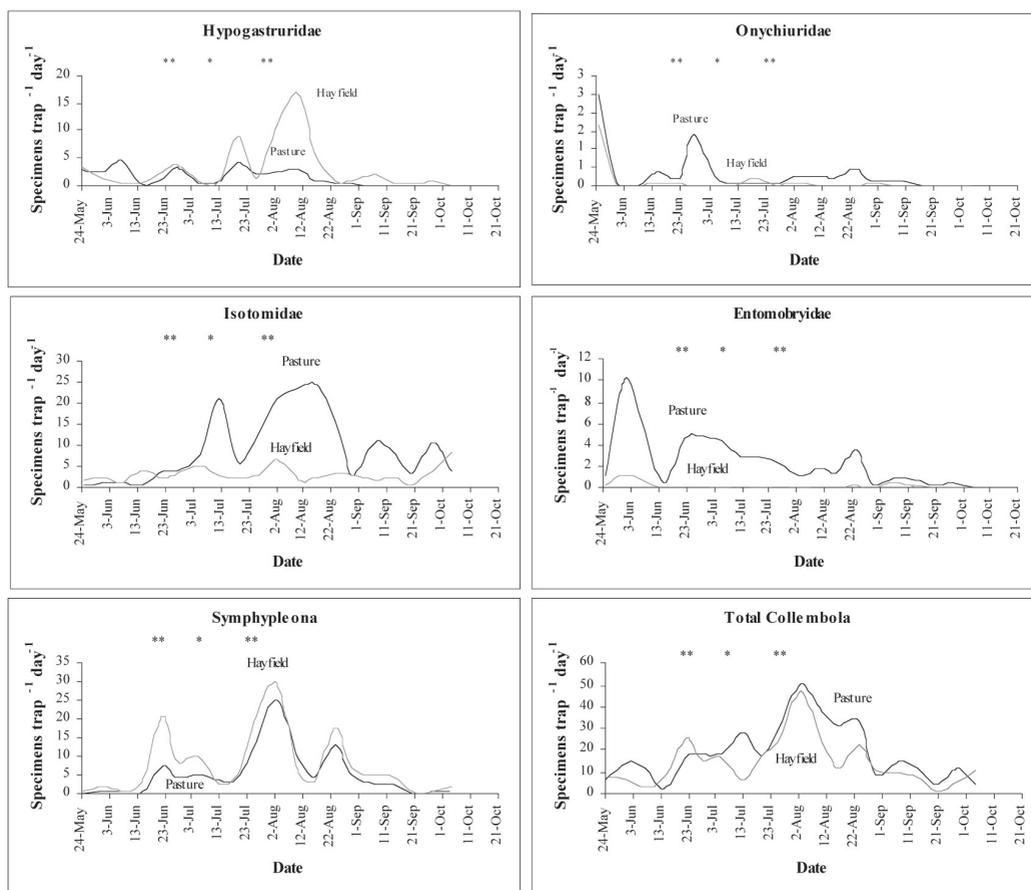
In Figure 1, where results of the DECORANA analysis are presented and environmental parameters are overlaid, the 5 or 6 replicates for each site are located in clusters on the basis of surface invertebrate species composition. Axis 1 separates hayfields and pastures.

Pastures were characterized by *Deschampsia* and *Agrostis* grasses while hayfields are related to *Poa* and *Phleum* as well as the high P and Ca content of the soil. Axis 2 is more related to soil characteristics. Sand and silt are related to high soil pH and Mg content while peat relates to high soil air and soil temperature.

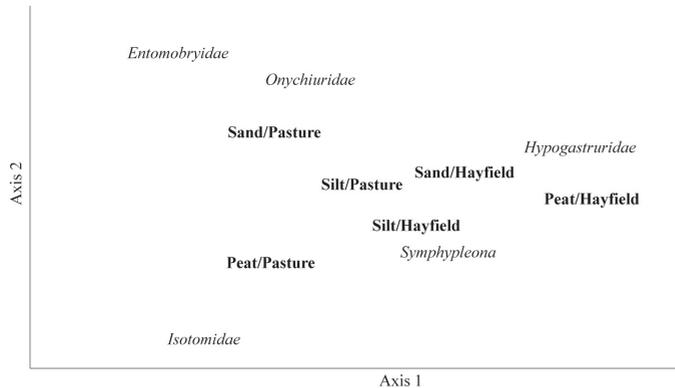
*Summer season activity*

The total number of Collembola culminates in late summer and early autumn and this was the case with Hypogastruridae, Isotomidae and Symphypleona, whereas Onychiuridae and Entomobryidae are most abundant in spring and early summer (Figure 2).

In Figure 3, where the six study sites are placed according to the results in Figure 1, the



**Figure 2.** Number of trapped specimens of four Collembola families and one subclass throughout the summer season. Mean of six pastures and five hayfields. Asterisks mark the date of hay cut in hayfields.



**Figure 3.** Results of DECORANA analysis of relationship between soil type/management and families or subclasses of Collembola.

Isotomidae family is placed at the lower left and is related to peat and pasture, while Entomobryidae at the upper left are related to sand and pasture. Hypogastruridae on the other hand are more related to hayfields.

The number of specimens collected in traps  $\text{day}^{-1}$  of the Collembola families on different soil types during summer is presented in Table 2 along with abundance under different management practices. Collembola, dominated by Isotomidae and Symphypleona, were significantly most frequently trapped on peat soil whereas Onychiuridae were most abundant on silt soil. The total number of Collembola was significantly higher in pastures than hayfields,

mainly due to Onychiuridae, Isotomidae and Entomobryidae. Hypogastruridae were slightly more abundant in hayfields while Symphypleona were fairly equally spread on hayfields and pastures (Table 2).

#### Winter season activity

From the end of the summer collection, 7 October 1996, sampling was continued through the winter in 2 out of 6 traps on each site until 27 May 1997.

Although winter activity was much lower than summer activity, Acari and Collembola were also the most active invertebrates during winter, and Collembola were more numerous than Acari. A mean of 1.9 specimens of Collembola and 0.4 specimens of Acari were trapped each day during the winter season. In Table 3 the results are divided into the periods of early winter, mid-winter and late winter. The total number of Collembola was significantly highest in late winter, as were Isotomidae, while Onychiuridae were most abundant in mid-winter (Table 3).

Collembola were fairly equally distributed on peat and sand whereas Entomobryidae and

**Table 2.** Number of specimens  $\text{trap}^{-1} \text{day}^{-1}$  of Collembola during summer season in different soil types and under different management practices. Mean of six pastures and five hayfields.

Family/Subclass	Specimens $\text{trap}^{-1} \text{day}^{-1}$						
	Sand	Silt	Peat	F-value	Hayfields	Pastures	F-value
Hypogastruridae	1.57	2.28	3.07	NS	3.13	1.80	NS
Onychiuridae	0.18	0.38	0.11	0.047	0.12	0.36	0.015
Isotomidae	1.56	3.10	14.70	<0.001	3.47	10.31	<0.001
Entomobryidae	1.86	1.35	0.93	NS	0.18	2.76	<0.001
Symphypleona	4.03	5.49	10.19	<0.001	7.74	6.29	NS
Total	9.20	12.60	29.00	<0.001	14.30	21.50	<0.001

Isotomidae dominated on peat and Hypogastruridae on sand. There was no significant difference in total catches of Collembola in pastures and hayfields. Hypogastruridae were significantly more numerous in hayfields than pastures and Entomobryidae in pastures (Table 3).

#### Soil-living Collembola

A total of 14 species of Collembola were identified from soil samples from a depth of 0-2 cm on 18 September 2004. The results are presented in Table 4. Between 4,000 and 10,000 specimens m<sup>-2</sup> of Collembola were collected. The most common species were the

Hypogastruridae species *Ceratophysella denticulata* (Bagnall) on peat soil, the Onychiuridae species *Protaphorura bicampata* (Gisin) on silt soil, the Isotomidae species *Isotoma caerulea* Bourlet in hayfields, and *Parisotoma notabilis* (Schäffer) on all three soil types.

#### DISCUSSION

In the present study surface-living invertebrates were collected for one year. Mites and springtails are the most numerous surface-living microarthropods in Icelandic grasslands, composing 88.5% of the specimens collected in this study, and almost 15 times more numerous than any other group of microarthropods caught in pitfall traps (Gudleifsson & Bjarnadottir 2002). The number of springtails in European grassland soils is similar to that of mites, over 100,000 specimens m<sup>-2</sup> (Curry 1994, Hopkin 1997). In the present study up to only 10,000 specimens m<sup>-2</sup> of Collembola were collected from soil. This low number is understandable as the activity of Collembola decreases substantially in September when sampling took place (Figure 2). In the present study Collembola in pitfall traps were more numerous than Acari, with Istomidae and Symphypleona the most abundant. Species of these two groups of Collembola are often associated with the herbage layer (Curry 1994).

The outcome of total abundance of families and subclasses in pitfall traps is the sum of many species behaving and responding differently. It is expected that a few species dominate in each family or subclass. In the park grassland experiments at Rothamstead, which started in 1856 (Edwards

**Table 3.** Number of specimens trap<sup>-1</sup> day<sup>-1</sup> of Collembola during winter. Mean of two traps in each site.

Family	Specimens trap <sup>-1</sup> day <sup>-1</sup>			F-value
	Early winter	Mid-winter	Late winter	
Soil temperature, °C	3.5	-0.9	3.5	
Hypogastruridae	0.16	0.27	0.88	NS
Onychiuridae	0.01	0.14	0.01	0.050
Isotomidae	1.22	0.04	1.33	0.007
Entomobryidae	0.71	0.06	0.48	NS
Symphypleona	0.06	0.00	0.36	NS
Total	2.19	0.51	3.05	0.026
	Sand	Silt	Peat	
Hypogastruridae	1.02	0.17	0.12	0.046
Onychiuridae	0.04	0.10	0.03	NS
Isotomidae	0.62	0.56	1.40	NS
Entomobryidae	0.20	0.08	0.97	0.005
Symphypleona	0.28	0.09	0.09	NS
Total	2.16	0.99	2.60	NS
	Hayfields	Pastures		
Hypogastruridae	0.82	0.05		0.020
Onychiuridae	0.09	0.02		NS
Isotomidae	0.84	0.87		NS
Entomobryidae	0.08	0.76		0.004
Symphypleona	0.25	0.06		NS
Total	2.08	1.75		NS

**Table 4.** Number of specimens of Collembola species identified from Berlese samples collected 18 September 2004. Mean of four replicates.

Species	Number of specimens m <sup>-2</sup>					
	Sand/ Hayfield	Sand/ Pasture	Silt/ Hayfield	Silt/ Pasture	Peat/ Hayfield	Peat/ Pasture
HYPOGASTRURIDAE						
<i>Ceratophysella denticulata</i> (Bagnall)				316	5891	421
ODONTELLIDAE						
<i>Xenyllodes armatus</i> Axelson	316					
ONYCHIURIDAE						
<i>Protaphorura pseudovanderdrifti</i> (Gisin)	105	947				
<i>P. fimata</i> (Gisin)		421				
<i>P. bicampata</i> (Gisin)			2946	6207		
<i>P. islandica</i> (Bödvarsson)		421				
<i>P. sp. juv.</i>		421	421			
ISOTOMIDAE						
<i>Folsomia quadrioculata</i> (Tullberg)	842	1262				
<i>F. manolachei</i> Bagnall	2104	1262				
<i>F. bisetosa</i> Gisin						105
<i>F. fimetaria</i> (Linnaeus)			105			842
<i>Parisotoma notabilis</i> (Schäffer)	1262	1473	4313			2104
<i>Isotoma caerulea</i> Bourlet			1999	316	3892	631
ENTOMOBRYIDAE						
<i>Lepidocyrtus lignorum</i> (Fabricius)		210				
SMINTHURIDIIDAE						
<i>Sphaeridia pumilis</i> (Krausbauer)			210	105		
KATIANNIDAE						
<i>Sminthurinus sp. juv.</i>	105			105		
Total number of specimens	4734	6417	9994	7049	9783	4103
Number of species	6	8	6	5	2	5

et al. 1975), the dominating species were *Isotoma viridis* Bourlet (Isotomidae), *Lepidocyrtus cyaneus* Tullberg (Entomobryidae) and *Sminthurus viridis* (L.) (Symphypleona). Bödvarsson (1957) identified species from Berlese traps in 6 grassland habitats in Iceland. The systematics used in that study are partly out of date, but comparing his result from 1957 and Fjellberg's (2007) species list, the following species are likely to comprise a large part of the populations collected in the present study: *Ceratophysella denticulata* (Hypogastruridae), *Protaphorura bicampata* (Onychiuridae), *Isotoma caerulea* (Isotomidae), *Lepidocyrtus lignorum* Fabricius (Entomobryidae) and *Sminthurinus aureus* (Lubbock) (Symphypleona).

The species most frequently identified from soil samples collected in Berlese traps in September 2004 (Table 4) were in agreement with the results from surface sampling (Table 2). The total number was low, between 4,000 and 10,000 specimens m<sup>-2</sup>. This is to be expected as the abundance of Collembola decreases substantially in September (Figure 2). In September Isotomidae species are most active in the soil (Table 4) and that is also the case on the soil surface (Figure 2). The Hypogstruridae species *Ceratophysella denticulata* was most frequently collected from hayfields on peat, the Onychiuridae species *Protaphorura bicampata* was collected only from silt soil and mainly pastures, and the Isotomidae species

*Isotoma caerulea* was most frequently collected from peat. Another Isotomidae species, *Parisotoma notabilis*, was not attracted by a specific environment. All this is in good agreement with the previously discussed surface-living species (Table 4).

The soil pH in the experimental sites was in all cases around 5.5, as well as for the peat soil (Table 1), which should be suitable for invertebrates (Curry 1994). Springtails are also most abundant in peat soil, and this applies mainly to the dominating groups, Isotomidae and Symphypleona (Table 2). In the peat soil the total air volume was greater (Figure 1) and the soil includes more organic matter to be decomposed; therefore the classes and families that inhabit litter dominated. On the other hand, Onychiuridae, which are a more soil-inhabiting family of springtails, were more abundant in silt soil where the pores were larger and the individuals found more suitable habitat conditions beneath the soil surface.

The impact of fertilizer on grassland invertebrates is largely a consequence of its effect on the vegetation and litter increase (Sigurðardóttir 1991). Moderate applications of mineral fertilizers generally have beneficial effects on invertebrate populations through increased plant production and increased return of litter to the soil, but high application rates of mineral fertilizer can be detrimental (Curry 1994), particularly high rates of ammonium sulphate (Gudleifsson 2002). The population differences in pastures and hayfields in the present study were an expression of the impact of long-term management (fertilizing, hay cutting) on Collembola, and management reduces the total number of Collembola and the abundance of Onychiuridae, Isotomidae and Entomobryidae. This was also the case with Isotomidae species in a study in the Netherlands (Siepel & van de Bund 1988). On the other hand, Hypogastruridae and Symphypleona seem to tolerate management practices slightly better and this effect was more pronounced in the winter collection (Table 3), as was also the case with Symphypleona species in France (Ponge et al. 2003).

Collembola were most abundant in late sum-

mer/early autumn (16 July-28 August) as were Hypogastruridae, Isotomidae and Symphypleona, whereas Onychiuridae and Entomobryidae were most abundant in early spring (Figure 2). In a study where soil invertebrates in grassland in the Eyjafjörður area in 1970 were collected in Berlese traps, the number of both mites and springtails culminated in spring and late autumn, with minimal activity during summer (Hallgrímsson 1976). In the present study this decrease in summer activity was only detected in Onychiuridae and partly in Entomobryidae (Figure 2).

Even though Collembola were also the most numerous group of invertebrates trapped during winter, the total number of Collembola was 9 times higher throughout the summer than during the winter. Isotomidae were most active in early and late winter, while Hypogastruridae and Onychiuridae dominated in mid-winter, probably because these families are more bound to the soil than the other families, which are more active on the soil surface.

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