

Dispersal and individual variability: laboratory experiments with the woodlouse *Porcellio scaber*

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Abstract

Laboratory experiments on the dispersal of woodlouse *Porcellio scaber* showed that the possibility to disperse diminished the intensity of intraspecific competition. The decision to disperse from local habitat to another one didn't depend on the weight of individual. The only category of individuals that tried to avoid dispersal were females carrying eggs. This can be connected with the Brownian way of movement of woodlouse during penetration of surrounding environment or with the arrangement of the experiment in which the costs of dispersal were low.

Key words

woodlouse, *Porcellio scaber*, dispersal, individual variability

1. Introduction

Intraspecific competition leads to uneven resource partitioning between competing individuals (Łomnicki 1988) which in consequence results in individual variability expressed mainly as individual differences in body weights. Such effects are clearly seen in classical competitive experiments with even-aged plant and animal populations (Uchmański 1985). The weight of an individual can be seen as the measure of its net energetic gains. The skewness of weight distributions in even-aged populations is a measure of the intensity of intraspecific competition: its positive value provides evidence for competition. The symmetric

weight distribution of interacting individuals or its negative skewness result from the lack of competition.

The amount of food available to individuals and the number of competing individuals have been considered as the main factors influencing the results of competitive experiments. A decrease in the amount food and an increase in the number of competing individuals lead to the increase in competition intensity expressed as an increase of individual variability and skewness of weight distributions. On the other hand, mortality during such experiments decreases the number of competing individuals, and individuals should be



Fig. 1. Woodlice *Porcellio scaber* used in the experiments



Fig. 2. Arrangement of the inner and outer dishes. One can see the location of food in the inner dishes and woodlice in some outer dishes

less variable and weight distributions less skewed in this case.

Similar effects can be expected when individuals can migrate or disperse from the place where they compete. Does dispersal or emigration decrease the intensity of competition in local population? Which individuals disperse or emigrate: heavier (winners of competition) or lighter ones (losers)? Answer to these questions is the aim of this paper.

2. The animal

The woodlouse *Porcellio scaber* is an epigeic terrestrial crustacean living in wet and shadow habitats, and feeding on dead plant material (Fig. 1). Its life span is approximately 2 years. It reaches maturity after 15 months when it is approximately 1.7 cm long, but it grows during the whole life. Mature females carry eggs until hatching.

Animals for the experiments described in this paper have been taken from a natural small islands surrounding trees in an alder swamp located in the Puszcza Kampinoska forest near Warsaw.

3. The experiments

Dishes 12 cm in diameter were used in each experiment. Each dish was located inside a greater dish. At the beginning of the experiments, 12 mature females of the same age

were placed in each inner dish, together with equal in each dish and in each experiment amount of litter (dry leaves) taken from the same place from which woodlice were taken. In each inner dish, the initial amount of litter was equal to 0.7 g. In each outer dish, the initial amount of litter was 0.35 g. Each inner dish had openings through which animals could get out into the outer dish. Animals couldn't escape from the outer dish. They had only two possibilities: to stay in the inner dish with food, but together with other individuals, and to compete with them, or to get out into the outer dish where the conditions at the beginning were unknown for them, and to stay there or go back to the inner dish.

Four experiments of different durations: 4, 7, 14, and 30 days, were performed to analyze the development of processes inside experimental dishes. Ten dishes were used in each experiment.

The aim of the experiments was to analyze the instantaneous presence of individuals in the inner and outer dishes, and their changes (movements between the dishes) with time. We observed the number and the quality of animals leaving the inner dish, in order to find differences between individuals leaving the dishes and staying in them. We supposed that the intraspecific competition for food inside the inner dishes could be the reason

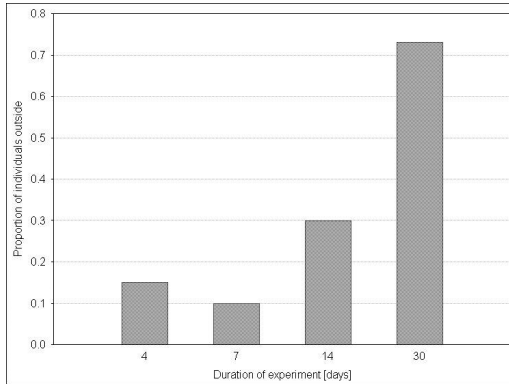


Fig. 3. Proportion of individuals found outside the inner dishes in experiments of different durations: 4, 7, 14 and 30 days. Total numbers of individuals from all 10 dishes in each experiment were used to calculate these proportions

for leaving them. As it was stated earlier, the weight of an individual can be a measure of its energetic gains during interactions with other individuals. Therefore, the amount of food inside and outside the inner dishes, together with the number and weight of individuals in these two locations, were the main results of the experiment.

4. Results

Fig.3 illustrates the proportion of individuals noticed outside the inner dishes over different time periods. After the first 4 days, 15 percent of the individuals were outside, then after 7 days, this proportion decreased to only 10%, after 14 days almost 30% of the individuals were outside the inner dishes and after 30 days over 70% were found in outer dishes.

The number of individuals present inside and outside the inner dishes found on subsequent days of the experiments was some instantaneous measure of the woodlice presence, which was rather a dynamic process, because individuals could freely move outside the inner dishes and back.

There were two cumulative measures of individuals' presence in both parts of the experimental space. One was the amount of food. Fig. 4 illustrates the amount of food

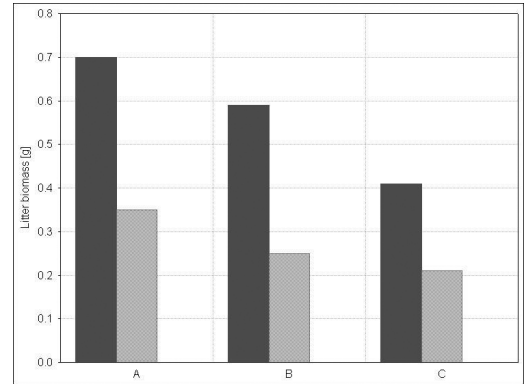


Fig. 4. Biomass of the litter in the inner dishes (dark bars) and outside of them (light bars) at the beginning of the experiments (A), after 7 days (B), and 14 days (C). For each experiment the average value from 10 dishes is presented

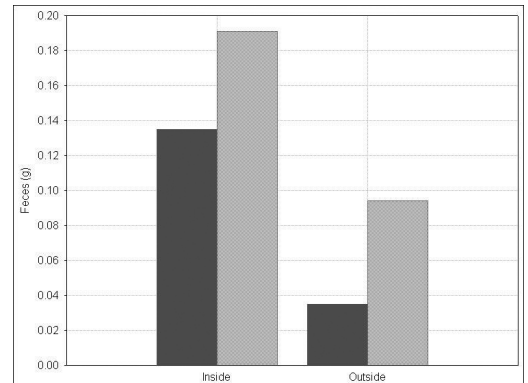


Fig.5. Amount of feces inside and outside the inner dishes found after 7 days (dark bars) and 14 days of experiments (light bars). For each experiment the average value from 10 dishes is presented

present inside and outside the inner dishes. It constantly decreased in time, which correlated with the activity of individuals present. One can notice that the rate of food decrease inside the inner dishes was greater than outside. The second cumulative measure of the presence of individuals was the amount of feces inside and outside the inner dishes (Fig. 5). It cumulated during

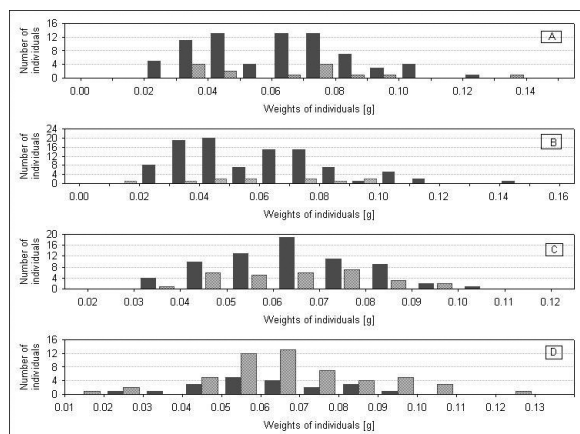


Fig. 6. Weight distributions of individuals found inside and outside of the inner dishes after 4 (A), 7 (B), 14 (C) and 30 (D) days of the experiments. Dark bars – in the inner dishes, light bars – outside the inner dishes. Total numbers of individuals from all 10 dishes in each experiment are presented

Table 1.

Basic statistics for experiments lasting different times. At the beginning 12 individuals were placed in 10 experimental dishes in each experiment. Number of individuals, mortality, average weights, standard deviations and skewness coefficients of weight distributions were calculated at the end of each experiment together for individuals inside and outside the inner dishes and for all 10 dishes present in the experiment together

Duration of experiment	Number of individuals	Mortality	Average weights [g]	Standard deviation	Skewness coefficient
4 days	88	0.27	0.057	0.024	0.408
7 days	106	0.12	0.052	0.022	0.363
14 days	99	0.17	0.059	0.016	0.150
30 days	73	0.39	0.061	0.021	0.220

the experiments, however their amount was at least two times greater inside the inner dishes than outside of them during experiment lasting different time.

The main aim of the experiments was to analyze the number and weights of individuals found in different parts of the experimental space. Fig. 6 illustrates the weight distributions of individuals noticed inside and outside the inner dishes in experiments with different duration. Basic statistics for these distributions together with information concerning mortality of individuals in experiments with different durations are presented in Tab. 1. In all cases all weight distributions of individuals found inside and outside the inner dishes showed

a relatively great degree of individual variability. Almost all distributions were also positively skewed. There were no statistically significant differences in the average weights of individuals between the inner and outer dishes during all inspections of them (Mann-Whitney test, $p > 0.05$). Also the average weight of individuals didn't increase significantly during 30 days.

Differences in the dispersal of marked females with and without eggs were analyzed in a 30-day experiment. Over that time, most females with eggs moved outside the inner dishes only once. Among females without eggs, the number of individuals which moved outside up to 5 times during 30 days was much greater (Fig. 7). The number

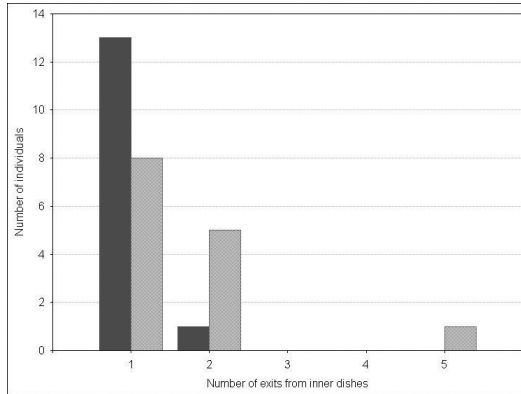


Fig. 7. Distributions of the number of exits from the inner dishes for females with eggs (dark bars) and without eggs (light bars). Results of the experiment lasting 30 days are presented

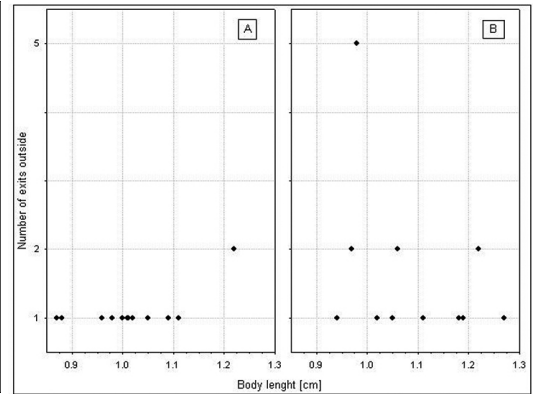


Fig. 8. Number of exits from the inner dishes for females with eggs (A) and without eggs (B) in relation to the size of females. Results of the experiment lasting 30 days are presented

of times when females without eggs moved outside the inner dish didn't depend on their sizes, while among females with eggs only those with biggest size moved outside the inner dish more than one time (Fig. 8).

5. Discussion

The amount of food in both the inner and the outer dishes decreased during the experiments. The decrease was faster in the inner dishes where initially the number of individuals was greater. Also the amount of feces cumulated during the experiments with different durations was at least two times greater in the inner dishes than in the outer dishes. Individuals were able to move freely outside the inner dish and back. In spite of this, the above evidences show that in the experiments lasting up to 14 days individuals were more active in the inner dishes. However, the number and proportion of individuals found outside the inner dishes increased with time, what was negatively correlated with the decreasing amount of food mainly in the inner dishes, and in 30 days of the experiment most individuals were found in the outer dishes.

Almost all weight distributions of individuals in the inner and outer dishes (see Fig.6) and calculated for individuals

from the inner and outer dishes together (see Tab.1) were slightly positively skewed starting from the fourth day until the end of the experiments on day thirty.

Positively skewed weight distribution in even-aged populations is an evidence for intraspecific competition, while a symmetric distribution indicates lack of competition (Uchmański 1985). Therefore, looking at the results of the experiments, we can assume that generally there was competition between individuals present in the experiments. However it is hard to decide where – in the inner or in the outer dishes – the weight distributions were more positively skewed.

In such type of experiments a decrease in the intensity of competition, together with a decrease in the positive skewness of weight distribution until its negative values, is normally caused by increasing mortality. Two other factors which are present in such type of experiments should increase the intensity of competition (together with the positive skewness of weight distributions): the decreasing amount of food available to individuals during the experiments, and the process of individual growth of them, which leads to the increase in energetic demands of organisms.

During our experiments the growth of individuals was negligible. So, this factor which can increase the intensity of competition (and positive skewness of weight distributions) was absent in the experiments described in this paper.

However, in all experiments the amount of food exploited by individuals decreased systematically with the duration of the experiment. Additionally, different mortality was observed in the experiments with different durations (see Tab.1 – there were no clear correlations between the duration of the experiment and the mortality of individuals).

Because individuals were able to move freely outside the inner dishes and back, let us treat all individuals – found during inspections inside and outside the inner dishes – as one population and analyze their total weight distributions.

In the 7-day experiment skewness of weight distribution was equally high as in the 4-day experiment (0.41 and 0.36 respectively – see Tab.1) in spite of a small decrease of the amount of food in the 7-day experiment (only approximately 0.15 in relation to the amount of food noticed in the 4-day experiment). This was probably caused by very low mortality in the 7-day experiment and small proportion of individuals found during inspection outside the inner dishes. We can see a great decrease of skewness in the 14-day experiment in relation to the 4-day experiment (0.41 and 0.15 respectively) in spite of almost 50% decrease of the amount of food after 14 days and relatively small mortality during this period. However, in the experiment lasting 14 days almost one third of individuals were found outside the inner dishes during the inspection. The possibility to disperse was probably the main reason for small skewness of weight distribution in the 14-day experiment. The result of the 30-day experiment can be analyzed in a similar way: despite small amount of food left in the experiment after 30 days the skewness of weight distribution is not much higher than

in the 14-day experiment because of a very high mortality during this period and very great number of individuals found outside the inner dish.

Therefore, generally we can infer that the possibility to disperse from the inner dishes where – looking at the amount of feces left by individuals – their activity mainly took place to the outer dishes was probably responsible for decreasing of the intensity of intraspecific competition in the experimental populations. However, woodlice probably didn't stay permanently in the outer dishes. They dispersed there for a short time, and then returned to the inner dishes where more food was initially provided and where they interacted with other individuals. But it was enough to decrease the intensity of competition for individuals which remained in the inner dishes.

There were no differences in weights between individuals found in the inner and the outer dishes. This can be an evidence that the decision to disperse outside the inner dish was random. It was not connected with the status of an individual. It was not so that heavier individuals (winners during competition) or lighter individuals (losers during competition) dispersed. The decision to disperse into the outer dishes was independent of the individual cumulative energy gains during interactions with other individuals, as measured by their weight. This may be a result of the Brownian way of the movement of *Porcellio scaber* during the exploration of the environment observed by Sutton (1972). There was only one category of individuals which tried to avoid the dispersal to the outer dishes – namely, females with eggs.

The costs of dispersal (except for females with eggs) in these experiments were very low, as the inner and outer dishes were put one into another, that is, they were not separated by a hostile environment. Individuals could easily get out of the inner dish and then come back without any extra energetic costs of such behavior. This probably

influenced the results of the experiments in such a way that the dispersing individuals didn't totally disappear from the local populations. Therefore, the influence of dispersal on the intensity of competition was rather low in these experiments.

The above mentioned lack of relationship between decision to disperse and the weight of the individuals can be also caused by the small costs of dispersal in this experiments. Probably only for females with eggs the costs of dispersal were too big. This is the reason why only the heaviest female with eggs was able to disperse more than one time.

References

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Dyspersja i zmienność osobnicza: eksperymenty laboratoryjne ze stonogą *Porcellio scaber*

Streszczenie

Laboratoryjne eksperymenty nad dyspersją stonogi *Porcellio scaber* pokazują, że możliwość dyspersji zmniejsza intensywność konkurencji wewnątrzgatunkowej. Decyzja dotycząca dyspersji z aktualnie zajmowanego siedliska do sąsiedniego nie zależała w tym eksperymencie od ciężaru osobnika. Jedyną kategorią osobników, które starały się unikać dyspersji były noszące jaja samice. Może to wynikać z tego, że stonogi tego gatunku penetrują środowisko poruszając się przypadkowo, ale mogło być także dodatkowo rezultatem tego, iż środowisko życia stonóg było w tym eksperymencie tak zaaranżowane, iż koszty dyspersji były niskie.

Słowa kluczowe

Porcellio scaber, dyspersja, zróżnicowanie osobnicze