

## The Role of Food in the Population Dynamics of *Orchesella cincta* (Linné) (Collembola)

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**Summary.** The feeding activity of the collembolan species *Orchesella cincta* (Linné) was studied in the laboratory and in the field. In the laboratory it was shown that at any one time only about 50–60% of the animals were feeding; the remainder were occupied with molting activities. Most of the time similar values were obtained in the field but during winter and during dry summer periods high percentages of empty guts could be demonstrated, indicating an absence or inaccessibility of food. When favorable weather returned, a high feeding activity was again observed. Laboratory experiments and field observations indicate that temporary starvation periods are followed by synchronization of the molting and reproductive rhythms and an apparent increase in longevity. These phenomena are important for the restoration of the population after unfavorable periods but reduce the stabilizing force of food scarcity.

### Introduction

The ecologic aspects of the nutritional biology of Collembola are discussed mainly in relation to the process of decomposition of litter material and the formation of the soil. Little is known about the significance of their nutritional biology for population dynamics, i.e., the effects of the feeding conditions on fecundity and survival. The distribution of Collembola depends greatly on the humidity conditions of their habitat; most animals can be found aggregated in humid places (Poole, 1961; Hale, 1966; Joesse, 1970). Long periods of drought lead to a decrease in number and size of such places where the animals can survive. Assuming that the animals become concentrated in these limited spaces, the local density will increase and competition for food might occur. On the other hand, Collembola are inactive during a great part of their life: they molt frequently and are immobile before and after each molt and do not feed for several days (de With and Joesse, 1971). Hence, at any one time the greater part of the population does not take part in the utilization of food resources,

which could result in a reduction of competition (Anderson and Healey, 1972; McMillan, 1975).

Studies on the food preferences of Collembola by examination of the gut contents of animals collected in the field, have nearly all led to the conclusion that most collembolan species are more or less unspecialized feeders (Petersen, 1971; McMillan, 1975). The differences in gut contents between individuals of the same species in different habitats are sometimes greater than between individuals of different species within one habitat (Gilmore and Raffensperger, 1970; Bödvarsson, 1970). In laboratory cultures most Collembola feed on a wide variety of organic material. This low degree of food specialization is thought to be associated with an excess of food available for decomposers (Anderson and Healey, 1972). However, where particular foods become rare at certain times, a strategy of adaptation to a varied diet would seem to be a distinct selective advantage (Emlen, 1973). Therefore it is important to investigate the availability of food for Collembola in field conditions.

Our knowledge is poor concerning the effects of variations in the availability of food. Usher et al. (1971) described laboratory experiments to investigate the effects of food availability on the growth and production of the parthenogenetic species *Folsomia candida*. Food appeared to play a major role in regulating the rate of population growth and in determining the maximum population density. Van der Kraan and Vreugdenhil (1973) demonstrated under field conditions that *Hypogastrura viatica* is sometimes limited in its food supply. This species feeds rather exclusively on unicellular algae that grow in great numbers in the surface layer of the soil. *H. viatica* cannot burrow and it can, therefore, only feed on algae growing at the surface of the soil, which can become rare when the soil is dried out or inundated. This causes periods of starvation, which may lead to a mass migration of animals searching for food (Jooisse, 1976).

In the present paper a description is given of an investigation into the nutritional state of individuals from a field population of *Orchesella cincta* (Linné). In laboratory experiments the relation between molting and feeding activity was studied at different temperatures and the effects of temporary food shortage on reproduction was investigated. The results are used to evaluate the field data on a population of *Orchesella cincta* with respect to the role of food availability in the population dynamics of this species.

## Materials and Methods

*Orchesella cincta* (L.) lives in the surface layer of forests, especially pine forests. The animals used in the laboratory experiments were sieved out of the litter of *Pinus sylvestris* plantations. They were kept in glass dishes (diam. 5 or 15 cm) with a layer (2 cm) of moistened plaster of Paris. The animals were fed with *Pleurococcus* sp. (green algae), taken from the bark of trees. The algae were washed and filtered. A homogeneous *Pleurococcus* suspension was offered in drops.

*Experiments on the Food Quality of Pleurococcus.* Studies on the effects of specific foods on growth and reproduction in Collembola are not numerous. Vail (1965) demonstrated that *Hypogastrura manubralis* showed the best results when fed on yeast. Snider (1971) had similar success with

*Onychiurus justii*. To determine the most suitable food for *Orchesella cincta*, six different diets were prepared that could all be administered easily and that did not prevent a direct observation of the animals.

These consisted of:

- malt agar (m.a.) with water (1:9)
- m.a. with milk (5:1)
- m.a. with milk and yeast (5:1:3)
- m.a. with milk, yeast, and glucose (5:1:3:5)
- m.a. with glucose and cellulose (5:5:3)
- algae (*Pleurococcus*)
- no food at all

Fifty animals were kept on each of these diets for 24 days, at a temperature of 20° C. Fecundity (number of eggs produced) was taken as a measure of food suitability.

*The Feeding Activity of Orchesella cincta in the Laboratory.* Feeding activity was assessed in isolated individuals and in mass cultures using two different methods. First, by counting the number of fecal pellets produced by one individual (this could be done only on isolated animals), and second, by counting the number of animals present on food. Non feeding animals always leave the food. Food was supplied in excess.

Isolated individuals were kept in glass dishes of 5 cm diameter. Three temperatures (10, 15, and 20° C) were studied and ten specimens used at each temperature. After an acclimation period of 3 weeks, the number of fecal pellets and the number of exuviae were counted daily. New food was given daily after each period of observation. There was a light period of 12 h per day.

The mass cultures contained 100 animals that were kept in glass dishes of 15 cm diameter. The number of animals present on the food was counted three times a day for 3 weeks. The mass cultures were maintained at different temperatures (2, 5, 10, 15, and 20° C) using one culture per temperature. The food was refreshed twice a week. This experiment was done initially with animals collected in June and then repeated in August.

*Laboratory Experiments on the Effects of Periodic Food Deprivation on the Fecundity, Growth, and Survival of Orchesella cincta.* The egg production of 100 discontinuously fed animals (a cycle of 2 weeks *Pleurococcus*, which was refreshed twice a week, followed by a week starvation) was compared with the egg production of 100 animals continuously fed on *Pleurococcus*. The experiments were continued until 50% of the animals had died. The animals were collected from the field in November and kept in glass dishes of 15 cm diameter at 20° C.

*Field Observations.* The percentage of animals with gut contents was determined several times between February 1973 and September 1976 in populations from different sampling sites. The animals were collected by pitfall traps, which were emptied once a week (De With and Joosse, 1971); from Tullgren samples (Joosse, 1969), and from hand-collected samples. The latter was done by sieving out the litter and humus layer. The Tullgren- and hand-collected samples were taken at random. The hand-collected samples consisted of at least 100 individuals of *O. cincta* that were fixed at the sampling site by the method of Gisin (1960). After some days they were cleared for 24 h in 10% KOH. The gut contents when present are then easily visible.

Temperature and rainfall data were obtained from the nearest weather station.

## Results

### *Food Suitability*

From Table 1 it is apparent that, of the different diets offered, *Pleurococcus* is the most suitable food for laboratory experiments with *Orchesella cincta*. A rough analysis of the gut contents of 25 specimens of *O. cincta* from a pine wood revealed that 45% of the determinable contents of the guts consisted

**Table 1.** Total number of eggs produced by 50 individuals of *Orchesella cincta* fed for 24 days on different foods

	<i>Pleurococcus</i>	No food	Malt agar	M.a. +milk	M.a. +milk +yeast	M.a. +milk +yeast +gluc.	M.a. +milk +yeast +gluc. +cell.
Total No. of eggs	997	0	41	0	4	38	26

of *Pleurococcus*. The guts of 10 animals from a mixed deciduous wood contained about 25%. Hence, *Pleurococcus* seems to be an important food for *O. cincta* also in natural conditions. For these reasons this diet was supplied in all subsequent experiments. It has the additional advantage that it can be administered very easily.

#### *Feeding Activity of Orchesella cincta under Experimental Conditions*

In previous work (De With and Joesse, 1971) it was demonstrated that the time spent feeding is limited by the molting process. Since the molting rhythm is influenced by the temperature (Joesse and Velkamp, 1970), the experiments were set up to establish the relationships between feeding activity and temperature and molting. Since the molting frequency at temperatures below 10° C is very low, reliable data could only be obtained at lower temperatures by using mass cultures.

#### *Observations on Individual Animals*

The daily production of fecal pellets and the times of ecdysis (arrows) of 5 arbitrarily chosen individuals from each temperature group are presented in Figure 1. The daily feces production, which is of course related to feeding activity, shows remarkable variations, which appear to be associated with molting.

It is clear that during each instar there is a regular pattern of feces production. The cessation of feces production some days before the molt is related to the development of a new cuticle (de With and Joesse, 1971). The pattern is similar in the different temperature treatments but the absolute duration of the feeding- and nonfeeding periods varies (Fig. 1). The mean number of days on which feces were produced per instar (calculated from the data of 10 individuals) decreases with increasing temperature (Table 2). However, the instar duration also decreases. It appears that for about 55% of the total instar duration the animals produced feces at all temperatures and at all moments (Table 2). This becomes apparent also from the mean percentage of filled guts; those animals that produced feces had filled guts.

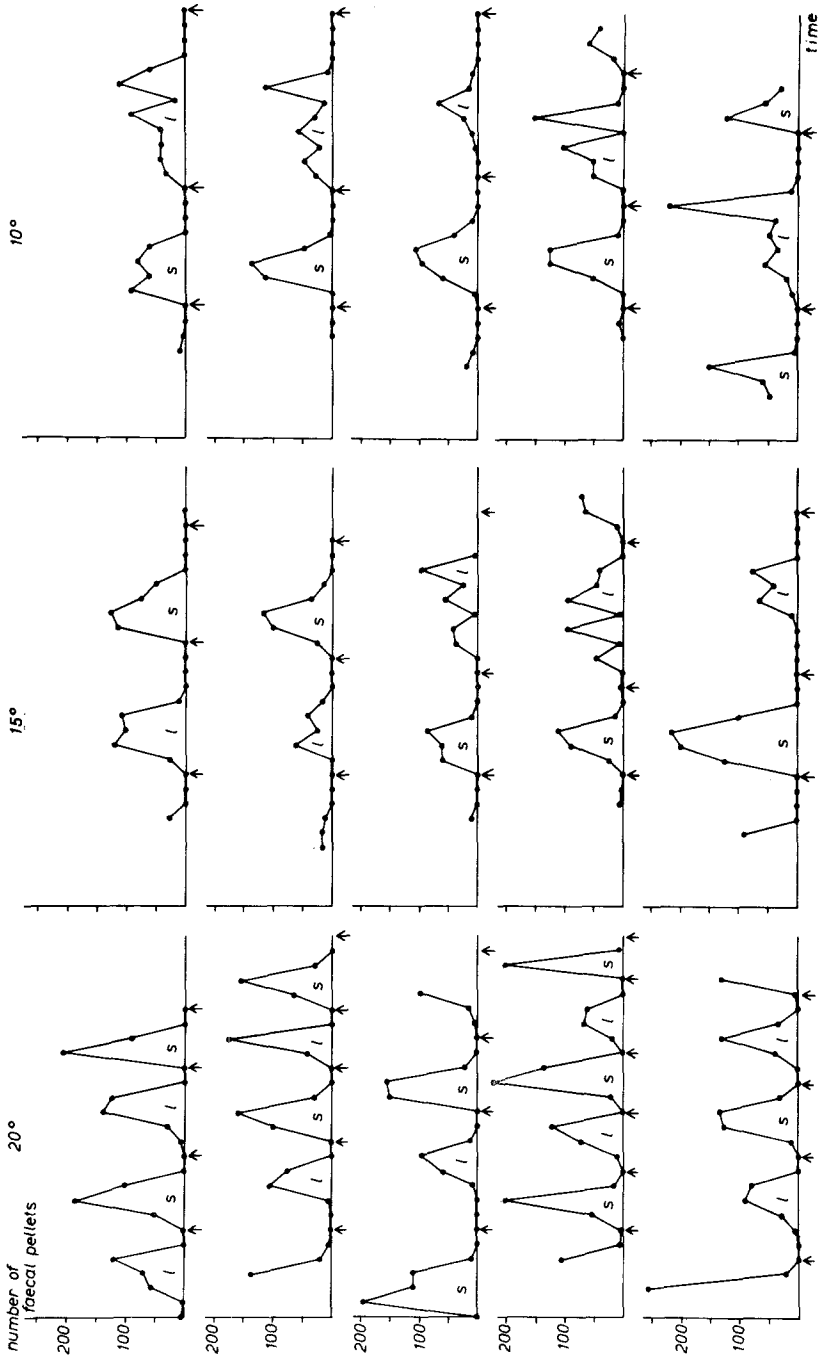


Fig. 1. Feeding activity in relation to molting and temperature in *Orchesella cincta*. *s* and *l* indicate short and long instar respectively;  $\uparrow$  molt

**Table 2.** Gut contents of isolated specimens of *Orchesella cincta* in relation to temperature

Temperature (°C)	Duration of feces production		
	In days per instar ± S.E.	As a % of instar time ± S.E.	Mean % filled guts ± S.E.
10	5.6 ± 0.5	54.5 ± 2.9	54.3 ± 2.9
15	4.5 ± 0.2	52.7 ± 2.2	51.0 ± 3.2
20	3.0 ± 0.1	59.5 ± 2.3	57.6 ± 3.7

**Table 3.** Feeding activity in experimental populations (mass cultures) of *Orchesella cincta* in relation to temperature

Temperature (°C)	Mean % feeding activity per observation ± S.E.		
	June population	August population	Isolated individuals
2	+	+	—
5	5.6 ± 0.7	3.8 ± 0.7	—
10	18.9 ± 1.7	18.5 ± 1.7	22.8 ± 0.3
15	21.0 ± 1.2	21.5 ± 1.2	23.8 ± 0.2
20	27.1 ± 0.8	23.9 ± 1.9	27.7 ± 0.3

On the basis of these individual observations, from 50 to 60% of the animals in a population could be expected to have food in their guts when temperatures are in the range studied. Provided that they can feed sufficiently and continuously during their feeding phase only 50–60% of the animals in a population are in a fed state at any one time.

### Mass Cultures

The feeding activity (i.e., the percentage of animals present on the food) observed in mass cultures of 100 adult animals is presented in Table 3. This measurement is different from the parameter feces production as a measurement for feeding activity, because after cessation of feeding the animals leave the food and still produce fecal pellets for at least 24 h. For comparison the percentage of animals present on the food observed on individual specimens (see previous Section) are added to Table 3. It appears that about 30% of the animals produce feces without being feeding-active.

It is clear that below 10° C the animals are completely inactive and die after a short time. The animals in the mass cultures seem to behave similarly with respect to feeding, to those kept individually. There is a tendency for a somewhat lower feeding activity of the animals in mass cultures, but this may be caused by disturbing effects between individuals. For the isolated individuals of Table 3 it was demonstrated that 50–60% had food in the gut (Table 2). It is assumed that a similar value would be obtained in the mass cultures. Conse-

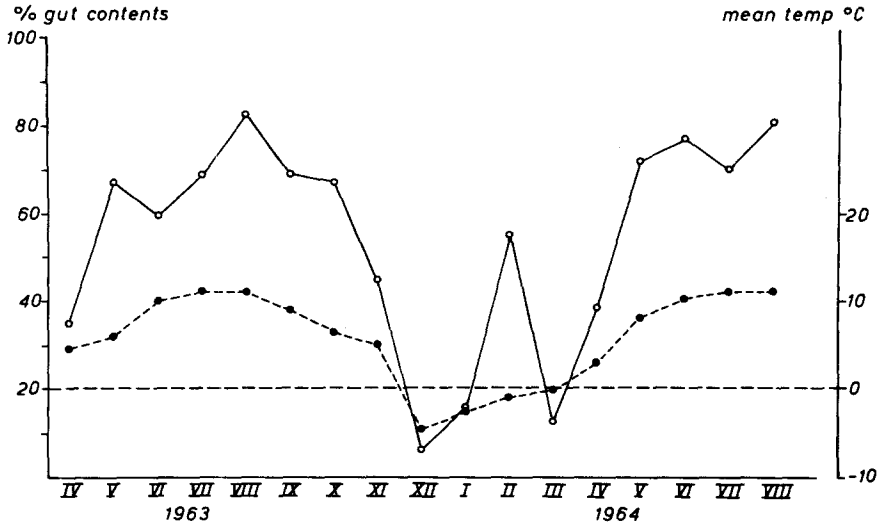


Fig. 2. Feeding conditions of field population of *Orchesella cincta* throughout the year. ○—○ % of animals with food in their guts; •—•—• mean monthly temperature

quently, it can be expected that in field conditions at temperatures above 10° C, when food is available, 50–60% of the animals will have food in their guts.

#### *Observations on the Feeding Activity of Orchesella cincta in the Field*

The data on the percentage of animals with food in their guts in field populations of *O. cincta* collected by pitfall traps are given in Figure 2. These data are derived from de With and Joosse (1971). Clearly the percentage of animals in which food was present in the gut shows a distinct pattern of change during the year that correlates with the mean soil temperature, suggesting a dependency of feeding activity on temperature. At temperatures below about 10° C, feeding activity appeared to decrease dramatically as it did in the laboratory experiments. During the winter months the gut is empty but rising temperatures in spring stimulate feeding activity. On the average the percentage of animals found to contain food in the gut at temperatures above 10° C is high in comparison to the values obtained in the laboratory experiments (75 and 50%, respectively). This difference may be an artefact since molting animals (one category that has an empty gut) are immobile for a few days (De With and Joosse, 1971) and are not caught in pitfall traps. Thus pitfall trapping is considered to be a selective sampling method, giving only relative information about the feeding state of Collembola.

A similar problem is raised by the Tullgren method since, in comparison with hand-collected animals fixed on the same date (12 July 1973), at the same sampling site a very low percentage of animals extracted by the former method had gut contents (Table 4).

**Table 4.** Effect of the Tullgren treatment on the number of animals with food in their guts (samples taken July 12, 1973)

	No of animals	% with gut contents
Tullgren	233	9.0
Hand-collected	249	82.3

From the extreme difference between Tullgren- and hand-collected data it can be seen that conclusions about the feeding conditions of field animals based on Tullgren samples, are unreliable. A stay of 7 days in the drying environment of the Tullgren apparatus results in a severe decrease in the number of animals with food in the gut. Therefore, for field studies on feeding activity, it is best to use hand-collected animals since it may be assumed that they allow reliable conclusions as to the feeding conditions.

For the present study, hand-collected samples were taken in a pine forest (Spanderswoud) near Hilversum (generally at intervals of about one month but additional samples were taken during and after dry periods). The results are presented in Figure 3 together with the mean temperature and total rainfall per day. On the basis of the laboratory experiments, the percentage of animals with food in the gut is expected to be 50–60% (at temperatures above 10° C). This expected range is indicated in Figure 3. The percentages of animals found in the samples with food in the gut are presented with twice the standard error (S.E.). Where the difference between the observed and expected values exceeds twice the S.E., this difference is judged to be significant ( $\chi^2$ -test;  $\alpha=0.05$ ).

It is clear from Figure 3 that many values are not significantly different from the expected range based on our laboratory results for animals with sufficient food supply. It is suggested that at those dates sufficient food was available. However, a number of samples showed values that were significantly different from the expected range. These are interpreted as follows. First, the low values observed on February 20, April 7, November 3, 1973, and on March 11, 1974, correlate with the fact that the temperature was below 10° C. In the laboratory experiments under these conditions similar low percentages of animals with food in the gut were observed.

Second, a number of extraordinary feeding conditions can be related to particular climatic conditions. The picture is most clear from a daily analysis of the gut contents during the dry summer of 1976 as presented in Figure 4. These data are based on at least 400 animals per sample. Very low percentages of animals with food in the gut were found during the dry periods indicated in the rainfall graph for June and end July-August. The drought apparently caused food shortage; until July 13 and August 24, 1976, the gut of nearly every animal was empty. Subsequent rainfall apparently had a sudden effect on the food supply: one day later, on July 14 and August 25, 1976, 98% and 95% respectively of the animals had food in the gut. This points to a synchronized onset of feeding activity related to the rainfall. From laboratory observations in starvation experiments it appeared that such a synchronization is related to the molting rhythm and can be traced for about 2 weeks. Subsequently the synchronization disappears as a result of individual variations in



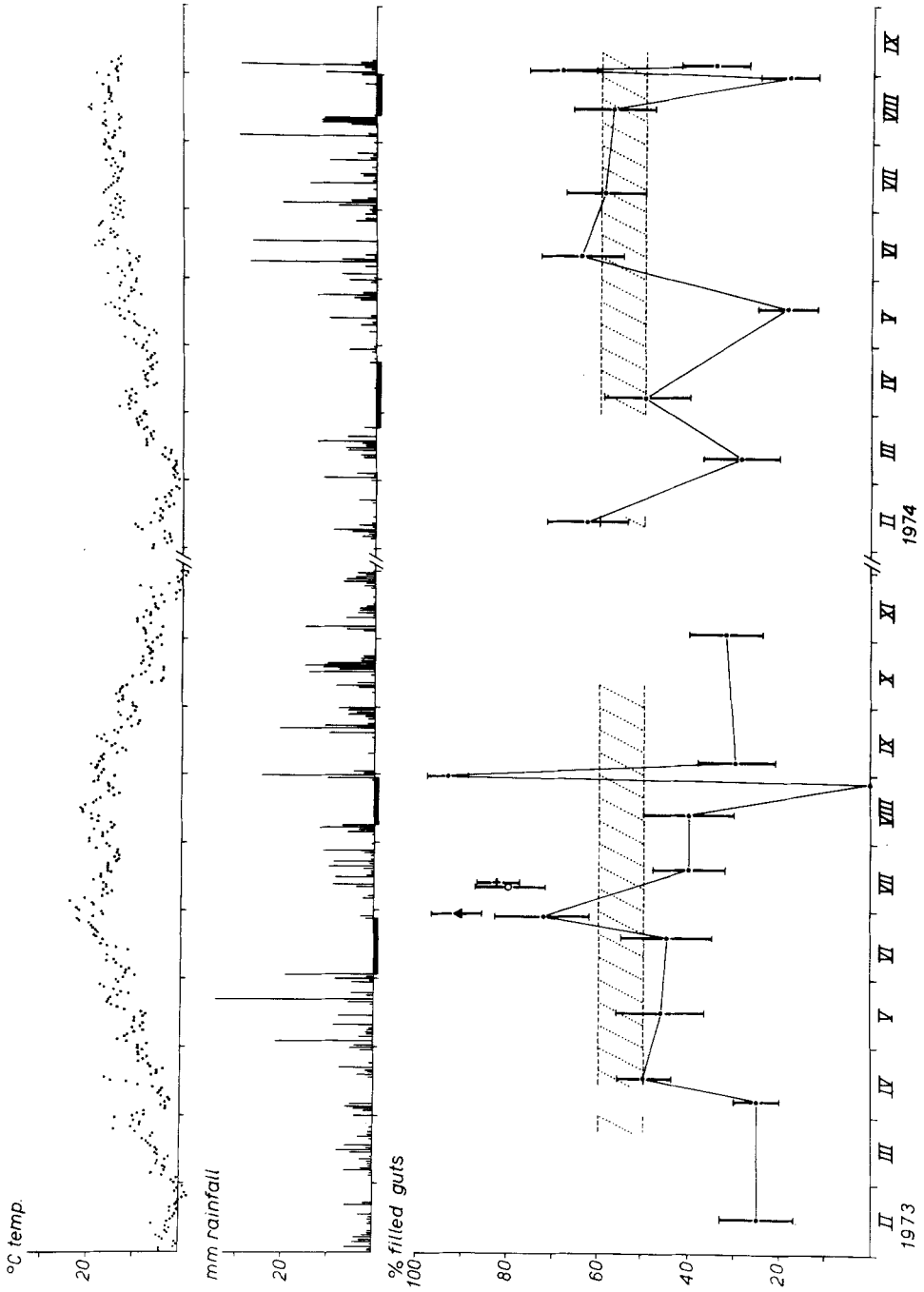


Fig. 3. Percentage of animals with gut contents in field populations of *Orchesella cincta*. The investigated dry periods are indicated below the abscissa. The shaded area indicates the expected percentages of filled guts at temperature above 10° C

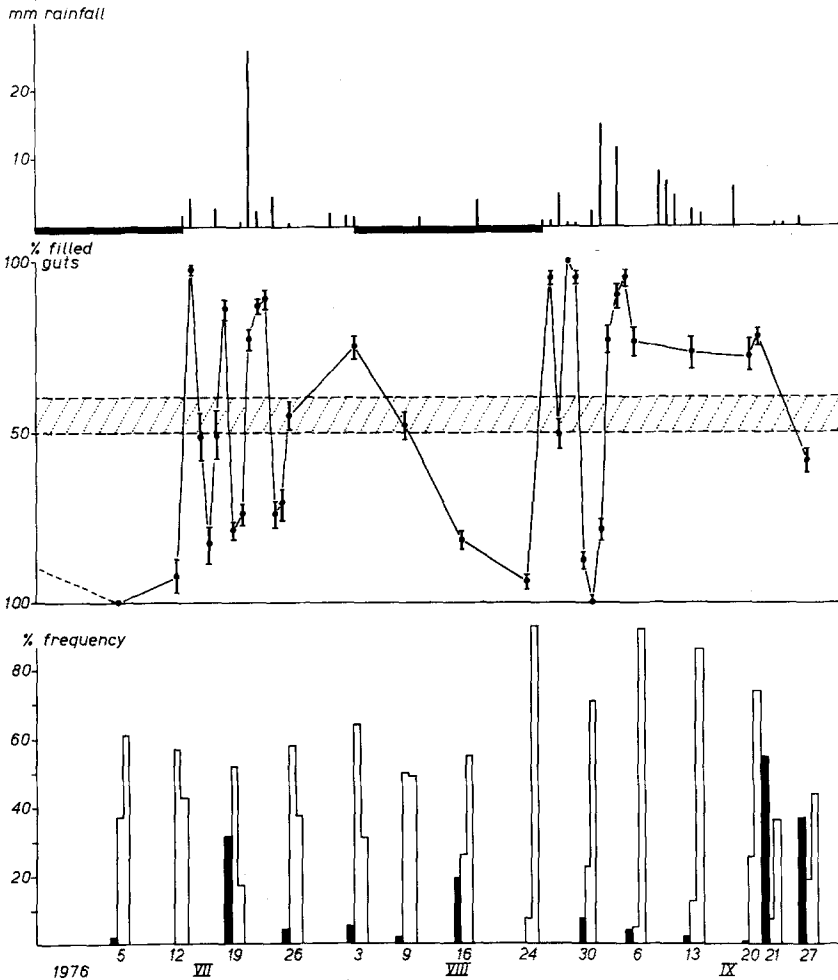
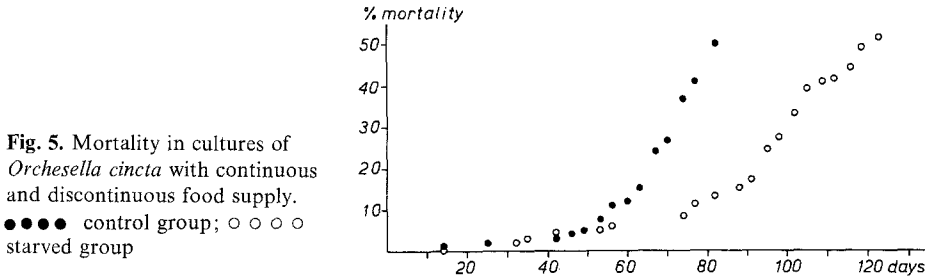


Fig. 4. Synchronization and reproduction in a field population of *Orchesella cincta* after food shortage. Black columns indicate % of animals just hatched. Each second column represents animals of 0.6–1.3 mm, the third column represents animals of > 1.3 mm

the duration of the instars (Jooose et al., 1973). A synchronized rhythmicity in feeding activity was also observed in the field in July and August 1976. The molting interval appeared to be about 4–5 days, which is similar to that found in the laboratory between 20° and 25° C (Jooose et al., 1973).

It is possible to recognize similar phenomena during the previous years (Fig. 3). Drought caused food shortage until August 27, 1973. A few days later, on August 30, after rainfall, 93% of the animals had filled guts. The low value of 30% on September 6, 1973, is probably related to a still synchronized molting activity. Thus, low values can be caused by dry conditions or by synchronization after rainfall following a dry period. The low value of August 30, 1974, was caused by the dry weather conditions and the low



values of July 19, 1973, and May 17, 1974, by synchronization. Other high values were also obtained under the same climatic conditions at three other sampling sites (Fig. 3, single points).

#### *Experiments on the Effects of Periodic Starvation on the Fecundity, Growth, and Survival of Orchesella cincta*

In the previous Section it was demonstrated that, in the field, food occasionally became rare for *O. cincta*. The question arises whether food limitation could have an effect on the population dynamics (i.e., the fecundity and survival) of the species. Therefore the effects of continuous and discontinuous food supply on survival, egg production, and molting activity were studied in the laboratory. The mortality data are presented in Figure 5. After 12 weeks, 50% of the animals of the group with continuous food supply had died, but in the culture with discontinuous food supply this point was reached after 18 weeks. Hence, the longevity of the periodically fed animals appeared to be increased in comparison to the animals with continuous food supply. The more rapid aging of the animals in the latter group may be connected with their higher metabolic activity (Joosse and Testerink, 1977), a feature perhaps reflected in their egg production. The results of the egg production are given in Figure 6. The total production of 8869 eggs in the cultures with continuous food supply was reached after 12 weeks. An equivalent number of 7904 eggs in the cultures with periodical food supply was reached after 18 weeks.

In Figure 7 the egg production of the starved group is compared to the molting activity. It is clear that a starvation period followed by feeding induces a synchronization of ecdysis and of egg production.

#### *The Effects of Starvation on Reproduction in Field Populations*

The effects of starvation on reproduction in field populations of *Orchesella cincta* are shown in Figure 4. A dry period in June/July 1976 resulted in very high percentages of animals with an empty gut. After rainfall (July 13) the individuals became synchronized in feeding activity and (according to the laboratory data) presumably in molting activity.

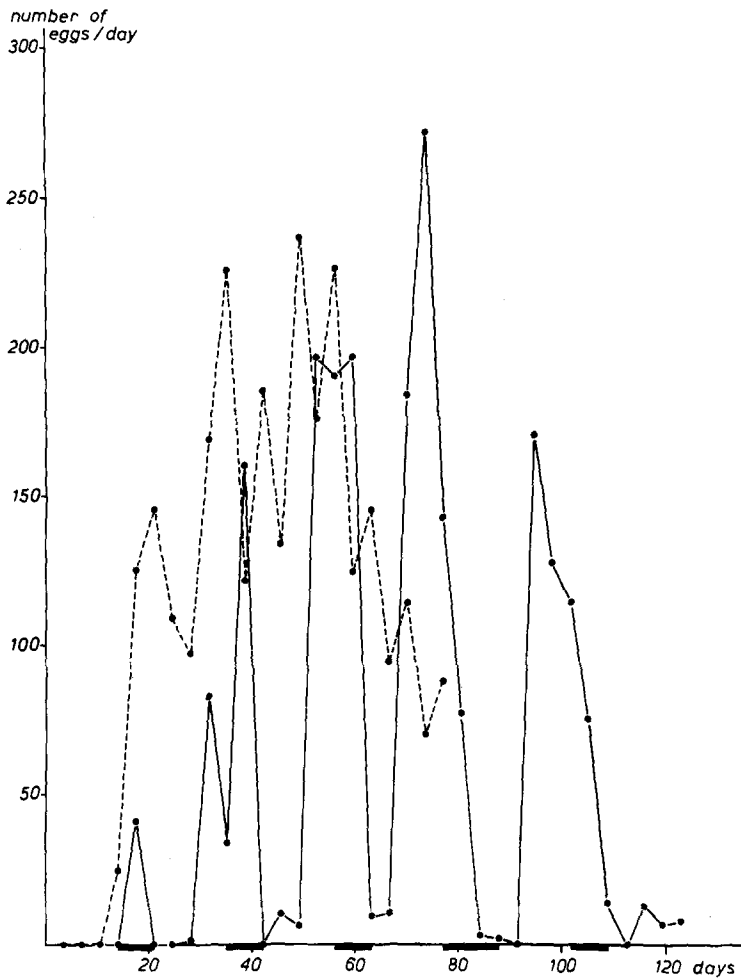


Fig. 6. The effects of continuous and discontinuous food supply on the egg production of *Orchesella cincta*. - - - control group; •—• starved group; ■ starvation period

The frequency diagrams of the lengths of the individuals, taken before and after the rainfall, demonstrate a sharp increase in the number of newly hatched individuals within one week of the resumption of feeding activity. Since from laboratory observations the egg development appeared to take 4 days at the prevailing temperature, the eggs must have been laid within three days of the start of the rainfall. In August the time interval between rainfall and appearance of newly hatched individuals seemed to be longer. The reason is not yet known.

Apparently the synchronization of reproduction remains for a rather long time. On September 20 no young animals were found whereas on September 21 a sudden explosion of newly hatched individuals was observed.

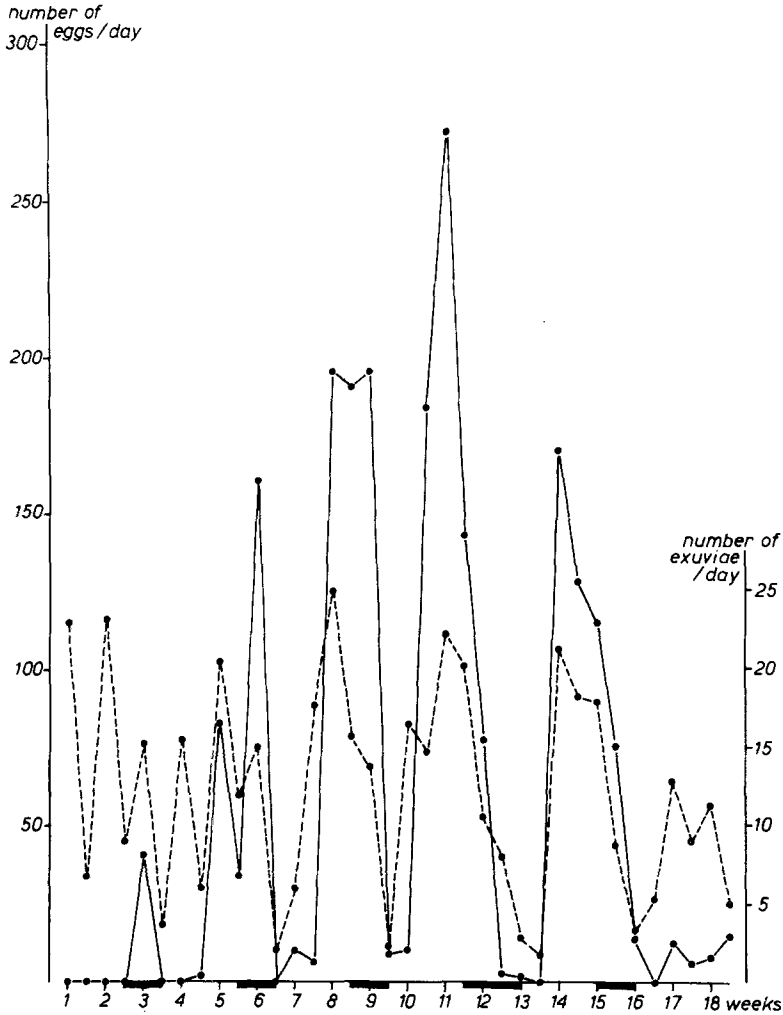


Fig. 7. Egg production in relation to molting in a culture of *Orchesella cincta* with discontinuous food supply. • - - - • number of exuviae; • — • egg production; ■ starvation period

### Discussion

The analysis of the feeding activity of *Orchesella cincta* in the laboratory shows that, when there is an excess of food at any one time, only about 50–60% of the animals are in a fed state. The remainder do not feed at all due to the molt cycle (de With and Joosse, 1971). The data from the temperature experiments reveal that below 10° C the percentage of fed animals is significantly lower. A similar temperature effect has been described for other soil arthropods, e.g., millipedes (Van der Drift, 1951; Barlow, 1957; Gere, 1962).

A comparison of the laboratory data on the feeding activity (Tables 2 and 3) with those obtained from the field (Fig. 3), reveals that most of the time

similar values are obtained. Only in dry field conditions is a difference from the expected value of 50 to 60% apparent. In extremely dry conditions even a value of nearly 100% for the incidence of empty guts can be recorded (Figs. 3 and 4). A similar phenomenon may be the cause of the differences between the percentages of springtails with an empty gut (31.3–52.5%) as found in southern Sweden by Bødvarsson (1970) and in a coniferous forest (up to 97.6%) in Hälsingland in northern Sweden (Bødvarsson, 1973). The Hälsingland forest is a relatively dry habitat, since it is dominated by the species *Anurophorus laricis*, which occurs especially in the litter. This corticolous species is xerophilous (Agrell, 1941). At the moment of sampling, Bødvarsson (1973) found the greatest concentration of individuals in the humus layer. This may point to the fact that at the sampling time the habitat was relatively dry, causing a food shortage and, therefore, a large number of animals had an empty gut.

Rainfall, following a dry period, induces a high feeding activity because new food becomes available or more accessible. A similar phenomenon has been demonstrated in the field for *Hypogastrura viatica* (Joesse, 1976). This species occurs on salt marshes. Periods of inundation of the habitat, during which the animals cannot feed and are washed ashore together in thousands are followed by a mass migration back to the original habitat as soon as the climatic conditions improve.

The renewed high level of feeding activity leads to a synchronization of the molting rhythm and from the present study it is apparent that this also synchronizes the reproductive cycle. Moreover, since food limitation increases the longevity of the individuals, their chances of survival during bad conditions increase. These phenomena are considered to be survival mechanisms. After unfavorable periods, when many local populations presumably become extinct, the few populations that happen to have been in the more favorable places will survive and, when favorable conditions return, these may act as foci from which the whole region is recolonized. A similar mechanism was described by Birch (1971) for the rabbit in semi-arid areas of Australia.

The role of food scarcity is considered to be an important source of stability reducing the amplitude of population fluctuations (Smith, 1972; Joesse and Testerink, 1977). The synchronizing responses of the collembolan population to starvation demonstrate a method of reducing the demand for energy in populations suffering from food scarcity and thus increasing the chances of survival of the population. By this means the stabilizing role of food scarcity is reduced, the population being less responsive to changes in food supply than it should be. Therefore the population numbers must be regulated by other stabilizing forces (Joesse and Testerink, 1977). Predation (Ernsting, 1977) and soil moisture conditions (Verhoef, 1977) are considered to be important in this respect.

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