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Navigation and behaviour of four Collembola species migrating on the snow surface

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Summary

In Norway, four species of Collembola, *Hypogastrura socialis*, *Vertagopus westerlundii*, *Isotoma hiemalis* and *I. violacea*, are regularly active on the snow surface during mild weather. In all species, each individual jumps in a rather straight line, using the sun as a “compass”. If the sun’s position was turned 180° using a mirror, the animal also turned 180°. As the sun does not have to be directly visible, the animals probably can use polarized light as well. Different individuals often migrate in quite different directions. At least three of the four species live in patchy and temporary habitats, and sooner or later have to find new patches. Winter migration on the smooth and moist snow surface is their only possibility to move over great distances.

Before each jump, the collembolan orientates its body relative to the sun either by rotating horizontally on the spot or by walking a little in a crooked line. *H. socialis* lands with extended anal sacks, which adhere the animal to the snow surface and enable it to position itself rapidly again.

Even in overcast weather, collembolans sometimes show a more or less directional movement. An experiment indicated that navigation under such conditions was by means of light and dark elements in the surroundings.

Key words: Collembola, winter, migration, navigation, behaviour

Introduction

Certain Collembola species are regularly active on the snow surface at temperatures around or slightly above 0°C (e.g. Leinaas 1981a, 1983; Zettel 1984, 1985; Hågvar 1995). The best known species with this behaviour is *Hypogastrura socialis* (Uzel)

(Hypogastruridae), a holarctic forest-dwelling species which may show mass occurrence on snow (Latzel 1907; MacNamara 1919; Leinaas 1981a). Hågvar (1995) showed that each individual of this species is able to keep a steady course by continuous jumping, using the sun's position for navigation. In this way, daily migrations of 200–300 m on snow is possible. Furthermore, it was observed that different individuals often migrated in different directions, resulting in an efficient spreading of the animals in the landscape.

This paper has two purposes: The first is to add more information about the behaviour of *H. socialis* on snow, including the ability to navigate in overcast weather. The second is to study the migratory behaviour on snow of three Isotomidae species: *Vertagopus westerlundi* Reuter, *Isotoma hiemalis* Schött, and *Isotoma violacea* Tullberg. These species also have the ability of directional migration on snow, using the sun's position as a "compass". Their behaviour has been studied in both sunny, partly cloudy and cloudy weather.

Materials and Methods

The studies were performed mainly during late winter (March and April) in the years 1993–1998. The habitat was usually spruce (*Picea abies* (L.) Karst.) forest, with a snow depth of 0.5–2 m. Two study areas were visited on skis: Area A was a high altitude forest, about 800 m above sea level at Vegglijfjell, Buskerud county, about 100 km west of Oslo. Area B encompassed forests at 100–500 m above sea level in Nordmarka and Østmarka close to Oslo, in Akershus and Buskerud counties. All four collembola species occurred in both study areas. Detailed observations on behaviour and jumping pattern were made on eighteen specimens of *V. westerlundi*, thirty-one specimens of *I. hiemalis* and eight specimens of *I. violacea*. By keeping a distance of approximately 1 m from the animals, my presence did not influence their jumping direction. When the sun was visible, its relative position to the animal's direction of movement was noted. The sun's position was sometimes manipulated with a mirror. Density estimates were recorded for *H. socialis* under various conditions, including animals crossing the ice cover of lakes. The observations also included an unusual mass migration of *I. hiemalis*.

Results

Densities on the snow surface

During all years in both study areas, *H. socialis* was the most abundant species on snow. Migration activity of this species was especially intense on warm and sunny days near the end of the winter, when the air temperature at 2 m height could reach 5–10°C. During the middle of April 1995, there were roughly 2 000–10 000 animals m⁻² snow surface within forest in the whole study area A (about 20 km²). The evenness of their distribution was illustrated by 25 squares (10×10 cm) randomly spaced across 20 m², which gave between 11 and 30 animals dm⁻² (mean value 21). In depressions in the snow, the jumping animals were often trapped and aggregated (Fig. 1), and ski tracks were coloured dark violet due to crushed collembolans (Fig. 2). Migrating specimens of *H. socialis* were also observed on frozen bogs and lakes. A density of about 1 000 animals m⁻² was observed on the snow-covered ice

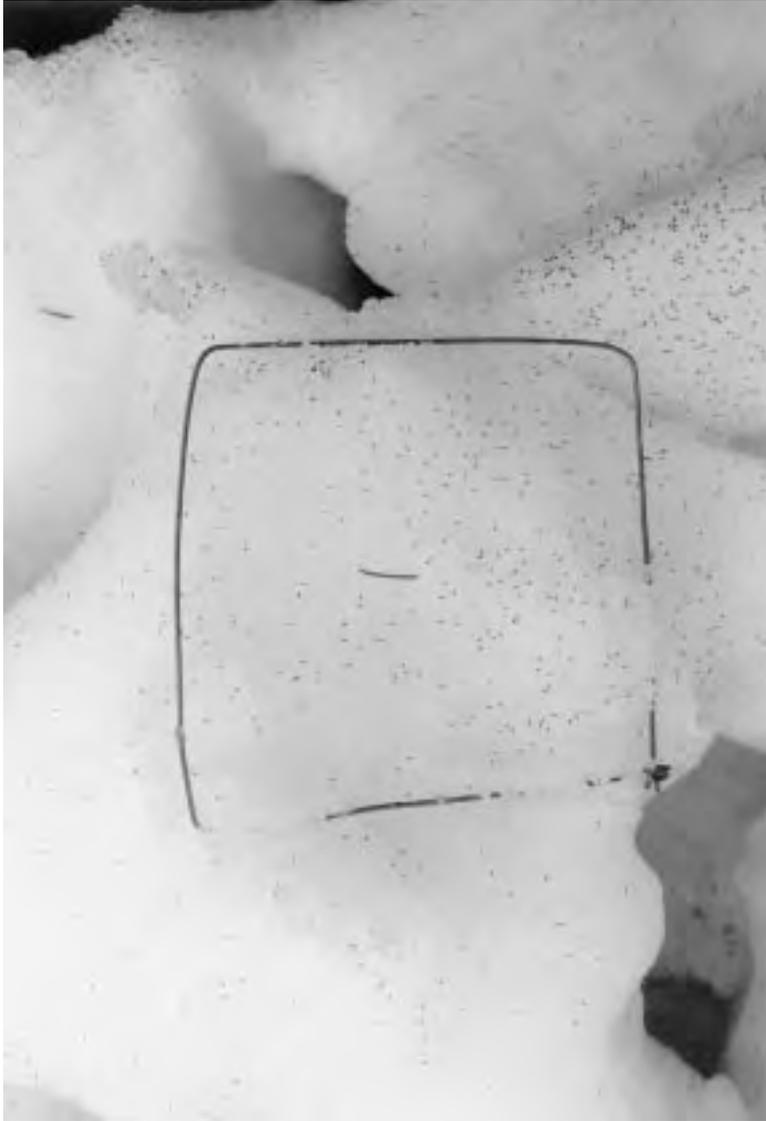


Fig. 1. A “moderate” concentration of *Hypogastrura socialis*, trapped in a depression in the snow. The frame is approximately 10×10 cm

in the middle of a 150 m wide lake, and about 25 animals m^{-2} in the middle of a 300 m wide lake. A few individuals were even recorded in the middle of a 1.5 km wide lake.

The density of the three Isotomidae species on snow was much lower, usually less than one animal m^{-2} . An exception, however, was a local mass migration of *I. hiemalis*, described below.



Fig. 2. During mass occurrence of *Hypogastrura socialis* on snow, great numbers may be trapped and killed in ski tracks, giving the tracks a dark violet colour

Directional movements

In sunny or partly cloudy weather, specimens of all three Isotomidae species showed the ability to jump consequently in a fixed direction. Typical examples of individual migration routes are given in Fig. 3A–C and Fig. 4A–D and G. A remarkable fact is that even in a given place, different individuals of the same species could migrate in

quite different directions. While highly individual migration directions in *H. socialis* were demonstrated by Hågvar (1995), Fig. 5 illustrates this for each of the three Iso-tomidae species. Individuals could migrate in all possible directions, both in relation to the cardinal direction (N) and the position of the sun at the time. There was no general tendency to migrate towards the sun.

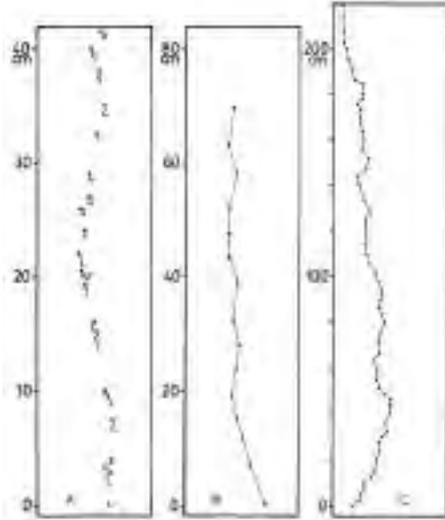


Fig. 3. Examples of directional jumping routes of *Vertagopus westerlundii* in sunny weather. Each dot represents a starting point for a jump. The animals moved upwards in the figure. The sinuous walking before each jump has been shown only in A

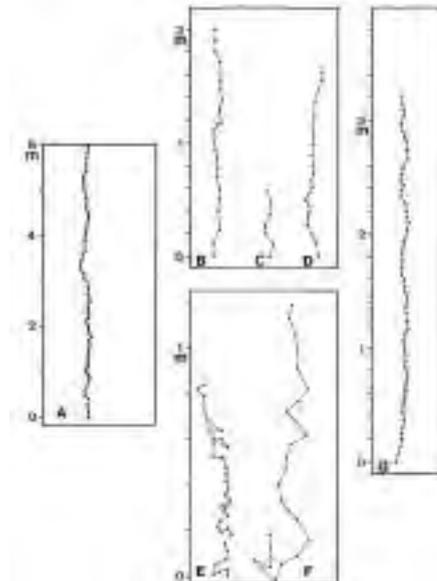


Fig. 4. Individual migration routes in *I. hiemalis* (A–F) and *I. violacea* (G). The animals moved upwards in the figure. Observations were made in sunny weather, except for D after sunset, and E–F in completely overcast weather

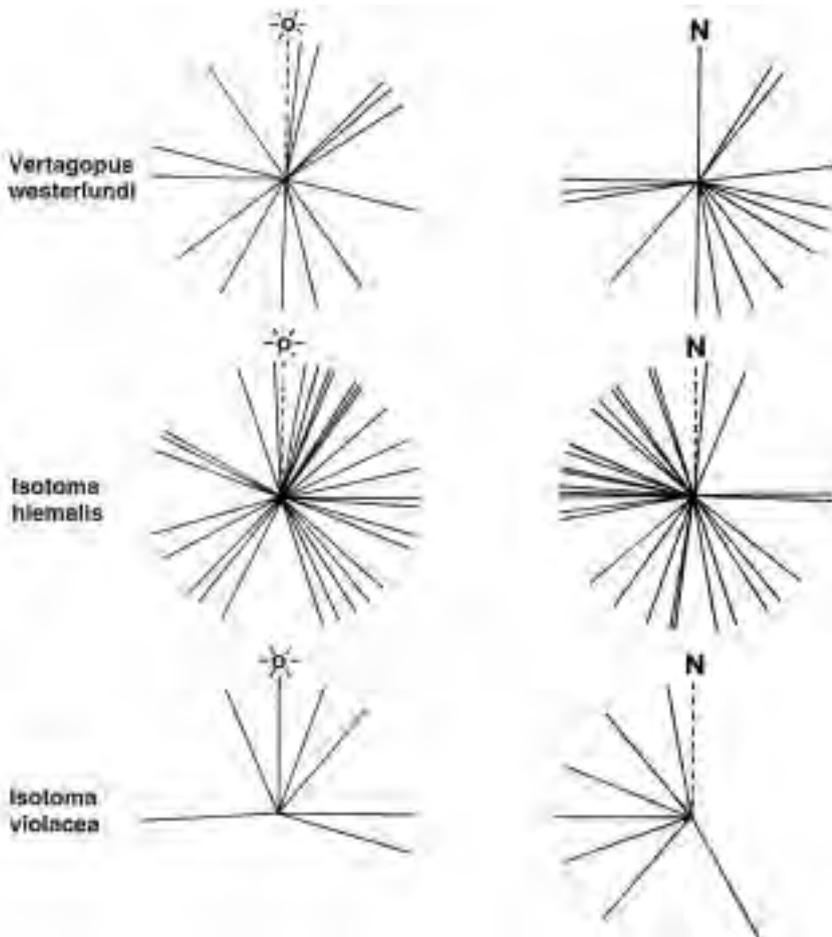


Fig. 5. Individual migration directions in the three Isotomidae species in sunny or partly cloudy weather (with at least some blue sky visible). The directions have been given both in relation to the cardinal direction (N), and in relation to the sun's position at the actual times

Navigation and behaviour

As demonstrated for *H. socialis* in a previous paper (Hågvar 1995), individuals of the three Isotomidae species also turned their direction 180° if the sun's position was turned 180° by using a mirror. During such manipulations, the actual position of the real sun was shadowed, so that the animal saw only the mirror image of the sun. When the mirror was removed, the animals resumed their original direction. This confirms that each individual finds its direction by consequently jumping at a certain angle relative to the sun's position. The short, sinuous walk after landing in the Isotomidae species (Fig. 3A) enables the animal to catch up the sun's position, and to position its body at a certain angle to the sun before the next jump. *H. socialis* finds the direction very efficiently by rotating the body horizontally on the spot immediately after landing (Hågvar 1995).

If the light patch from the mirror on the snow was not in good contrast to the general light conditions on the snow, the animals often hesitated long before jumping, changed their direction in an unpredictable manner or simply stopped migration. This may be due to a conflict between the “new” sun and the polarized light from the real sun, giving contradicting information. The probable use of polarized light as a substitute for a directly visible sun was indicated by three types of observations: a) A constant direction was easily kept by all species without a visible sun (i.e. in partly cloudy weather), as long as some blue part of the sky was visible. b) Animals could keep the direction through shady patches, and c) Directional migration continued even after sunset (e.g. Fig. 4D).

In completely overcast weather, all four species showed a low jumping activity. If jumping occurred, it was often random, and the animals hesitated long before jum-

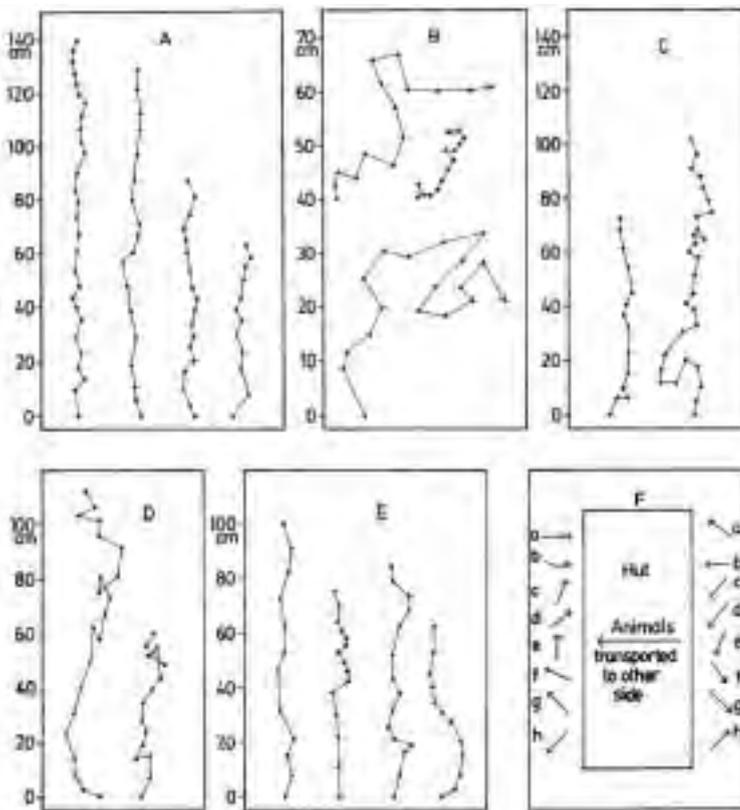


Fig. 6. Individual migration routes of *Hypogastrura socialis* in completely overcast weather. Each dot represents a starting point for a jump. The animals moved upwards in the figure, if not otherwise indicated. A: Examples of successful navigation. B: Examples of more random jumping, with shorter jumps (new scale). C: Two migration routes in foggy weather, and D: two routes in wet snowy weather. E: Directional migration by four animals close to a dark hut wall. F: When eight animals (a–h) were transported to the other side of the dark hut, their migration direction turned approximately 180°. Further explanation in the text

ping. However, some individuals showed a more or less constant jumping direction, as shown for *I. hiemalis* in Fig. 4E–F. It was decided to make a more systematic study of the behaviour of the most abundant species, *H. socialis*, in overcast weather with no patch of blue sky. All degrees of directional migration were found: Random walking or jumping, a tendency toward directional migration (Fig. 6B), a directional migration with some deviations (Fig. 6C–D), or successful navigation along a rather straight line (Fig. 6A). It was hypothesized that the animals might use the surrounding pattern of dark and light elements for short-distance navigation in overcast weather. The hypothesis was tested by manipulating specimens which navigated rather well 30–70 cm from a dark wall of a hut (Fig. 6E). First, it was confirmed that individuals, picked up and released again, resumed their direction of movement. Then, eight individuals with different migration directions close to one side of the dark hut, were moved to the other side of the hut and released. They all changed their directions approximately 180°, indicating that their clue for orientation was the position of the dark wall in contrast to the white snow on all other sides (Fig. 6F).

Among the four species, *H. socialis* shows a quite special feature in jumping behaviour. Upon landing, it often stands in a vertical position with head up. Then it bends forward to grip the snow. This movement takes about one second. Evidently, an adherent at the tip of the abdomen stops the rotation of the body at the landing point. Even animals landing on their back would often first raise to a vertical position before bending forward. This behaviour was easily seen if the animals were allowed to land on a sheet of paper. J. and U. Zettel (pers. comm.) noted that the closely related species *Ceratophysella sigillata* (Uzel) has a similar ability of sticking to the landing surface. Their information and discussions with Leinaas and Fjellberg (pers. comm.) makes it clear that the glue-like mechanism is the everted anal sacks described by Leinaas (1988). Including earlier observations by Hågvar (1995), we can distinguish between six behavioural phases for each jump in *H. socialis* (Fig. 7).

Only one case of mass migration on snow was observed among the Isotomidae species. It was a directed migration of an *I. hiemalis* crowd, observed on 11 January 1998 in Nordmarka, study area B. A half meter thick snow cover of a 5 m wide forest road was densely covered with collembolans over a length of about 200 m. All animals eagerly jumped in the same direction, following the road. Under this intense migration, the animals did not walk between the jumps, but simply rotated on the spot for about four seconds to decide the direction of the next jump. It is noteworthy that the

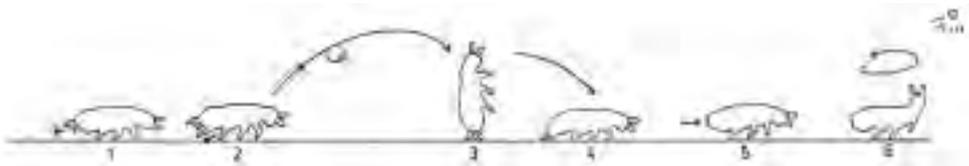


Fig. 7. Six phases during one jump in *Hypogastrura socialis*. 1: The animal contracts its body and extends the anal sacks. 2: The furca is released and the animal jumps. 3: Anal sacks “glue” the animal to the snow at landing and stops rotation. 4: The animal bends forward and grips the snow. 5: The anal sacks are withdrawn. 6: The animal rotates horizontally on the spot and positions itself for another jump at a certain angle relative to the sun

sky had a thin cover of clouds without a visible sun, but with a few spots of a faint blue colour. There were about 5 000 animals per m², which gives a population of about 5 million animals over the mentioned area of 1 000 m². However, these are minimum numbers, since animals also migrated in lower densities outside the “core population”.

Migration rates

Fig. 8 illustrates migration rates of the four species under different conditions. The fastest rate was observed during the above mentioned mass migration of *I. hiemalis*, with 15 jumps, each 8 cm, per min., resulting in 120 cm per min. Thus, the population of several million animals moved about 70 m per hour. The fastest migration rate in *H. socialis* was observed during mass occurrence in very mild, sunny weather, with 8 jumps corresponding to 80 cm per min. A maximum migration rate of 50 cm per min. was observed in *I. violacea*, and 22 cm per min. in *V. westerlundii*. At temperatures close to zero, all species showed low migration rates, and in combination with overcast weather, *H. socialis* moved very little. The two fastest migrators, *I. hiemalis* and *H. socialis*, are the two which also show mass migrations. During optimal conditions, they may migrate about fifty meters or more per hour, indicating that one individual should be able to cover several hundred meters per day.

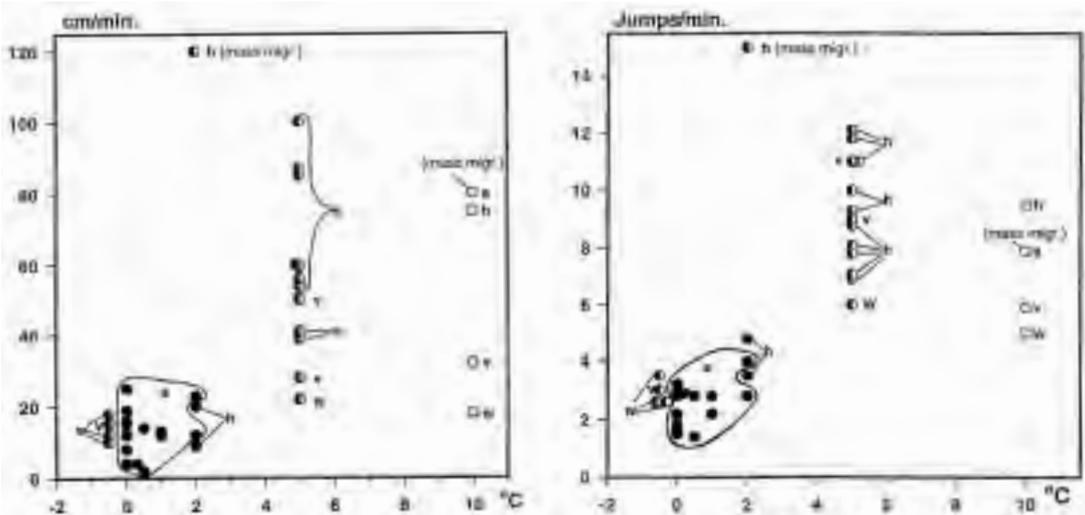


Fig. 8. Jumping rates (cm or number of jumps per minute) in the four species in different weather conditions. Temperature was measured in the shade at 2 m height and may be different from the air temperature close to the snow, but still indicates the conditions. Dark dots: completely overcast, partly dark dots: partly cloudy, and open dots: bright sunshine without clouds. h = *Isotoma hiemalis*, v = *Isotoma violacea*, w = *Vettagopus westerlundii*, s = *Hypogastrura socialis* (as well as dark dots not marked). The fastest rates in *I. hiemalis* and *H. socialis* were observed during mass migrations

Discussion

Why migrate, and why during winter?

Brummer-Korvenkontio & Brummer-Korvenkontio (1980) and Leinaas (1981a, 1983) showed that most edaphic Collembola species in coniferous forest migrate up into the lower snow layers during winter. Leinaas (1981a, 1983) assumed that surface-living Collembola by this general behaviour avoided unpredictable and harmful water-logging or freezing of the uppermost soil layer. He regarded the horizontal activity on the snow surface as being an evolutionary extension of the vertical migration within the snow layers, and assumed that surface activity had developed further into a dispersal behaviour in *Hypogastrura socialis* and *H. lapponica* (Axelson). Both of these species live in patchy and temporary habitats during summer, and sooner or later these colonies have to find new suitable patches. The colonies of *H. socialis* are situated in thick needle mats below selected spruce trees, and those of *H. lapponica* under the bark of old birches (Leinaas 1981a,c).

In Norwegian coniferous forests, the summer habitat of *I. violacea* is restricted to needle heaps below spruce trees, and that of *V. westerlundi* to lichen at the base of certain spruce trunks (Leinaas 1980, 1981a; Leinaas & Fjellberg 1985). In fact, the habitats of *I. violacea* and *V. westerlundi* are so restricted that these species are not found in ordinary soil samples (Hågvar 1982). In these two species, the dependence on patchy and temporary habitats may explain their need of dispersion. According to Leinaas (1981a), *I. hiemalis* is distributed all year over the whole forest floor under Norwegian conditions. However, in Switzerland, where the species is active on the snow surface in subalpine spruce forest, it occurs only in moist accumulations of needle litter during summer (Zettel 1984, 1985). So at least in parts of its distribution area, migration is important for the species. The local and unusual mass migration observed in *I. hiemalis* in area B could have been triggered by water logging of the soil in an area with very high densities of the species. During the two preceding days, it had been unusually mild, so that melting water from the snow layers seeped into the ground. Zettel (1984) showed that changing barometric pressure led to increased surface activity of *I. hiemalis* in Switzerland, thus being responsible for mass appearances. However, the present mass appearance was not connected to large changes in the barometric pressure.

Leinaas (1981a) assumed that *V. westerlundi* found in the snow had first climbed trees and then fallen down by accident. However, sweep-netting of spruce branches up to 3 m in the present study yielded no Collembola. Probably also the three Isotomidae species are able to migrate up and down through the snow layers like *H. socialis*, alternatively along tree trunks. It was observed several times that Collembola on the snow surface could disappear downwards into the snow, for instance when temperature dropped in the evening.

“Patch-dwelling” forest Collembola have little chance to find new habitats in summer, due to the adverse conditions between the ecological islands. Migration on the snow surface in winter is the only existing possibility to move over great distances, partly to establish new colonies and partly to exchange genes between colonies (cf. Zettel 1985). The snow surface has few obstacles and sufficient air humidity. The migration occurs outside the breeding and feeding season, and is rather safe from predators (cf. Leinaas 1981c; Hågvar 1995). According to Leinaas (1981a), nearly the

whole population of *H. socialis* is present on the snow surface on favourable days. Knowing that the winter activity of this species starts from very local colonies, their even distribution on the snow throughout the landscape reflects an intense migration activity in all directions. Leinaas (1981a) repeatedly measured a density on snow of approximately 4000 animals m⁻² during February and March, and concluded that *H. socialis* was the most numerous edaphic collembolan in the area. My estimates were in the same order of magnitude. Furthermore, the observations of migrating animals in the middle of frozen lakes suggest that whole landscape elements as lakes, bogs and rivers can be crossed, -an impossible task for a collembolan during summer. It cannot be excluded that wind may promote long-distance transport on snow. However, it was never observed that Collembola were blown along the snow surface. Migration activity was highest on calm days, and the observed migration rates alone could easily explain the ability to cross lakes.

Adaptations to winter migration

All four species show the following adaptations to migration on the snow: They have a tolerance for low temperatures, are able to penetrate the snow layers if the snow is coarse, and appear on the snow surface when the air temperature rises to zero or a few degrees above. Instead of random jumping, each animal jumps in a fixed direction by using the sun or probably polarized light as a "compass". The direction is checked before each jump by rotating or twisting the body. Because different individuals for some reason choose different directions, the animals are efficiently spread out in the forest. A certain navigation is sometimes possible even in completely overcast weather, probably by referring to dark and light objects in the surroundings. During temperature fall, the collembolans simply retract into the snow and reappear when the temperature increases again. These various adaptations may have developed independently in Hypogastruridae and Isotomidae.

An observation that even three specimens of *Isotoma viridis* Bourlet showed a directional migration on snow may indicate that an even larger number of species has this ability.

In alpine habitats during summer conditions, the movements of *V. westerlundii* were found to be independent of the sun (Leinaas & Fjellberg 1985). Instead, the animals headed toward tall objects, according to the fact that in the mountains, *V. westerlundii* lives on top of boulders. Another species, *V. sarekensis* (Wahlgren), living on the ground, migrated in a certain angle to the sun. However, their daily route would make a bow, since they did not compensate for the sun's movement (Leinaas & Fjellberg 1985). It is not known whether collembolans migrating on snow can compensate for the sun's movement. Hågvar (1985) found indications of this ability in *H. socialis*, since animals which retreated into the snow during the cold evening seemed to resume their direction the following morning.

Another question is: what induces different migratory directions in different individuals? One possible explanation is that a given animal begins migration towards the most open (and light) direction in order to avoid obstacles, and subsequently maintains this direction. During the observed mass migration of *I. hiemalis*, the animals followed the open forest road, without penetrating into the dense, dark forest on the sides. Also in *H. socialis*, Hågvar (1995) observed that whole populations often followed a main direction. When many populations gradually meet and cross, animals in

the same place may be seen to migrate in all possible directions. Since we do not know how far an individual observed in the field has jumped, this question needs an experimental approach.

H. socialis has two morphological specializations for winter migration. The first is a cyclomorphosis in the furca. During winter, the dens has larger teeth, improving the animal's grip on the snow surface (Leinaas 1981b). The other specialization is the use of the anal sacks as an "anchor" at landing. When Leinaas (1988) described the anal sacks in the Poduromorpha group of Collembola, the function of the sacks was unknown. However, he observed that, in culture, the anal sacks became everted, and thus visible outside the body, immediately before a jump. Leinaas (pers. comm.) also observed that the animals may be "glued" to the wall of the culture vial at landing. J. & U. Zettel (pers. comm.) made similar observations in cultures of the winter active species *Ceratophysella sigillata*. Even *Hypogastrura vernalis* (Carl) and *Xenylla humicola* (Fabricius) jump with everted anal sacks (Leinaas 1988), hence the phenomenon is not limited to winter active species. An interesting parallel is the use of the ventral tube for self-righting from a dorsal position in the Sminthuridae springtail *Sminthurus viridis* (L.) (Brackenbury 1990).

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