Notes and Discussion

Overland Migration of Collembola (Hypogastrura nivicola Fitch) Colonies

ABSTRACT: Dense aggregations of Collembola (*Hypogastrura nivicola* Fitch) move across the surface of the forest floor in central New England in the autumn and spring for distances of 20-25 m before disappearing. Colonies 30 cm in diam have populations of 0.5-1 million individuals. Hourly movement is as much as 75 cm and daily movement as much as 6 m. Overland movement ceases at night or when colonies are covered by black plastic sheeting.

INTRODUCTION

Black, moving, 20-30 cm diam colonies of the Collembola, *Hypogastrura nivicola* Fitch, are common on and in the forest floor in central New England in the spring and autumn. These springtail colonies have a slightly purplish hue and resemble accidental spills of lubricating oil and are thus often overlooked. Each colony consists of hundred of thousands of individuals 1 mm long and most colonies exhibit continual daytime unidirectional movement over the surface of the forest floor. Colony edges are sharply defined and the constantly jumping individual insects on the surface of the soil are so small they are not readily evident until a piece of paper or one's hand is placed near the advancing colony.

In early spring the flea-sized, black insects are conspicuous on snow, hence the name, snowfleas. On snow, however, individuals as a rule are spaced 5-10 mm apart and are not clustered into colonies, although occasionally thousands may occur together temporarily in footprints or other small depressions from which they cannot readily jump. After snowmelt, many individuals can be observed floating on small pools of water along the edges of small streams. They aggregate into black, moving colonies after the snow has gone.

Students seeing these moving clusters on the forest floor generally ask how many individuals there are in a colony, how fast the colonies move, whether they move in straight lines and how long a colony remains intact. Continuous observation of a small area at the Harvard Forest, in central Massachusetts, over a period of about 3 weeks in autumn 1971, when colonies were numerous and very active, provided answers to some of these questions. The same site also was observed frequently during 1972 and 1973 and, although there always seemed to be more colonies here than elsewhere in the vicinity, they were never as numerous as in 1971.

Congregating habits of Collembola are well known and swarms have been reported a number of times in the literature. Conspicuous swarms of *H. nivicola* (*Achorutes socialis* Uzel) have been described by Macnamara (1919), Judd (1950) and Cass (1951) on snow in Ontario. Maynard (1951) in New York and Snider (1967) in Michigan also called attention to large numbers on snow and, in addition, noted their fondness for maple sap made them a nuisance for maple sugar producers. Brown (1921) described swarming of *Achorutes* and others in England and Park (1949) reported a large outbreak of *A. bengtssoni* Agren in Illinois.

METHODS

Numerous colonies of *H. nivicola* were suddenly noted 21 September 1971 on a small watershed within the Prospect Hill 1 tract of the Harvard Forest where daily observations of water tables were being made. About 50 colonies

varying from 30-100 cm in diam were seen in both hardwood and conifer stands over an area of about 6 ha. Most of the colonies were localized in a 30-m wide, sloping depression in a 46-year-old red pine (*Pinus resinosa* Ait) plantation. Here, several colonies in an already gridded 91 x 122 m (300 x 400 ft) area were outlined with string and the shape and location plotted. On 3-5 occasions daily over the next few days the new positions of the colonies were reoutlined and plotted to provide information about the hourly rate of movement and changing shape of colonies. All colonies not outlined with string were marked at each visit by flags and the successive locations plotted. Observations continued through 14 October.

Three small colonies, each about 30 cm in diam, were collected *in toto* and the individuals driven from the sample by use of a Berlese funnel. Number of individuals in each colony was determined by counts on small subsamples.

During the autumn of 1972 several actively moving colonies were covered with black plastic sheeting at midday to simulate nighttime conditions. The sheeting was suspended about 30 cm above the soil to allow freedom of movement and all light was excluded. In front of several small colonies metal barriers 30 cm wide and 1 m long were placed on edge to see whether forward movement could be stopped. These barriers extended downward through the forest floor to the mineral soil.

RESULTS AND DISCUSSION

Various characteristics of migrating colonies are illustrated in Figure 1. During migration, colonies about 30 cm in diam tend to keep a roughly circular outline (Fig. 1A), although the advancing front itself is faintly crescentic. Large colonies a meter or 2 in width are distinctly crescentic (Fig. 1B), and the shape and size change noticeably in detail over periods as short as 5 min. A colony with long backward-curving tips tends to split into smaller colonies because the individuals in each arm advance in a more or less straight line (Fig. 1F).

Not all individuals of the colony are on the surface during migration. Removal of the forest floor litter shows at least 10, if not 100, times more within the loose upper 2-3 cm of forest floor than on the surface. In fact, an easy way to collect a sizable supply of the insects (Figs. 1C, 1D) is to find a colony where there are loose, whole hardwood leaves in the litter. The congregated springtails on the leaves can be picked up and poured almost like sand into a receptacle. The enormous number of insects under the surface perhaps accounts for the rapidly changing shape and size of the colonies. Considering the number within the forest floor, it is conceivable that most of the forward movement is done by crawling rather than jumping.

All colonies exhibited unidirectional movement (Figs. 1E, 1F) and their nearly straight-line advance was no more than temporarily halted by stumps or stones. They gradually moved around these small obstructions. Most movement in the small study area was downslope and toward the SW although several colonies moved upslope and toward the W (Fig. 1E). All overland movement was during the day. With the approach of darkness the colonies retreated into the forest floor and could be observed by flashlight just under the surface. By 8 AM the next day the colonies were on the move again. When taken to the laboratory and placed on a table, the insect's first movement was toward a bright light. Not enough observations were made to determine response to light in the forest. Certainly it is not great because patches of sunlight did not cause obvious response. On the other hand most, if not all, migrating colonies seem to move to the W or S. When a moving colony was

covered at midday by black plastic sheeting, the colony stopped forward movement. If, after 2 or 3 hr, the colony was uncovered, it continued forward movement until night. If covered for 4 hr or so, the colony disappeared into the forest floor. Metal barriers set on edge and penetrating the forest floor to the mineral soil below stopped forward movement of small colonies. Colonies

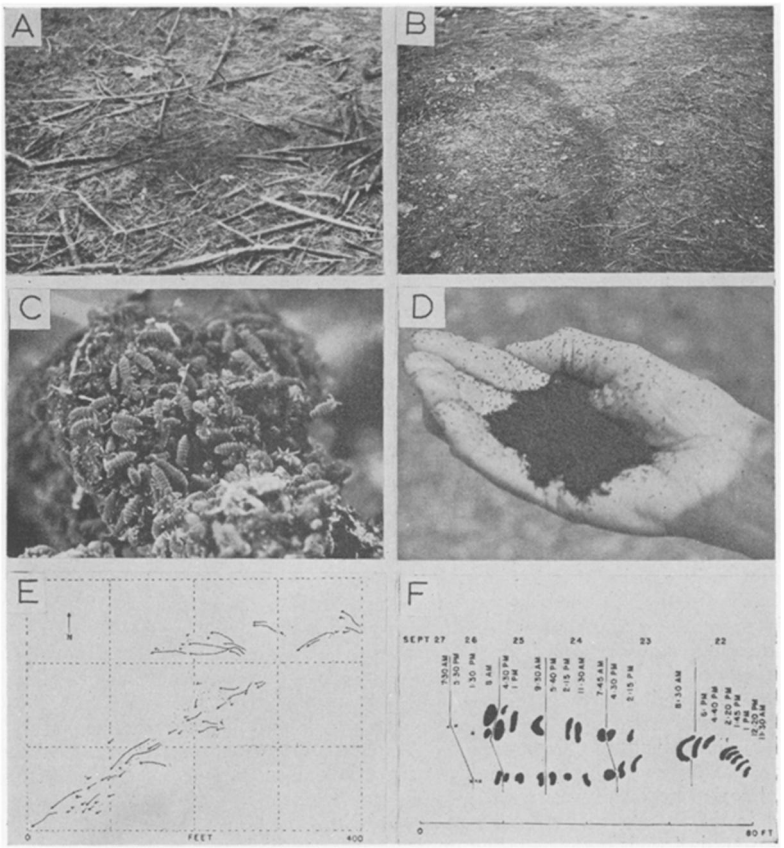

Fig. 1.—Characteristics of migrating colonies of *H. nivicola:* A. The dark blotch in the center of the photo is a medium-size, more or less circular colony ca. 30 cm in diam. B. The narrow streak extending vertically across the middle of the photo is a 3-m-long crescentic migrating colony moving toward the right. C. A group of springtails in late September. The individuals are about 0.7 mm long. D. In a medium-size colony there are hundred of thousands and they are easily collected in large numbers. As a guess there are about 0.5 million in the hand. E. Migrating colonies were localized in a small narrow area from 22 September to 3 October 1971. The lines with arrows show distances and directions traveled by migrating colonies. Dots show the location of colonies where overland movement was not actually observed. F. Diagram showing the changing shape and rate of movement for a 5-day period of a colony that divided during the 2nd day

remained in place and many individuals molted, leaving behind white exuviae. These are conspicuous against the brownish-black color of the forest floor.

Colonies were first observed on 21 September. From 22 September to 3 October 1971 inclusive the numbers of colonies on successive days in the 91 x 122 m study area were 17, 27, 38, 50, 46, 27, 3, 1, 25, 2, 0, 0. No observations were made on 4 October but on 5 October there were 25-30 colonies in the small study area and also a good many in other parts of the adjacent watershed where none had been seen since 22 September. From 5 October until daily observations ceased on 14 October only one or two colonies per day were seen. There was no obvious reason for the varying number of colonies. Daytime weather conditions did not seem to be the cause. In the autumns of 1972 and 1973, colonies appeared at the same time as in 1971 but in only half as great numbers. In the spring, isolated individuals are frequent on snow when the air temperature is above freezing. After the snow melts, colonies are common in forested areas during March, April and May but never as frequent as in the autumn. In some instances the insects cluster on the trunks of trees as well as on the soil.

During the period of detailed observation in the autumn of 1971 the longest distance traveled by a single colony was 25 m. Many colonies moved 10-15 m before disappearing altogether. Some colonies moved only 0.5 m, others seemed stationary. Those colonies that migrated for distances of 10-15 m moved an average of about 3 m per day; one colony moved over 5 m in 1 day. Hourly movement was about 30 cm and the greatest hourly movement observed, either in spring or autumn, was about 75 cm. Mature individuals in the spring often move rapidly for 1 day, then slow down the next. The greatest daily distance noted for travel in the spring was 6 m.

Many colonies completely disappeared overnight and were never seen thereafter. In these instances no individuals could be found in predicted advance positions even by removing the forest floor. The longest time one colony existed as an entity on the 91 x 122 m plot was 5 days.

Migration of Collembola was barely mentioned by Macnamara (1919), and his observations and those of others suggest that the insects generally return to the soil from the place where they emerged. This seems to be the case for *H. nivicola* at the Harvard Forest when on snow, since no migrating colonies have been observed under those conditions. It is also true, of course, for those colonies that remain in one place for a day or 2 during migration.

Individuals in the September and October colonies are roughly one third the size of adults seen in the spring. In three colonies sampled in late September and early October insects were 0.7 mm long, whereas those collected in November in the same area were 1.3 mm long. The mature insects are so heavy that the sound of their bodies landing on dry leaves can be heard distinctly.

Molting within actively migrating colonies was not observed but seemed to be common in stationary colonies. Macnamara (1919) and Brown (1921) postulated that swarming might result from lack of food. Another possibility is that swarming, in some manner, is related to molting. For example, a colony molted when its forward progress was stopped by an artificial barrier, and within a day or 2 a multitude of white cast skins were noted within the forest floor. In another instance molting took place at the junction of melting snow and the forest floor during several days of unusually warm weather in January. Molting and moribund groups of insects were observed under remaining patches of snow and large clusters of white exuviae were conspicuous on the surface of the forest floor where the snow had just melted. Also relevant is the observation that the white cast skins are rather common within the forest floor and always tend to be in groups rather than as isolated individuals. As a

matter of fact, Macnamara (1919) himself noted that white patches of cast skins were left next day after a large explosion of insects from a log.

Three medium-size colonies, sampled *in toto,* consisted of approximately 700,000, 600,000 and 400,000 insects. These are conservative figures because they are based on insects driven from samples over a period of 5 days in Berlese funnels where extraction was probably far from complete. Park (1949) estimated that somewhat more than 4 million insects emerged from an area of 6 sq ft and others have commented on the large numbers in swarms. At first, such enormous numbers seem unreasonable, but the counts of the three colonies at the Harvard Forest indicate that any colony a meter or more in width consists of at least several million insects. Figures in the tens, or even hundreds, of millions are indeed reasonable.

Estimation of the total population of *H. nivicola* in any one area is dependent on a sampling technique that takes account of the gregarious habits of the insects. Bellinger (1954), for example, in a broad study of Collembola occurrence in Connecticut sampled several areas during the course of the year and found *H. nivicola* in only one sample. If this insect tends to stay in localized colonies and in relatively small areas, it is easy to see how a whole population might be missed.

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Yearly Variation in the Phenology of California Annuals

ABSTRACT: The phenological development of seven annual plants growing in the chaparral climate of southern California was followed for periods as long as 6 years. Initiation of growth varied greatly from year to year as did the commencement of rain. Variability of the timing of subsequent phenophases was less, and was generally strongly correlated with the elapsed time from a previous phenophase rather than with climatic events. Time of reproduction was less variable than growth response, presumably reflecting different selective forces.

A large percentage of the rich California flora is composed of annuals. In general these plants germinate with the first rains of winter and complete their