Dispersal of the collembolan, *Folsomia candida* Willem, as a function of age

D. L. JOHNSON[1] AND W. G. WELLINGTON
Institute of Animal Resource Ecology, University of British Columbia, Vancouver, B.C., Canada V6T 1W5
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The tendency of *Folsomia candida* to disperse varies with age. In laboratory experiments, the youngest individuals rarely moved from the release sites in dispersal trays, while the older *F. candida* showed a tendency to move into more distant areas. Distance travelled is an approximately linear function of body length, and length is a power function of age in this species. The same linear relationship between dispersal and age was apparent over short (2 h) and long (24 h) dispersal periods. When food was present on the release site, the dispersive behavior of the youngest and the oldest classes was unchanged. However, the presence of food restricted travel of medium-sized springtails, many of which remained in the release site to feed. Since these young adults begin oviposition while still growing at a relatively high rate, their food requirements are higher than younger and older springtails. This change in behavior significantly altered the relationship between size and distance travelled. In natural situations, it is advantageous for the youngest individuals to remain in the area in which they hatched, where ample food and moisture are likely to be found. Because of their greater tendency to disperse, the older individuals spread their eggs over a larger area.

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La propension à la dispersion varie avec l'âge chez *Folsomia candida*. En laboratoire, les individus les plus jeunes s'éloignent rarement de leur point de libération sur une aire expérimentale, alors que les individus plus âgés ont tendance à s'éloigner considérablement. La distance parcourue est une fonction linéaire de la taille et celle-ci est une fonction géométrique de l'âge. Cette relation s'applique à la fois dans les expériences de courte (2 h) et de longue durée (24 h). Malgré l'addition de nourriture au point de libération, les comportements de dispersion des jeunes et des vieux restent les mêmes. Cependant, plusieurs collemboles de taille intermédiaire demeurent au point de libération pour se nourrir. Puisque ces jeunes adultes commencent à pondre tout en maintenant une croissance rapide, ils ont des besoins alimentaires plus importants que les jeunes et les vieux. Ce comportement modifie significativement la relation entre la taille de l'insecte et la distance parcourue. En nature, il est avantageux pour les jeunes de demeurer à l'endroit où ils ont éclos et où ils ont plus de chance de trouver une abondance de nourriture et d'humidité. Les insectes plus âgés, qui ont une forte tendance à se disperser, répartissent ainsi leurs œufs sur une grande surface.

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Introduction

Although dispersal is a major determinant of population change, dispersers are not necessarily typical members of a population: certain types of individuals seem obliged to disperse, whereas others do not. Such differential dispersal, achieved through differences among age classes, genetic groups or physiological types, is an effective means of dealing with a highly unpredictable world (Southwood 1962; Johnson 1969; Wellington 1979, 1980; Stinner *et al.* 1983). Dispersal therefore should not be treated as the simple diffusion or "leakage" from a population that Elton (1930) once suggested (Wellington 1980).

Short-distance dispersal may be vitally important to soil arthropods, particularly those collembolans which live in small patches of choice habitat. Although springtails inhabit the litter, fermentation, humus and, in some cases, mineral layers of the soil, for a number of environmental reasons they occur there in aggregated or "underdispersed" spatial patterns (Christiansen 1964, 1970; Butcher *et al.* 1971). Despite the frequent reports of swarming collembolan populations (i.e., mass migrations over the snow or soil surface) the details of their short-distance ambulatory movements have been largely neglected. This study examines the differences in dispersive tendencies among *Folsomia candida* individuals of different ages.

Folsomia candida is a relatively well-known isotomid, found in forests and grasslands throughout Europe and North America. It is apparently parthenogenetic, and has an ametabolous–monophasic developmental sequence in which periodic moults throughout life produce up to 30 instars. It is soft-bodied, blind, and for locomotion is equipped with six clawed legs and a short spring (furcula) arising from the ventrum of the fourth abdominal segment. Detailed observations on the life history and biology of *F. candida* have been published by Milne (1960), Marshall and Kevan (1962), Green (1964*a*, 1964*b*), Snider (1971), Snider and Butcher (1973), Gregoire-Wibo and Snider (1977), Hutson (1978*b*), and Johnson and Wellington (1980*a*). Ecological experiments with this species have been conducted by Christiansen (1970), Usher *et al.* (1971),

[1]Present address: Research Station, Agriculture Canada, Lethbridge, Alta., Canada T1J 4B1.

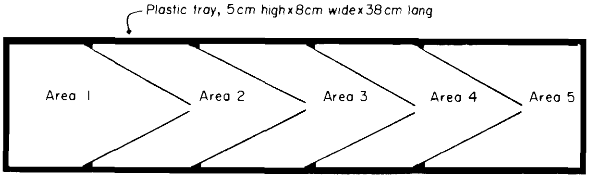

FIG. 1. The design of the trays used in the dispersal experiments. The floor consisted of the same plaster of Paris – charcoal mixture used in the culture jars. The angled glass dividers separating areas 1–5 were arranged to channel any dispersing springtails from their starting place in area 1 towards areas 2–5.

Torne (1974), Usher and Hider (1975), and Usher and Stoneman (1977). Christiansen (1970) also investigated its ambulatory movement in relation to environmental conditions, but without regard to age.

Materials and methods

Folsomia candida cultures were obtained from stock maintained by Dr. V. G. Marshall of the Pacific Forest Research Centre, Victoria, Canada. Populations were kept in 150-mL plastic specimen jars, 12 h at 14°C : 12 h at 18°C. Each jar had a floor 1.0–1.5 cm deep (area = 18 cm^2) of technical plaster of Paris mixed 40:1 with charcoal. The charcoal was a mixture of 2 parts powdered activated charcoal to 3 parts powdered animal charcoal, providing a dark substrate with a pH of 5.5–6.0 (Hutson 1978*a*). Floors were kept saturated, but not visibly wet, with distilled water. The populations were fed once a week on powdered yeast. Populations were intermixed regularly to ensure a homogeneous source of experimental animals.

In each of the following experiments, a population of *F. candida* was introduced into area No. 1 of a plastic tray similar to the illustration in Fig. 1. Glass dividers sunk into the substrate were arranged to channel movement in one direction and, in practice, effectively prevented movement against the outward-bound traffic. The distances of areas 1–5 (Fig. 1) from the release site were, respectively 0, 8, 16, 24, and 32 cm. Thin plastic was stretched over the top of the tray to maintain the required high humidity. *Folsomia candida* only tend to "spring" upon encountering dry air, so they do not normally use this type of movement to disperse. All the dispersing individuals in our populations walked.

Age and body length are closely related in these springtails. (Fig. 2). The body lengths (measured from the anterior of the head to the posterior of the anal segment) were recorded at the end of each experiment with a micrometer mounted in a binocular microscope. The length classes used ranged from 0.20 mm (approximate length at eclosion) to 1.60 mm (length at age > 3 months).

Experiment 1

Hypothesis—Some age-classes have greater tendencies to disperse than others. To test this hypothesis and determine the relationship between age (i.e., body length) and dispersive tendency, a population of springtails was released into area No. 1 of a tray held at 16°C and allowed to move into the other areas for 24 h. After this period the numbers and sizes of springtails in each area were recorded.

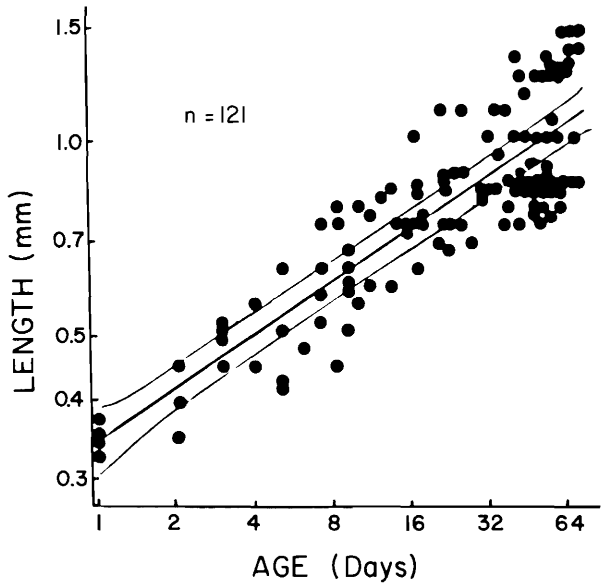

FIG. 2. The relationship between length and age of *F. candida* reared at 14 and 18°C. The graph shows length in millimetres. The length in micrometres is described by the equation $\ln L = 5.853 + 0.271 (\ln A)$, $r^2 = 0.749$. 99% confidence boundaries are shown for the estimated mean length (ln).

Experiment 2

Hypothesis—The presence of food may reduce the tendency of springtails to disperse, but the responses of different age-classes (i.e., size classes) should differ. Two trays were used, to avoid possible effects of pheromones and (or) feces. One tray had 10 grains of yeast in the release area and the other had none. The numbers and ages of the insects in each area of the trays were determined after 2 h.

The insects used in these two experiments were not fed for 24 h before they were placed in area No. 1 of their trays.

Results and discussion

Experiment 1

Older *F. candida* showed a greater tendency than the younger, smaller individuals to move into more distant areas of the trays (Fig. 3). These results were produced by actual differences in behavior and level of activity, not by differences in velocity; e.g., observations showed that the distance from area No. 1 to area No. 5 (some 32 cm) could be easily traversed in 24 h by even the smallest individuals. Nevertheless, the majority of those <0.6 mm in length remained in the first two areas, even after 24 h.

There was no threshold size at which the population divided into dispersers and nondispersers. The relationship between size and distance travelled along the trays was continuous and linear. The statistical relationship

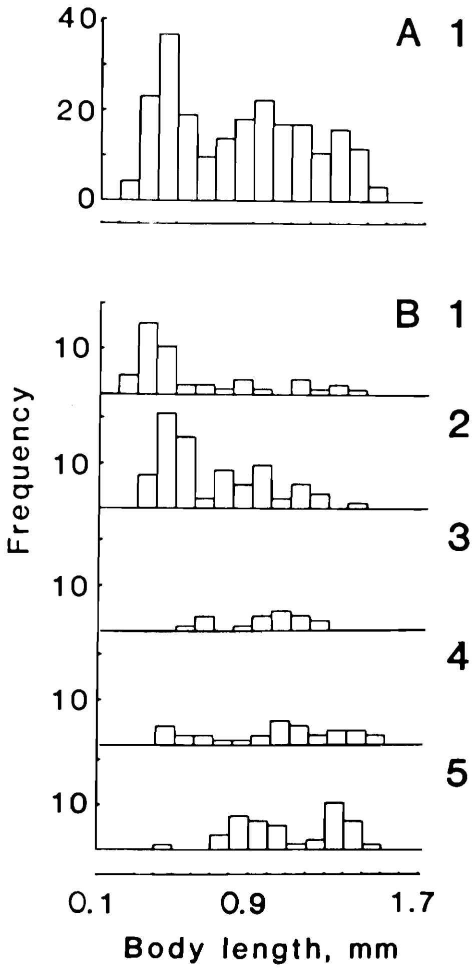

FIG. 3. Initial (A1) and final (B 1–5) distributions of 215 springtails 0.2–1.5 mm long through areas 1–5 of the dispersal trays during 24 h of travel.

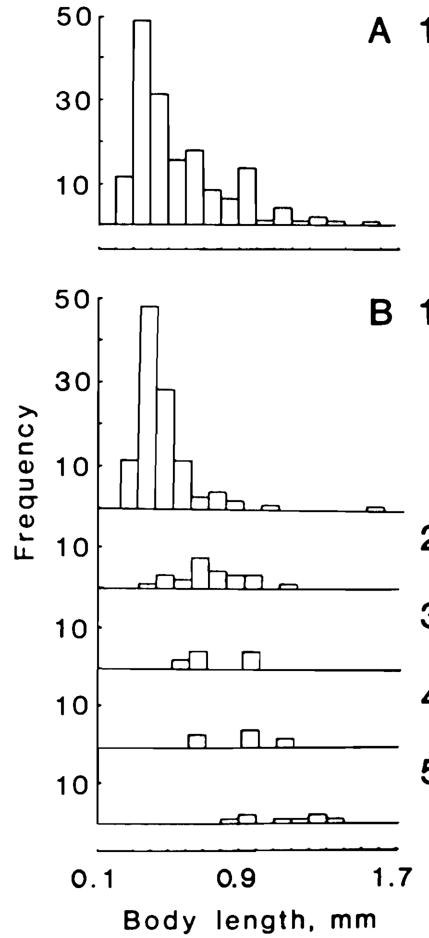

FIG. 4. Initial (A1) and final (B 1–5) distributions of 157 springtails 0.2–1.6 mm long through areas 1–5 of the dispersal trays during 2 h of travel in the absence of food.

between size and distance travelled (Fig. 3) is adequately described by the linear equation:

$$\text{distance} = 18.2(\text{size})$$
$$(r^2 = 0.32,\ s_b = 0.77,\ F_{1,213} = 564.9,\ p < 0.0001)$$

where distance is measured in centimetres and size in millimetres. The least squares regression line was forced through the origin since, without this constraint, the intercept did not differ significantly from zero (a = 0.047, s_a = 1.53).

Experiment 2

Movement over 2 h, without food

Decreasing the time allowed for movement reduced the number of individuals that moved beyond area No. 1, but did not alter the basic relationship between distance and size (Fig. 4). The relationship remained linear (Fig. 4 and the following equation):

$$\text{distance} = 24.1(\text{size}) - 7.1$$
$$(r^2 = 0.52,\ s_b = 1.86,\ F_{1,155} = 168.0,\ p < 0.0001)$$

but the slope did not differ significantly from the slope of the 24-h model (t = 0.72, $p > 0.2$).

Movement over 2 h, with food

When food was included in area No. 1, the larger individuals moved farthest during the 2-h period. However, many medium-sized individuals (between 0.7 and 1.0 mm in length) remained to feed in area No. 1 (Fig. 5). This difference in behavior is illustrated by the significantly reduced slope in the distance–size regression:

$$\text{distance} = 11.3(\text{size}) - 4.4$$
$$(r^2 = 0.37,\ s_b = 1.14,\ F_{1,166} = 98.8,\ p < 0.0001)$$

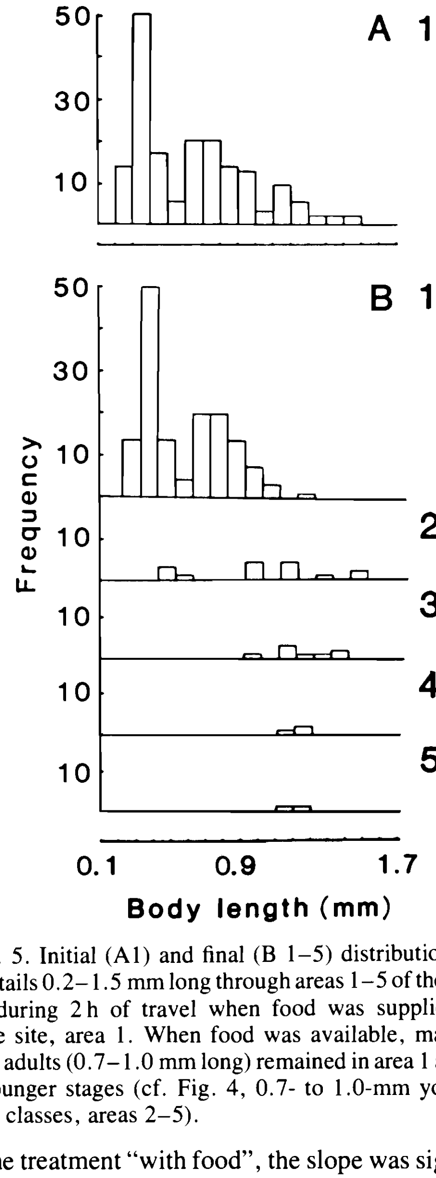

FIG. 5. Initial (A1) and final (B 1–5) distributions of 168 springtails 0.2–1.5 mm long through areas 1–5 of the dispersal trays during 2 h of travel when food was supplied on the release site, area 1. When food was available, many of the young adults (0.7–1.0 mm long) remained in area 1 along with the younger stages (cf. Fig. 4, 0.7- to 1.0-mm young-adult length classes, areas 2–5).

For the treatment "with food", the slope was significantly lower than that for the treatment "without food" (t = 2.30, df = 321, $p < 0.05$), mainly because of the greatly reduced amount of travel by the medium-sized animals.

Older *F. candida* showed a greater tendency to disperse than the young adults and juveniles in all these experiments. These differences arose from age-specific differences in activity. The smallest individuals travelled only a few centimetres, exhibiting the same relationship over short (2-h) and long (24-h) periods.

The presence of food at the release site reduced the travel of the medium-sized, not the larger, springtails. This middle group (0.7 to 1.0 mm in body length) was composed of young adults that had recently attained sexual maturity. The studies of Marshall and Kevan (1962), Snider (1971), Snider and Butcher 1973), and Johnson and Wellington (1980*a*) suggest that *F. candida* begins to oviposit in the 6th instar, when individuals usually vary from 0.7 to 0.8 mm in length and are 16–21 days old (see also Johnson and Wellington 1980*b*). Since this age group begins to oviposit while its individuals are still maintaining a relatively high growth rate (Johnson and Wellington 1980*a*), its food requirements are higher than those of younger and older groups.

In our experiments, these young, still growing adults were sufficiently attracted to the localized supply of food to delay their dispersal during the observation period. In contrast, since the larger, older springtails had already laid at least one batch of eggs and had already achieved nearly all their growth, they were more compelled to move than to stay and feed.

In natural situations it would often be advantageous for the youngest individuals to remain in the area in which they hatched. That home area would usually have a sufficiently high humidity to meet their requirements, since the local microclimate already would have encouraged their parents to oviposit and allowed the eggs to develop and hatch. In addition, food would rarely be scarce in the hatching area, because adult springtails not only lay eggs where they feed; they also leave potential food (e.g., feces, exuviae, and some growing microbial populations) behind. The smaller radius of activity of the youngest individuals would allow them to take full advantage of these food sources, whereas the greater tendency of older individuals to disperse when conditions permit travel would remove the threat of their competition for this remaining food (cf. Johnson and Wellington (1980*c*) for the age-specific effects of different population densities in closed systems).

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