

Intraspecific Competition in an Island Environment: Variability and Dispersal of Terrestrial Snail *Helix aspersa aspersa* Müller, 1774 (Gastropoda: Helicidae)

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Abstract: Positive skewness of the weight distribution of individuals from even-aged populations is a measure of the intensity of competition between them. Skewness coefficient decreases during the growth of individuals in such populations because of the mortality of individuals. Such results are typical for experiments with plants. Terrestrial plants are sedentary organisms. Animals can disperse or migrate. This paper answers the question how the dispersal of individuals influences intraspecific competition. The results of experiments with the snail *Helix aspersa aspersa* are presented. They show that: (a) the average weight of individuals in experiments with the possibility of dispersal is greater than the average weight from closed local population without possibility of dispersal, (b) the skewness of weight distribution is smaller and decreases faster with the course of experiment when individuals can disperse as compared with the results of control experiment without dispersal, (c) when the costs of dispersal are greater (when distances between local populations are greater) only individuals with greater weight (better competitors) disperse on longer distances.

Key words: intraspecific competition, individual variability, skewness of weight distribution, *Helix aspersa aspersa*

Introduction

Intraspecific competition leads to uneven resource partitioning among competing individuals: some individuals obtain more, other less resources needed for growth, survival and reproduction (ŁOMNICKI 1988). How resources are partitioned among individuals is difficult to measure and to analyze, but we can observe indirect results of competition, namely individual variability in weight among competing individuals (UCHMAŃSKI 1985). The weight of an individual is a result of the amount of resources the individual obtained minus costs of its life (its respiration measured, for instance, in energetic units).

In an even-aged population of competing individuals weight distributions are positively skewed: most individuals have small weights, and the number of heavier individuals is always small. The skewness of weight distribution can be measured by the coefficient of skewness q , which is given by the following equation:

$$q = \Sigma(w_i - w_a)^3 / (\Sigma(w_i - w_a)^2)^{3/2}$$

where w_i is weight of i -th individual from the even-aged population, and w_a is the average weight of an individual in this population.

The value of the skewness coefficient of weight distribution is related to the intensity of competition. A greater coefficient of skewness in an even-aged population consisting of individuals of the same species at the same age and of the same sex means a greater competition between individuals (UCHMAŃSKI & DGEBUADZE 1990). The skewness of weight distributions depends also on population density. For constant resource level available to individuals, a greater population density obviously means a greater intensity of competition. This is the reason why skewness coefficient is greater for more dense populations.

In even-aged populations of individuals competing during their growth, skewness of weight distribution will change with the age of individuals. It

is almost equal to zero for initial stages of growth (weight distributions of young individuals starting the growth and competition are symmetric). It increases during growth of competing individuals, along with the increasing variability of individuals. However, as it was stated earlier, competition means unequal resource partitioning, so when competition is sufficiently strong, an additional effect can be observed. When competition is strong enough, weak competitors obtain such a small amount of resources that they can not survive on it, and they die. This is the reason why in experiments with strong intraspecific competition we observe an increase in the mortality of competing individuals with their age. This leads to a decrease in the population density. In consequence, it diminishes the intensity of competition, and results in a decrease in the skewness of weight distribution of the competing individuals with their age.

Such results were obtained many times in experiments with sedentary organisms, for instance, with terrestrial plants (KOYAMA & KIRA 1956). However, most animals can move. This is an additional factor which can influence the competition process and its outcome – the skewness of weight distribution. If a species lives in the form of a set of local interconnected populations, individuals can disperse or emigrate from one local population to another one. It means a decrease in the local population density, and should change the skewness of weight distributions in the local population (and consequently also in the global population) in the same direction as mortality does – skewness should decrease. However, immediately an additional question arises: who disperse or emigrate? Is it a weak individual which loses the competition and “hopes” to find better conditions in other local population, or is it a strong one which obtained sufficiently large amount of resource in the past, and is able now to invest them in a dangerous and energy

consuming process of dispersal or emigration. In both cases we can expect additional and probably different influence on weight variability in both the local population and global population. Animal dispersion is an important ecological factor and was subject of many ecological investigation (for review see for instance CLOBERT et al. 2001, 2012), but its influence on shape of weight distribution of competing individuals has been never investigated before.

Materials and Methods

To answer the above questions, the following field experiments were performed in which conditions for the dispersal of animals between many local populations were provided.

The animal species. *Helix aspersa aspersa* Müller, 1774 (Gastropoda: Helicidae) is an edible North African snail introduced for the first time to Southern Europe for cultivation as a food (Fig. 1). Now its cultures are widely established also in Northern Europe. The cultivation procedure is very simple. The standard dry food for *Helix aspersa aspersa* cultures is also easily available in commerce. Snails used in each experiment were of the same age and they originated from the same commercial culture.

Local population. It consisted of plastic garden dishes 60 cm in diameter filled with soil, covered by grass, and watered. In the centre of each dish a wooden table was placed with the area much smaller than the dish surface. Food for snails was placed on the top of the table. The same arrangement is applied in commercial cultures of *Helix aspersa aspersa*.

Conditions for dispersal. In the experiments, except for the control, 36 dishes in rectangular arrangement 6x6 were used. Each dish was marked with a number. A hostile environment was arranged between the dishes – dry, filled with small stones,

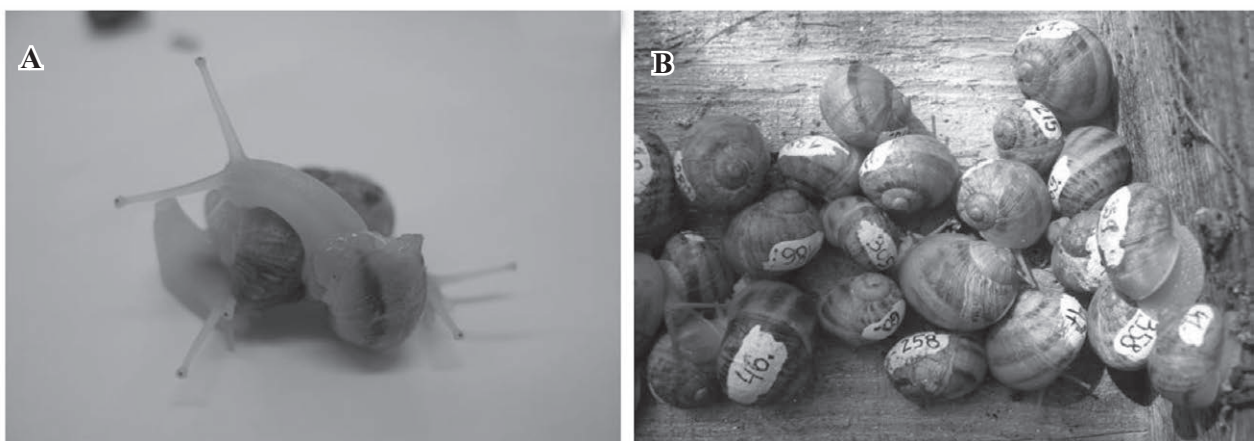


Fig. 1. Snails *Helix aspersa aspersa* (A) and the way how they were marked (B).

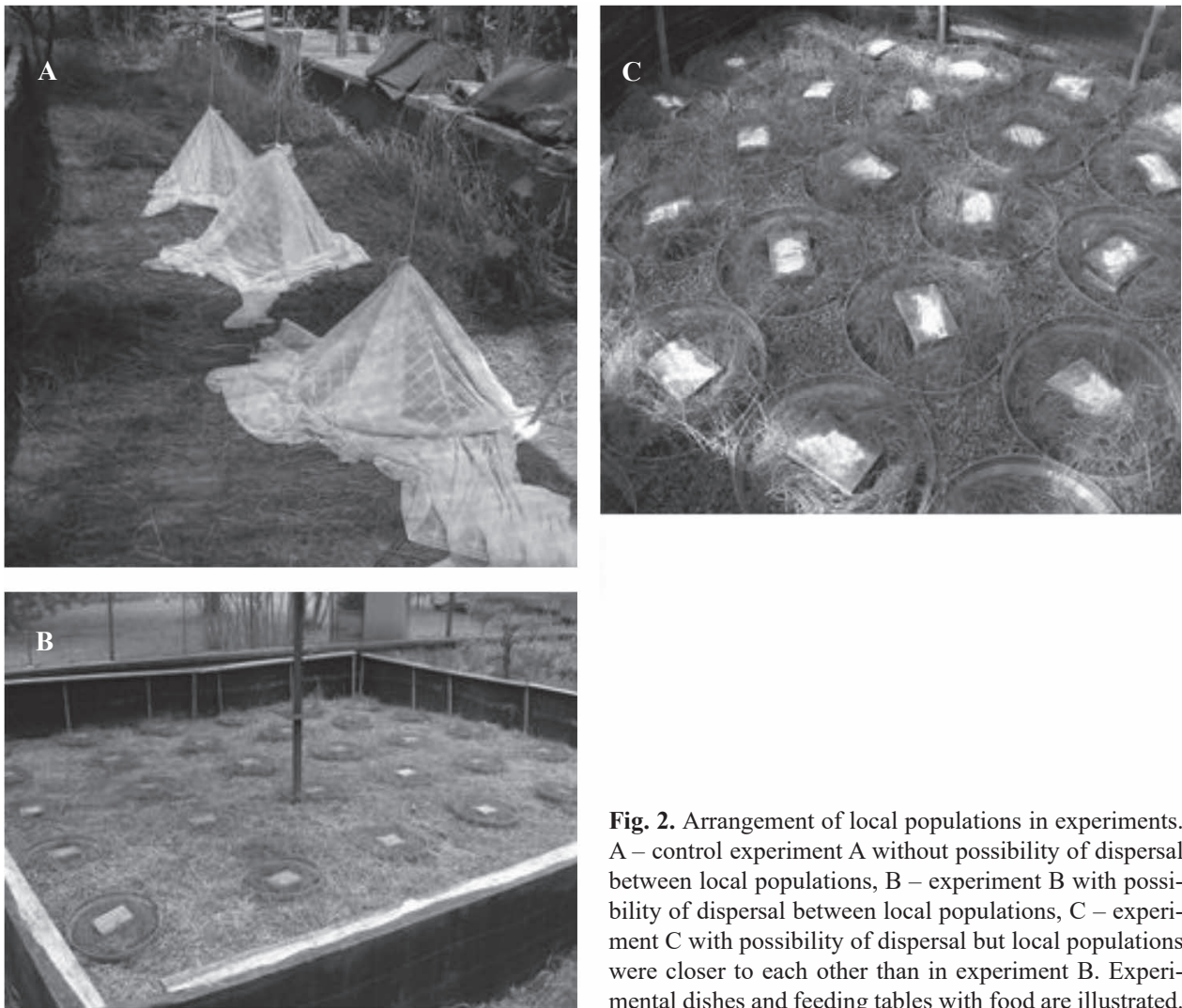


Fig. 2. Arrangement of local populations in experiments. A – control experiment A without possibility of dispersal between local populations, B – experiment B with possibility of dispersal between local populations, C – experiment C with possibility of dispersal but local populations were closer to each other than in experiment B. Experimental dishes and feeding tables with food are illustrated.

without grass and food. To prevent escapes of snails from the experiment, the sets of dishes were surrounded by a fence covered with substance unpleasant for snail. Additional dishes were kept in a bigger enclosure to prevent predation on snails. The enclosure had a deep concrete base, and it was covered with a metallic net from the sides and from the top.

Differences between experiments. Three experiments were performed with different possibilities of dispersal between local populations (Fig. 2). In experiment A the dispersal between local populations was not possible, because each dish was separated with a net from the outside dish environment. The results of this experiment were treated as a control for the two following experiments. In experiment B the distances between centers of local populations were equal to two dish diameters (120 cm – it was possible to put one dish between two neighboring dishes). In experiments C neighboring dishes stayed close one to another. The distances between them were equal to one dish diameter (60

cm). 36 dishes were used in experiments B and C. In experiment A only 3 dishes were used.

Experiments A and B were performed in 2007, experiment C in 2006. Experiment A, the control performed in 2007, lasted 12 weeks (from 23 July to 12 October). In 2007, experiment B lasted also 12 weeks and was performed in the same time as experiment A (from 23 July to 12 October). In 2006, experiment C lasted 7.5 weeks (from 16 August to 13 October).

Initial conditions. At the beginning of each experiment, snails were gradually introduced in portions consisting of approximately 50 individuals, and distributed over local populations. The recruitment to each portion was random. The number of snails introduced into each experiment was such that on average 10 or a little more individuals could be assigned to each dish. Each snail was marked with its unique number at the beginning of the experiment. The period of the introduction of snails to the experiments and their adaptation lasted approximately

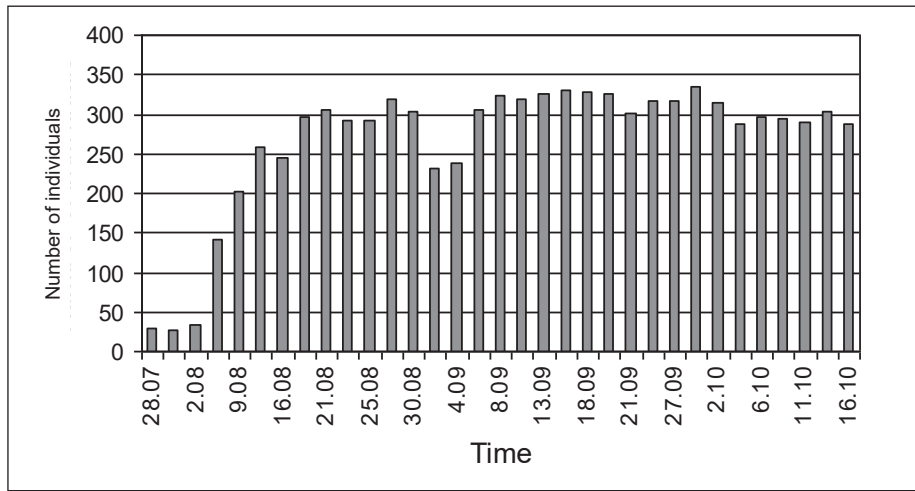


Fig. 3. Experiment C. The total number of snails noticed during subsequent inspections in all local populations.

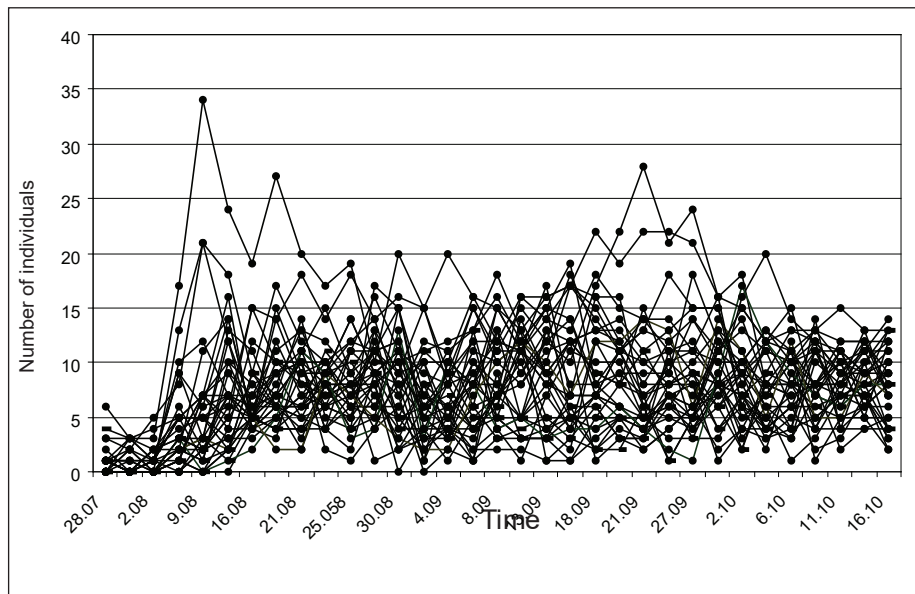


Fig. 4. Experiment C. The number of snails noticed during subsequent inspections in each local population.

three weeks after which the proper experiment started.

Feeding. Three times per week (on Mondays, Wednesdays and Fridays) dishes were inspected and food was put on the tables. The amount of food offered to snails on each table was such adjusted that the tables were empty on the next day after feeding. The standard food used in *Helix aspersa aspersa* commercial cultures was used in the experiments. The amount of food offered to snails on the tables was constant during the whole experiment and the same in different experiments.

Measurements. The location of each snail (the number of the dish in which it was found during each inspection) was recorded. These data were used to calculate the distance covered by each snail:

two-day distances covered by each individual (from Monday to Wednesday and from Wednesday to Fridays) and the average two-day distance covered by each individual during the whole experiment. Twenty two-day periods were chosen for recording snail movements in experiment B. Fifteen two-day periods were defined during which distances covered by snails were recorded in experiment C.

All individuals noticed in dishes were weighted tree times during each experiment: at the beginning (during the introduction to the experiment), in the middle of it and at the end of each experiment.

Each individual was characterized by: (1) its weight (w_p) at the beginning of the experiment, (2) its weight (w_m) in the middle of the experiment, (3) its weight (w_k) at the end of the experiment (this

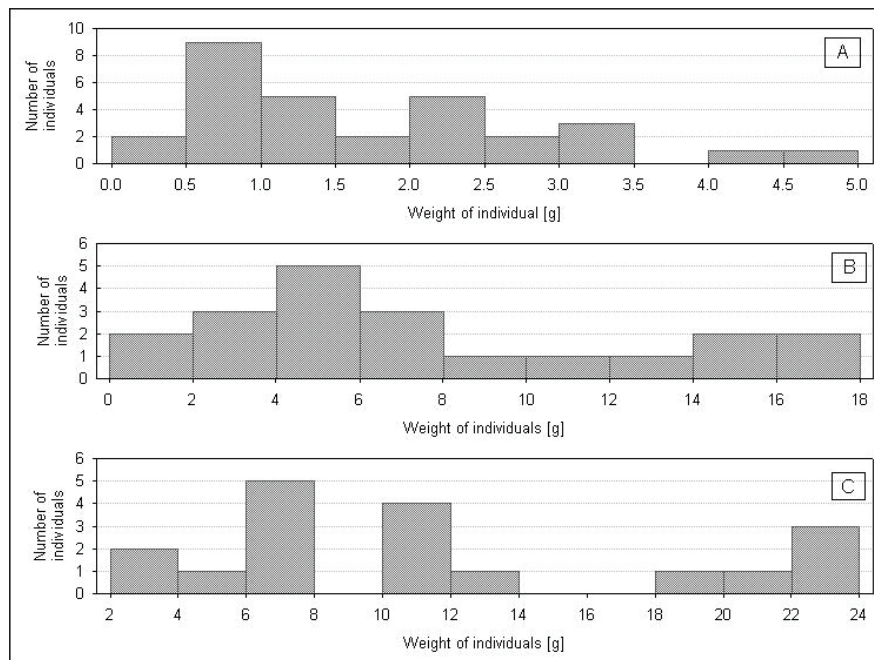


Fig. 5. Weight distributions at the beginning of the experiment (1), in the middle (2) and at the end of it (3). Experiment A. Control experiment – individuals could not disperse.

enabled us to calculate the weight increase during the whole experiment ($w_k - w_p$), and (4) average distance (d) covered by the individual in two-day periods during the whole experiment. Additionally, real (not average) two-day distances of all individuals were analyzed together with the densities of local populations from which individuals dispersed.

At the end of all experiments, all survived snails were analyzed for the presence of parasites. In each experiment the result was negative. No parasites were found.

Results

Population dynamics. In the control experiment A, a high real (not including individuals which escaped from the experiment – their number in the experiment A was equal to 0) mortality was observed during the first half of the experiment. 30 individuals were introduced into experiment A and only 19 of them were found in the middle of the experiment (mortality rate was equal to 0.37 during this time). Later mortality was not practically observed – 18 individuals were noticed at the end of the experiment, which gives mortality rate equal to 0.40 during the whole experiment A.

Changes of the number of individuals over time during experiment C are shown in Fig. 3. After the period of the introduction of individuals to the experiment and their acclimation, which lasted approximately three weeks from 28 July until 16 August,

when the proper experiment started, the number of individuals found during each inspection was more or less constant, fluctuating a little around 300 of individuals. Fig. 4 shows temporal changes of the number of individuals in each experimental dish during experiment C. Despite great fluctuations, the number of individuals in most dishes stayed in limits 5-15 individuals, and events when dishes were empty during inspections were very rare. Only 14 snails were found dead during experiment C. It gives real mortality rate equal approximately to 0.04. Other individuals that were not noticed during the inspections of dishes in experiment C stayed during the inspection time outside dishes: in the hostile environment between dishes or on the fence surrounding the dishes. 380 snails were introduced to experiment C at the beginning and 320 were noticed at the end of it in the dishes and outside them. It gives mortality rate equal to 0.16 including individuals which died and these which escaped from the experiment.

In experiment B the real mortality rate of snails was similar to that in experiment C. However, the proportion of snails which during inspections stayed outside the experimental dishes or escaped from the experiment was greater. The same number of snails as in experiment C – 380 individuals – were introduced to experiment B but only 187 were found at the end of the experiment in the dishes and outside them. This was the direct result of a much greater space between the experimental dishes in experiment

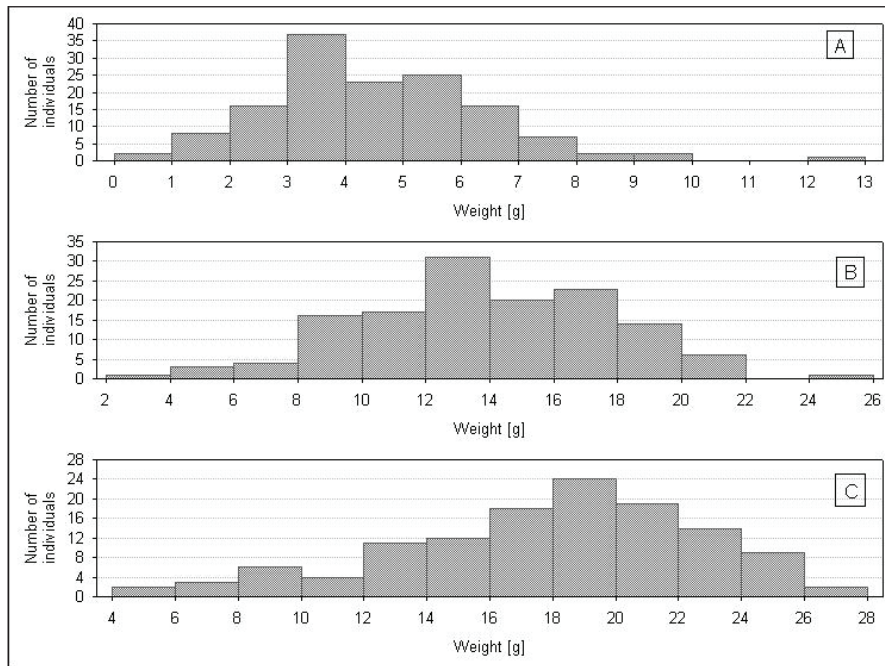


Fig. 6. Weight distributions at the beginning of the experiment (1), in the middle (2) and at the end of it (3). Experiment B. Individuals could disperse, however distances between experimental dishes were greater than in experiment C (they were separated by a hostile environment).

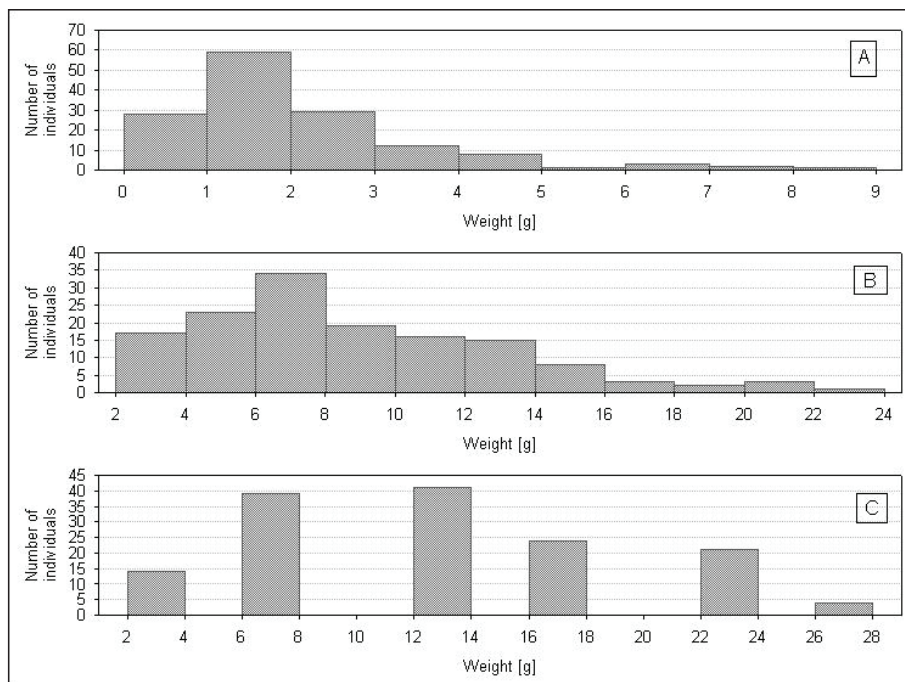


Fig. 7. Weight distributions at the beginning of experiment (1), in the middle (2) and at the end of it (3). Experiment C. Individuals are able to disperse, however distances between experimental dishes are smaller than in the experiment B (experimental dishes stayed in close contact).

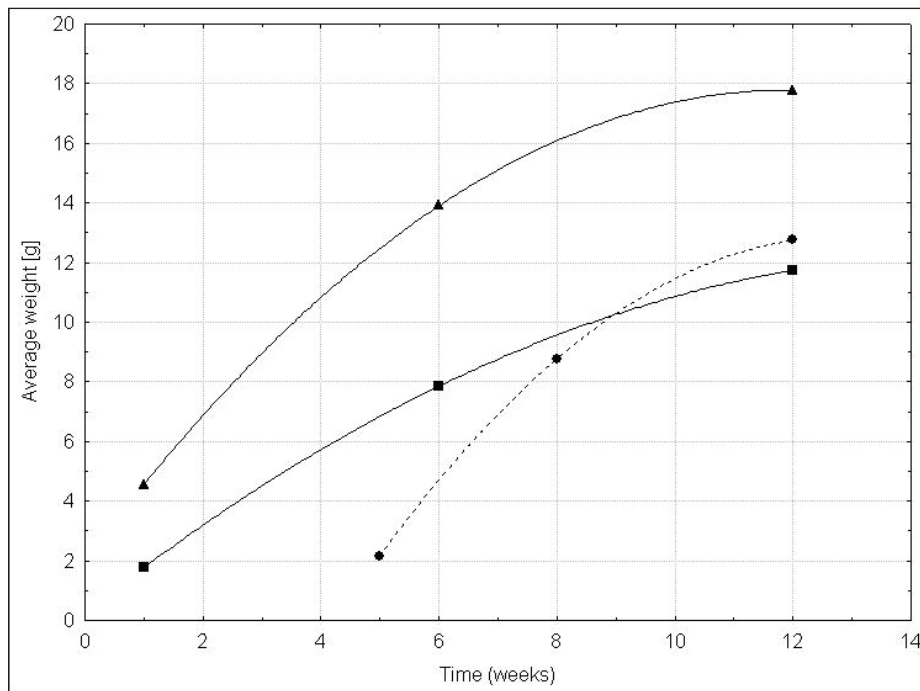


Fig. 8. Average weights of individuals from the experiments with dispersal of individuals (solid triangles – experiment B, solid circles and dotted line – experiment C) compared with the average weights from the control experiment A without dispersal (solid squares), at the beginning, in the middle and at the end of experiments. Experiments A and B were conducted simultaneously, experiment C in previous season, it started later in the season, but ended in the analogous moment as experiments A and B. The regression lines have been drawing here to indicate only to which experiment the given set of points belongs.

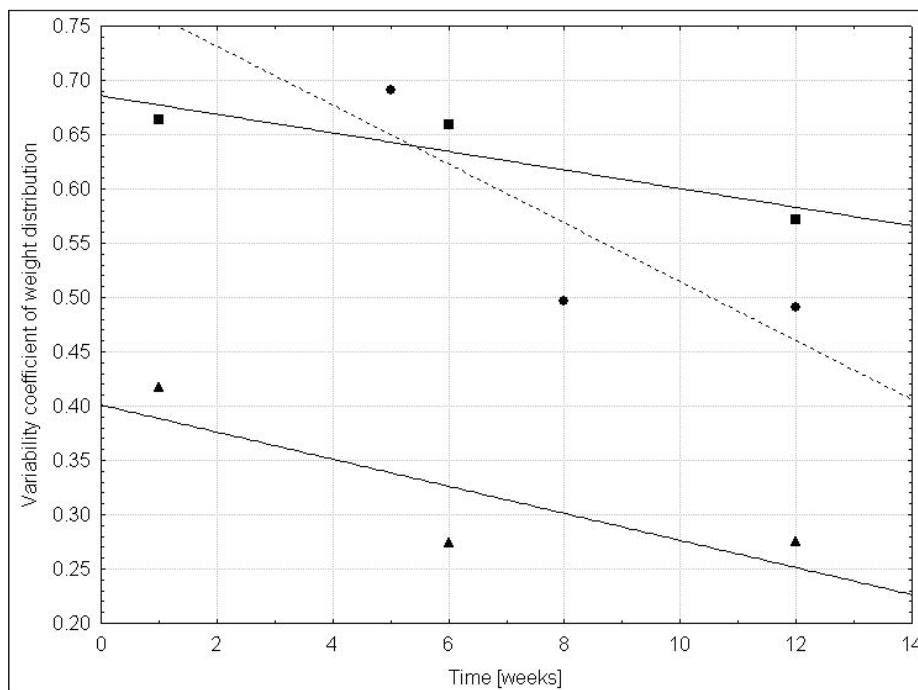


Fig. 9. Coefficient of variability of the weights of individuals from the experiments with dispersal of individuals (solid triangles – experiment B, solid circles and dotted line – experiment C) compared with coefficient of variability of the weights from the control experiment A without dispersal (solid squares), at the beginning, in the middle and at the end of experiments. The regression lines have been drawing here to indicate only to which experiment the given set of points belongs.

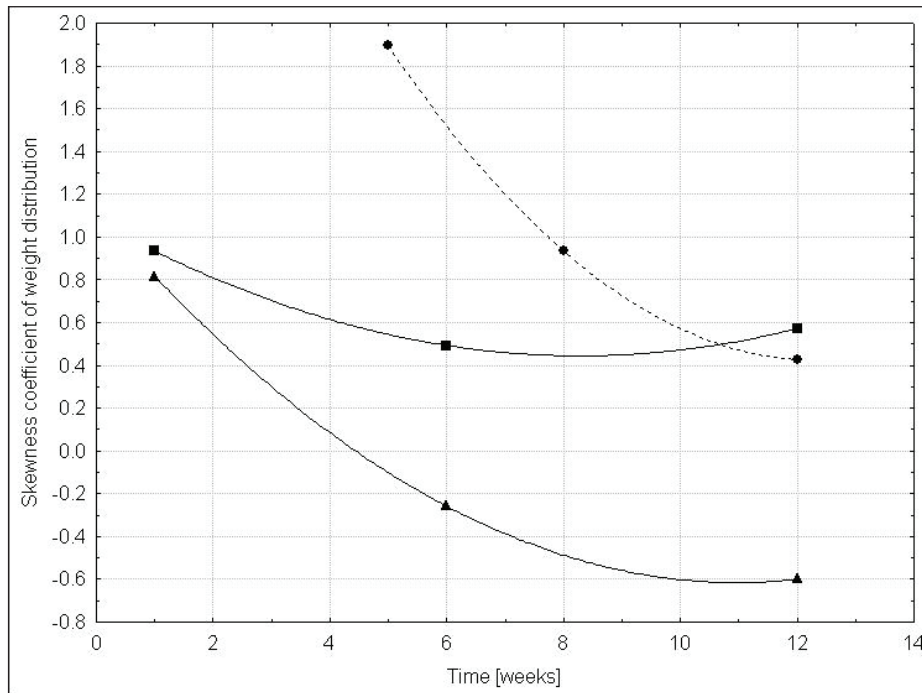


Fig. 10. Skewness coefficient of weight distribution from the experiments with dispersal of individuals (solid triangles – experiment B, solid circles and dotted line – experiment C) compared with skewness coefficient of the weight distribution from the control experiment A without dispersal (solid squares), at the beginning, in the middle and at the end of experiments. The regression lines have been drawn here to indicate only to which experiment the given set of points belongs.

B than in experiment C. Individuals not found at the end of the experiments either died during the experiments or escaped from the experiments, or hid in the space of the experiment. All of them did not participate in interactions with other individuals, but probably for different periods, which gives mortality rate equal to 0.51 including individuals which died and these which escaped from the experiment

All individuals present in experiment A were used in further analysis. In experiments B and C only the snails noticed not less than nine times in experimental dishes were used in analysis of the results. These were 139 snails in experiment B and 143 snails in experiment C. In this way we eliminated from further analysis the snails which preferred to stay outside dishes or moved too slowly between them to be noticed in two subsequent inspections of the dishes. We analyzed only individuals which stayed in local populations or were sufficiently motivated to leave the local population and to reach another one during a short period (not longer than the time period between two subsequent inspections of the dishes).

Weight distributions: individual variability with and without dispersal. Weight distributions of individuals from the control experiment A are

illustrated on Fig. 5. Weight distributions from experiments with possibility of dispersal are illustrated in Fig. 6 (experiment B) and Fig. 7 (experiment C). All the above figures illustrate changes in the weight distributions over time of the experiments (at the beginning, in the middle and at the end of each experiment). Snails grew during the experiments, so the distributions show the weights of individuals on different stages of their life. Individuals at the end of experiments were several times heavier than at the beginning, but also the variability of individual weights (measured as their coefficient of variation and skewness coefficient of weight distribution) changed during this time.

The average weight of individuals during experiments B was greater than the average weight of individuals from the control experiment (see Fig. 8 for the results of experiment B compared to the results of experiment C and the control experiment A). In experiment C the average weight was more or less similar to average weight in the control experiment A. Differences between average weights from experiment B and control increased with time.

Variability of individual weights measured by coefficient of variability was almost two times greater in the control experiment A without dispersal than in

experiment B with possibility of dispersal, and in both cases it decreased at a similar rate with time of the experiments (Fig. 9). In experiment C the variability coefficient was at the beginning similar to its value in control. Later, starting from the middle of the experiment, its value was smaller than in control, but still almost two times greater than in experiment B.

Skewness coefficient of weight distribution in the control experiment A was greater than zero during the whole experiment. It decreased with time but at the end of the experiment it was still positive. In experiment B with the possibility of dispersal, the coefficient of skewness was at the beginning similar to its value from the control experiment A, but later decreased quickly and reached negative values starting from the middle of the experiment time (see Fig. 10 for the results of experiment B in relation to the results of experiment C and the control experiment A). The highest values of skewness coefficient were in the experiment C. Only at the end of this experiment its value was little smaller than in the control experiment A.

Influence of the costs of dispersal on individual variability. Experiment C in 2007 was shorter than experiments A and B from 2006 (7.5 weeks in comparison with 12 weeks, respectively). All of them, however, lasted sufficiently long to assume that we can compare the results of them despite the fact

that they were done in two different but subsequent years. We assumed that duration of all experiments guarantee similar growth conditions for snails in different years because they encountered all possible weather conditions during summer in the middle of Poland. Additionally all experiments ended approximately on the same day of the year (in the middle of October in two subsequent years). This enables us to compare the results of these experiments.

Table 1 presents average weights of individuals, coefficients of variation and skewness coefficients of weight distributions at the beginning, in the middle and at the end of experiments A, B and C. In experiment B, when costs of dispersal were greater, the coefficient of variation and skewness coefficient of weight distributions were much smaller during the whole experiment than in the experiment C with dispersal still possible but smaller dispersal costs due to shorter distances between the local populations. In experiment C, coefficient of variation decreased with time faster than in experiment B. In the middle and at the end of the experiment it reached values smaller than in the control experiment A. The skewness coefficient of weight distributions in experiment C decreased with time also faster than in experiment B, however in the middle of the experiment it was still greater than in the control experiment A, and

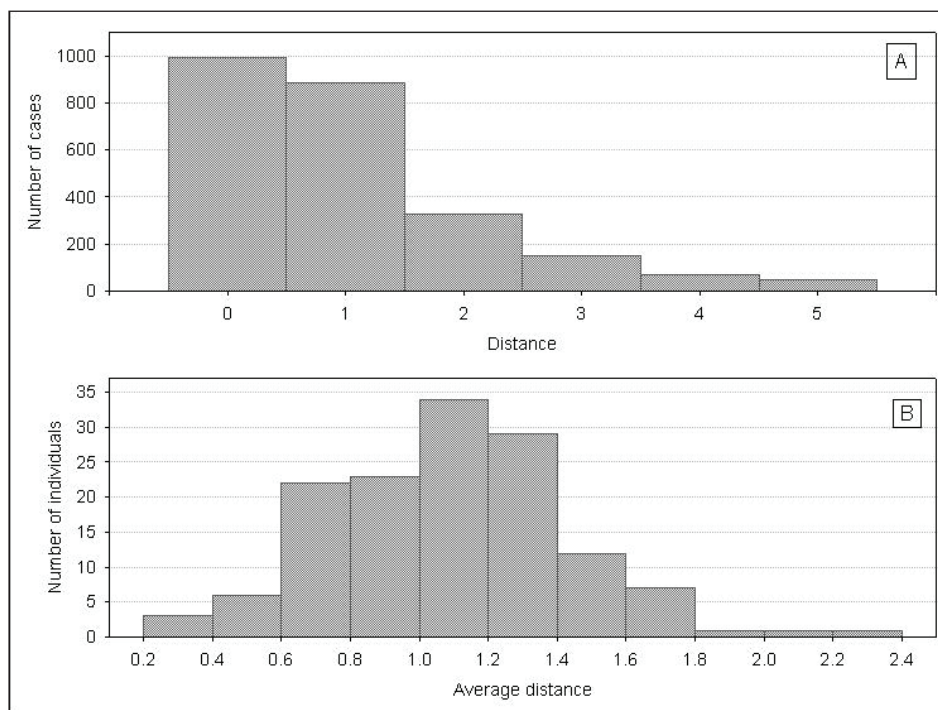


Fig. 11. Experiment B. Illustration of the movements of snails between the experimental dishes. (1) Distribution of two-day distances covered by all individuals during the whole experiment. (2) Distribution of the average two-day distances covered by individuals during the experiment as measured in the number of dishes visited (real distance between centres of two neighbouring dishes was equal to 120 cm).

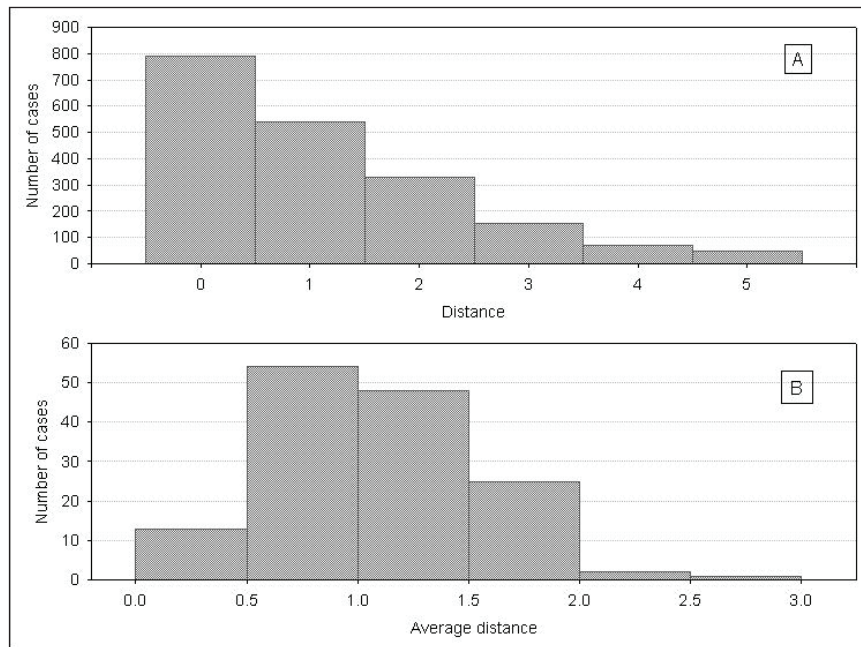


Fig. 12. Experiment C. Illustration of the movements of snails between experimental dishes. (1) Distribution of two-day distances covered by all individuals during the whole experiment. (2) Distribution of the average two-day distances covered by individuals during the experiment. Real distance unit was two times smaller than in the experiment B because distances were measured in the number of dishes visited.

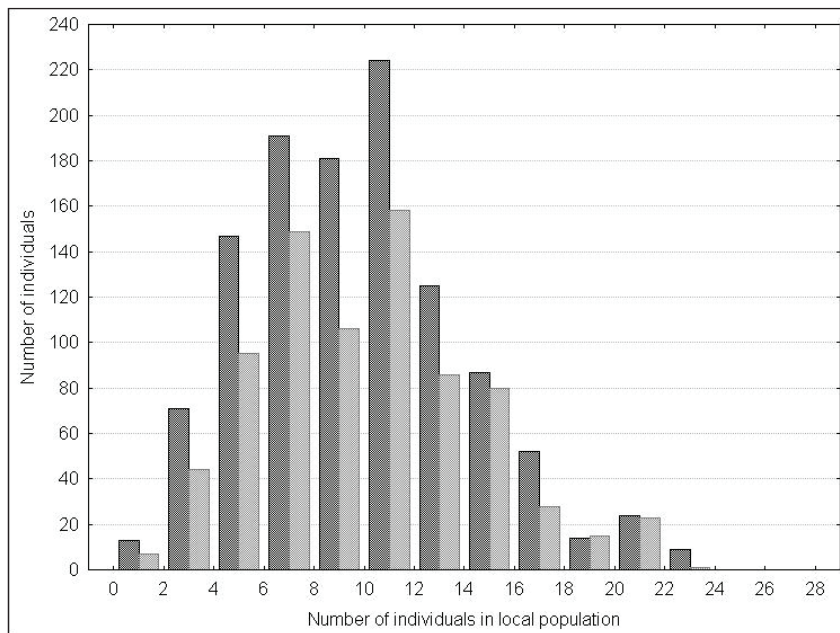


Fig. 13. Experiment B. The distribution of the number of individuals in the dishes from which individuals dispersed (dark bars) compared with the distribution of the number of individuals in the dishes in which individuals stayed during two subsequent inspections (light bars).

only at the end of experiment C it reached the value comparable with the skewness coefficient from the control experiment A.

Dispersal. The distribution of distances covered by all individuals during the two-day periods

for experiment B with the possibility of dispersal between experimental dishes is illustrated in Fig. 11.1. The average two-day distances covered by individuals during experiment B are illustrated in Fig. 11.1. The same data for experiment C from 2006 are

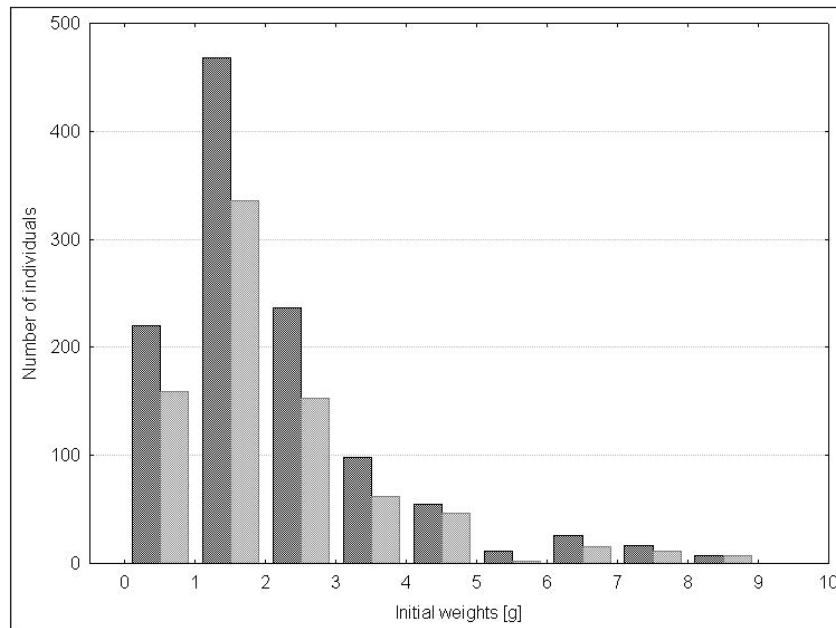


Fig. 14. Experiment B. The distribution of the initial weights of individuals which dispersed from the dishes (dark bars) compared with the distribution of the initial weights of individuals which stayed in the dishes (light bars).

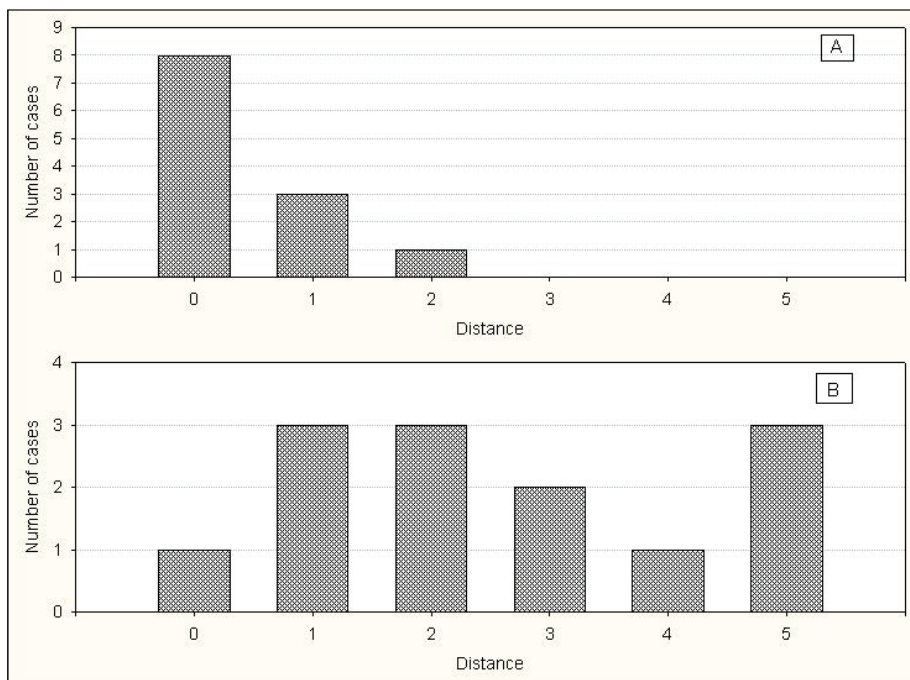


Fig. 15. Experiment B. (1) The distribution of two-day distances covered by individuals with small weight at the end of the experiment (3.4 g), (2) The distribution of two-day distances covered by individuals with much greater weight at the end of the experiment (25.3 g).

illustrated in Fig. 12.1 and Fig. 12.2, respectively.

During each inspection of the dishes in experiment B, the locations of all individuals found in the dishes were noticed. If an individual was found in the same dish as during the previous inspection, the number of individuals in the dish was noticed. If, however, an individual was found in the dish different than in

the previous inspection, the number of individuals in the former dish was also noticed. This enables us to construct two distributions: the first one illustrating the distribution of the number of individuals in dishes in which individuals stayed, and the second one illustrating the distribution of the number of individuals in dishes from which they dispersed. This was done

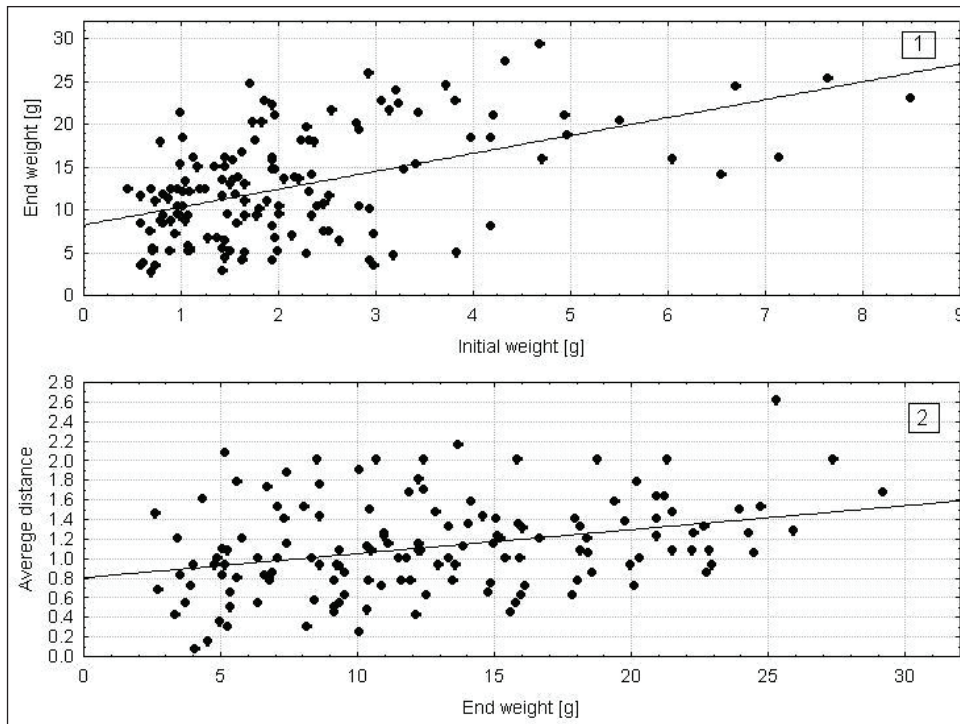


Fig. 16. Experiment B. (1) Correlation between the end and initial weights of individuals ($r = 0.50$). (2) Correlation between the weight of individuals at the end of the experiment, and the average distance covered by these individuals during the experiment ($r = 0.30$). Both correlations are significant.

together for all individuals found in the dishes and for all inspections during experiment B (Fig. 13). There were no statistically significant differences between the average values of these two distributions (Mann-Whitney test, $p > 0.05$).

There were statistically significant differences between the distribution of initial (at the beginning of the experiment) weights of the individuals which during the inspections in experiment B were found in the same dish as in the previous inspections and the initial weight distribution of individuals found in another dish than in the previous inspections (Fig. 14). The average initial weight of dispersing snails was greater than the average initial weight of not dispersing individuals (Mann-Whitney test, $p < 0.05$).

The analysis of variance was performed to test the dependence between the weights of individuals at the end of the experiment and the average distance they covered during the whole experiment. Each individual from the experiment was classified into one of four classes according to its weight at the end of the experiment, and the significance of differences in average distances between individuals from different weight classes was tested. There were statistically significant differences in the average distances covered by snails from different weight classes in

the case of experiment B (ANOVA, $F = 6.74$, $p = 0.00014$).

This can be illustrated also by examples of two snails with different weights at the end of experiment B. The distribution of two-day distances covered by snails with the weight at the end of the experiment equal to 3.4 g is shown in Fig. 15.1. The same kind of the weight distribution but for snails the weight of which equalled to 25.3 g at the end of the experiment, illustrates Fig. 15.2. Heavier snail had a much greater proportion of dispersals over up to twice longer distances than the lighter snail.

The above results of experiment B can be also presented in the following form: as a positive correlation between initial and end weights of individuals (Fig. 16.1) and as a positive correlation between the weights of individuals at the end of experiment B and the average distances covered by these individuals during the experiment (Fig. 16.2). Both of them were statistically significant.

There were no differences in the average distances covered by individuals with different weights at the end of experiment C with local populations located closer to each other, and smaller than in experiment B dispersal costs (ANOVA, $F = 1.21$, $p = 0.112$)

Discussion

When analyzing the weights of individuals, one can see all symptoms showing that food conditions in the experiments were poor. They led to competition for food between individuals. It was strong in the control experiments A without possibility of dispersal, where the weights of individuals were low, and the skewness of weight distribution had in all cases highest positive values. The positive skewness of the weight distribution means that the population was numerically dominated by individuals with small weights, and the number of heavy individuals was relatively small. But the weights of heavy individuals were much greater than the weights of most individuals in the population.

A decrease in population density – smaller number of competitors – always diminishes the intensity of competition. The skewness of weight distributions decreased with time in the control experiment A (especially during the first half of the experiment). It was correlated with the increasing number of dead individuals in the course of the control experiments. Such a situation is very typical for competitive experiments, and was observed before in many such experiments.

The highest mortality rate was observed in the control experiment A. It was equal to 0.40 if we compare the number of individuals at the beginning and at the end of the experiment. On average, at the end of the control experiment A, we had 6 snails per dish, which was the result of a real mortality of individuals during experiment A. This mortality took place mostly in the first half of the control experiment (there were 19 snails found in the middle of the experiment). Therefore, we can assume that all 18 remaining snails participated in competition during the whole control experiment A.

In experiment B with the possibility of dispersal only 187 individuals were found at the end of the experiment. It gives an average density of 5.1 individuals per dish at the end of the experiment. However, it wasn't the result of a real mortality exclusively. The number of dead individuals found in experiment B was similar to the number of dead individuals in experiment C. All other snails not found during the inspections of dishes in experiment B were those which preferred to stay outside the dishes, and not to participate in competition for food located inside the dishes, so that they were not noticed during inspections. We can therefore assume that the real average density of snails in the dishes in experiment B was equal to or higher than in the control experiment A. Despite the higher density, the skewness coefficient of weight distribution in experiment B was smaller,

and decreased faster with time than in the control experiment A. This is a direct result of the possibility of dispersal to other local population in experiment B.

The skewness of the weight distribution of individuals in the situation when it was possible to disperse was not only much smaller than in the control experiment and decreased with the course of experiments B faster than in the control experiments A, but additionally starting from the middle of experiment B, and also at the end of it the skewness was even negative – individuals with greater weight dominated in the experiment. A negative value of the skewness of weight distribution in an even-aged population is always connected to a weak intra-specific competition or its absence. If densities in experiment and in control are more or less equal (as it was in experiments A and B), the difference in the skewness coefficients and in the rates of decrease in the skewness coefficient over time in the experiments with and without possibility of dispersal can be treated as a measure of the influence of dispersal on the intensity of competition.

The statement that in experiment B with possibility to disperse, the intensity of intraspecific competition was relatively low is supported by the fact that the average weight of individuals was greater in experiments B with possibility of dispersal than in the control experiment A when snails had to stay in closed local populations.

The possibility of dispersal from the local population changed the intensity and results of competition between individuals. We observe the symptoms of a decreasing intensity of competition between individuals, when they can leave the local population. However, dispersal of an individual from the local population is not the same as the death of it. The individual does not disappear and stop competing with other individuals. It continues to live and compete in another local population. What is the difference for the results of competition between the mortality of individuals and their dispersal?

There are two main results of dispersal observed in the experiments. Both of them concern the differentiation of individuals, which took place on two levels. Some individuals died during the experiment with the possibility of dispersal, but others preferred to stay most of the time outside the experimental dishes or to visit them seldom. We can estimate their number using information on the number of individuals noticed at the end of the experiments. The number of such individuals depended on the size of the space between the experimental dishes. In experiment C 16% of the initially introduced individuals chose such a way of life, but in experiment B

with approximately four times greater space between the experimental dishes it was 51% of the introduced individuals. These numbers include the real mortality, but it was similar in experiments B and C (approximately 0.04 of initial population in both cases). Other individuals from this category preferred to avoid competition and to stay most of the time outside the dishes. The second category consists of individuals which preferred to participate (however with different intensity) in competition in local populations, dispersing between them and treating hostile environment between the local populations only as a transient zone.

The second level of the differentiation of individuals took place among these individuals which decided to compete in the island environment. We chose to further analysis only these individuals which did it especially intensively (they were met more than 9 times during inspections of the experimental dishes). The number of them was constant in different experiments (139 individuals in experiment B and 143 in experiment C, which gives 37% and 38% of initially introduced individuals, respectively). This probably reflected the equal number of experimental dishes and the same amount of food offered to snails in all experiments.

In all experiments with the possibility of dispersal, individuals, most often stayed in one local population. 38% of the two-day distances in experiment B were equal to 0. If they dispersed they preferred to go for a short distance. 34% of the two-day distances in experiment B were equal to 1 (individuals moved to the next experimental dish). In all experiments only a small part of the distances covered by individuals during the two-day periods were longer, up to the fifth dish from the current one. The analysis of the average distances covered by individuals show, however, that there were no individuals staying in the same local population during the whole experiment B.

In experiment B dispersal of individuals was connected with some energetic costs of such behaviour, because local populations were located at some distances one from another, and separated by a hostile environment. In this spatial arrangement only large individuals were able to disperse on longer distances. Probably only winners of competition in local populations were able to cover the costs of dispersal in this case. Because weight distributions of competing individuals were positively skewed, the number of large individuals was relatively small. This small number of large individuals relatively frequently dispersing over long distances didn't increase the intensity of competition in local populations. In the local

populations deprived large individuals (because they dispersed and visited local population seldom and for a short time only) the intensity of competition decreased. The individuals that preferred to stay in the local population or disperse over short distances were able to grow faster and to achieve greater weights as a result of the decreased competition in the local population. Therefore, the left part of the weight distribution moved toward its centre, thus increasing the average weight. On the other hand, large individuals that dispersed on long distances obtained benefits from this behaviour. If we analyze Fig. 4, we can see that the number of snails in the dishes changed very dramatically between two subsequent inspections. Moving on long distances, large individuals visited different local populations and could easily find local populations with a small number of other individuals, probably small, weak competitors. This gave large individuals access to a much greater amount of food than they would obtain if they stayed in one local population. They grew faster and achieved greater weights as compared to individuals from experiment A. But large individuals have to bear energetic costs of dispersing on long distances. Due to the costs of dispersal, the right part of the weight distribution moved relatively slower and was not able to escape from its left part. The average weight increased relatively to results of the experiment without dispersal but the skewness of weight distribution decreased.

Despite the possibility of dispersal between local populations, the degree of separation of local populations and the associated dispersal costs of individuals could modify the results of the experiments in different ways. When dispersal is related to some cost (as in experiment B), it leads to the reduction of competition intensity: the average weight of competing individuals is greater and weight distributions are less skewed. The situation is different, however, if local populations stay close to each other, individuals can easily move to the neighbouring dish, and the costs of dispersal are small as it was in the case of experiment C. Much more compact space in the case of experiment C didn't give individuals possibility to hide or escape from the experiments. Due to this, the average density in local populations was much higher than in experiment B. 320 snails were noticed at the end of the experiment C. This gives an average number of snails per dish equal to 8.9, which is a much higher value than in experiments A and B. This is the first reason for the highest skewness and variability of the weight distribution in experiment C. Additionally, in experiment C all individuals irrespective of their weight and status during competition could easily disperse to the

neighbouring local population, but only some of them did this. Because the average distance of dispersal didn't depend on the weight of an individual, these individuals which decided to disperse were recruited from all weight classes. Instead of a pure situation with separated local populations we have in this case local populations with most snails staying in them for most of the time, and competing there locally (but travelling from time to time on short distances irrespective of their weights), and the rest of individuals of different weights dispersing on different distances and competing globally with other individuals in many local populations. These local and global components of competition make it relatively strong, even stronger than in the case of local populations strictly isolated with no possibility of dispersal.

Despite greater costs of dispersal in experiments B with long distances between local populations the tendency to disperse was the same as in experiments C with local populations close to each other (compare Fig 11 and Fig. 12). The distributions of two-day movements and average two-day movements were similar in both experiments (the share of small average distances is greater in the case of experiment C), however note that distance 1 in experiment B was in fact two times longer than the same distance in experiment C and, additionally, the neighbouring dishes were separated by a hostile environment in experiment B. Different was only the quality of dispersing individuals. In experiment C all snails could easily disperse, making the space of the whole experiment one big experimental dish with a high average number of snails per dish, because the space outside the dishes was very small. This produced conditions for intense competition. In experiment B only large individuals could move on long distances, using this opportunity for increasing their access to more food in the dishes they visited, and releasing food for other individuals in the dishes they left.

Generally, the possibility to disperse to other local environments gave competing individuals access to a greater amount of resources. This increased the consumption and assimilation rates of individuals. When the costs of dispersal were small, all individuals used this opportunity. This converted

environmental conditions into one big local population and intensified competition. This was the situation similar to competition in one isolated local population with a comparable number of competing individuals. However, when the costs of dispersal were high, only large individuals could benefit from dispersal. However, their dispersal diminished the intensity of competition in general.

It looks like that in the first case – when local populations are close together and the cost of dispersal are small – individuals sensed the condition in the neighbouring local population without going there, and decided to change the feeding place only when in the new place conditions were better. In the second case – when local populations are separated by hostile environment and the cost of dispersal are high – individuals had to check conditions in the neighbouring local population only by going there, and because of the high costs of dispersal only stronger competitors (individuals with greater weight) could do this. The second situation is probably much more common in nature.

We think that this is a proof that dispersal to other local habitats is an important component of snail behaviour which evolved as a competition avoidance mechanism. But the value of such mechanism depends on spatial arrangement of the environment.

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