



## Resource Partitioning among Competing Individuals: an Experiment with Bean Weevil *Acanthoscelides obtectus* (Say, 1831) (Coleoptera: Chrysomelidae)

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**Abstract:** The aim of this study is to prove that intraspecific competition leads to unequal resource partitioning. Bean weevil *Acanthoscelides obtectus* larvae were used in the experiment. They foraged inside bean seeds drilling corridors. Different numbers of larvae can live together in one seed. The corridors were filled with a dentistic material. Following variables were measured in the experiment: weight of bean seed before and after the experiment, the number of larvae living in each seed, weights of filling which is a measure of the amount of resource consumed by a larva and the weight of adult individual emerging from each marked corridor of known size. Weights of fillings and weights of adult individuals are variable even when they are taken from seeds with only one larva living inside. However, in this case there are no other relations between variables measured in the experiment. When many larvae are living together in one seed, the variability of weights of fillings is greater and the distribution of weight of adult individuals is positively skewed. Additionally there is statistically significant positive relationship between weight of fillings and weight of adult individuals and negative relationship between the length of larval period and weight of adult individual together with weight of filling.

**Key words:** bean weevil, *Acanthoscelides obtectus*, intraspecific competition, resource partitioning, individual variability

### Introduction

Intraspecific competition between individuals in even-aged populations leads to an unequal distribution of resources that are the subject of competition among competing individuals (ŁOMNICKI 1988). However, the number of papers documenting this fact is very little. Most often, it is indirectly inferred from the shapes of weight distributions in even-aged populations (UCHMAŃSKI 1985, 1987).

JOBLING (1993), in a review article on fish bioenergetics, stated that interactions between individuals of the same age resulted into the formation of a social hierarchy among them. This in turn caused

unequal distribution of resources and differences in body weight with low level of resources. The individual being the strongest competitor had the highest position in the social hierarchy and was usually the heaviest.

NAKANO (1995) studied small, local populations of the salmon *Oncorhynchus masou ishikawai* in mountain streams in Japan. Direct observations of marked fish revealed the existence of a social hierarchy. The individuals with the highest positions in this hierarchy were territorial, had the largest territories and occupied the most food-rich places. They also spent most time outside their hiding places and ate the largest victims. This led to large differences in

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the amount of food eaten between territorial individuals. There was also a positive correlation between the rank of an individual in the social hierarchy and the amount of food eaten. The same relationship was observed between the rank of an individual and its weight. The fishes at the bottom of the social hierarchy were not territorial, moved over a much larger area and often migrated to other reservoirs.

YAMAGISHI (1962) studied small, laboratory populations of the rainbow trout *Oncorhynchus mykiss* (Walbaum, 1792) (originally reported as *Salmo gairdneri* Richardson, 1836). The results confirmed the existence of variability in body weight and food consumption in even-aged fish populations but also showed that this variability was greater when environmental conditions allowed dominant individuals to monopolize resources. Similar results were obtained by SYMONS (1968) for the Atlantic salmon *Salmo salar* Linnaeus, 1758 and by MAGNUSON (1962) for *Oryzias latipes* (Temminck & Schlegel 1846). It turned out that the observed increase in the differentiation of the growth rates of individuals and the rates of food consumption in deteriorating food conditions may be associated with the strengthening of the social hierarchy in the population.

In sedentary organisms such as terrestrial plants, their uneven distribution in space also leads to their unequal access to light and soil resources. There are various measures in ecological literature that attempt to quantify these aspects of interactions between sedentary organisms (BENJAMIN & HARDWICK 1986, KENKEL 1990, CZÁRÁN 1998, BERGER & HILDEBRAND 2000, BAUER et al. 2004, GRABARNIK 2007, BERGER et al. 2008). WYSZOMIRSKI et al. (1999) modified the above-mentioned approach of Benjamin and Hardwick to such a form that it can be used to describe the effects of unequal distribution of resources between globally competing non-sedentary animal organisms.

In even-aged populations, not only individual weights and assimilation rates vary. The respiration rate also shows a considerable degree of variability. KLEKOWSKI et al. (1967) showed this for the oxygen consumption rate of adult individuals of *Tribolium castaneum* (Herbst, 1797) (Coleoptera: Tenebrionidae). Similar results were obtained by CIANCIARA (1980) for *Cloeon dipterum* (L., 1761) (Ephemeroptera). There is a purely physiological positive relationship between the growth rate of an individual and the rate of metabolism of the growing individual (KONARZEWSKI 1995). Additionally, competition with other individuals means not only unequal distribution of resources among competing

individuals but also different energy costs of individuals' lives related to obtaining different amounts of food during competition. The correlation between the rates of assimilation and respiration of individuals competing in even-aged populations may have a different sign. It may be positive. The assimilation of more food may be accompanied by higher energy costs of obtaining this food. METCALFE et al. (1995) showed that in *Salmo salar* the rate of standard metabolism increased with the position of the fish in the social hierarchy. Additionally, in this species, fish of higher position in the social hierarchy had a higher growth rate. The costs of being a dominant and having more resources can be so great that the net energy gains of the dominant may be less than the net gains of the lower-ranking individual. YAMAGISHI et al. (1974) described a social hierarchy in small, laboratory populations of freshwater goby *Odontobutis obscurus* (Temminck & Schlegel, 1845). The social hierarchy has been reconstructed based on aggressive and territorial behaviour. The food ration of individual fish was measured directly. The fish dominating the social hierarchy defended the best territory and had the highest food consumption. However, the second fish in the social hierarchy was heavier than the dominant fish because the dominant's energy expenditure was the highest and it was able to devote only a smaller amount of its energy to the growth of its own body. Considerable amounts of energy were spent in maintaining the dominant position. On the other hand, the dominant fish showed the lowest variability of the food ration over the duration of the experiment.

For animal species in which no social hierarchy or territorial behaviour have been observed, there is lack of information about the distribution of resources among competing individuals. It should be noted, however, that such experiments are very difficult as, for most species, it is virtually impossible to measure the amount of food consumed by each individual in a case of scramble competition. In the studies presented above, the size of an individual's territory was a measure of the amount of resources that it obtained in competition with other individuals. In the case of non-territorial species, a different trace of the individual's activity must be found, a trace that would allow an estimate of the amount of food consumed by the individual. Direct measurement of an individual's consumption in a population of competing individuals is possible only in the case of large vertebrates, using expensive and complicated equipment. On the other hand, it seems that the unequal distribution of the resources as a result of competition being a common phenomenon

also occurs, e.g. in those animals that do not have territorial behaviour. The aim of this work is to show the variability in the amount of food obtained by individuals in conditions when they exploit common resources, the competition is scrambler and there is no social hierarchy or territorial behaviour. The subject of the research is an insect species whose larvae leave clear traces of feeding, which makes it possible to measure the amount of food obtained by each individual.

## Materials and Methods

The experiment described in this study used a bean weevil culture that was kept at optimal temperature and humidity throughout the experiments. The breeding was carried out in a way to obtain even-aged groups of adult males and females. Bean seeds of a variety preferred by the bean weevil larvae were used. The bean variety was selected based on the literature on the breeding of the bean weevil and preliminary experiments conducted before the main experiment.

In the main competition experiment, a number of male and female bean weevils were introduced into a number of seeds. Each seed was weighed and labelled. From the eggs laid by the females, the larvae hatched and bit into the bean seeds. After metamorphosis, the adult insects of the next generation left the bean seeds. Each emerging adult was individually marked, weighted and assigned to an appropriate corridor hollowed out by the larva from which it had arisen. The amount of the food consumed by each larva was measured by filling the corridor it left inside the bean with dental material (with a known specific weight) and subsequent weighting of the “filling”. The adult weight was related to the amount of food eaten by the larva from which it had emerged. In turn, the amount of food eaten by the larva was related to the weight of the bean seed in which it developed and the number of other larvae present in the seed.

The cultivation of the *Acanthoscelides obtectus* beetle later used in the main experiment began in May. Over a period of approximately three months, the beetles were successively multiplied for the main experiment. In early September, 120 previously weighed and marked beans were infected with 120 adult insects of both sexes. Two weeks after the start of the experiment, 91 live adults and 29 dead were recorded. After four weeks, 23 live adults and 97 dead were recorded. At the end of October, only four live and 116 dead individuals were recorded.

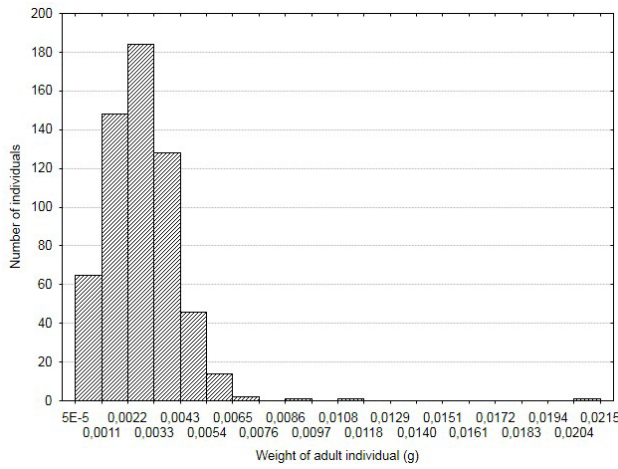


**Fig. 1.** Seeds analysed in the experiment as appearing at the end of the experiment. Note the different number of windows in each of the seed.

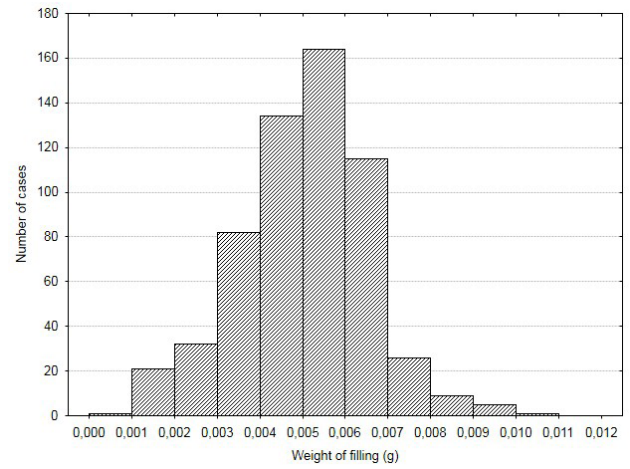
About six weeks after the experiment was set up, the first descendants were obtained in the first days of November. The period of the appearance of descendants lasted until January of the following year. The descendants were preserved in test tubes in 70 % ethanol solution immediately after leaving the bean windows (Fig. 1), which were marked with colour. Each individual was then individually dried in an incubator at 40° C for 24 hours to obtain a dry weight of the beetle. After the period of the appearance of progeny individuals, 26 bean seeds were observed, in which no traces of the presence of a beetle were noticed. In the remaining 94 seeds, traces of the presence of insects in the form of holes left by them were noticed with the naked eye. The coloured holes formed by insects were sequentially filled with a dental mass of the company *Zhermack Hydrogum 5* prepared according to the manufacturer's instructions. After extraction, each filling was weighted using an electronic balance. When the last individuals had emerged from the seeds, each bean was weighted using an electronic balance.

## Results

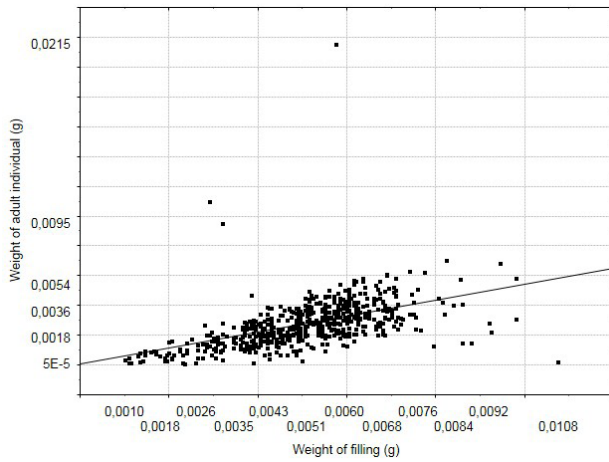
In the experiment, there was a relatively low mortality of larvae, i.e. c. 4 %. There were 26 reports of larva deaths inside beans. The average weight of dead larvae was  $1.408 \times 10^{-3}$  g (the minimum weight was  $0.5 \times 10^{-4}$  g, and the maximum was  $2.95 \times 10^{-3}$  g); it was significantly lower than the average weight of a live adult that emerged from the seed (*t* test,  $t = 4.5$ ,



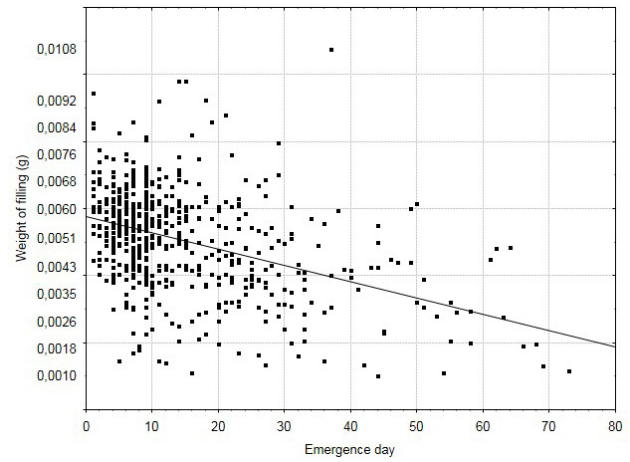
**Fig. 2.** Weight distribution of all 590 adult individuals obtained in the experimental culture. Average weight  $2.793 \times 10^{-3}$  g, minimum  $5.0 \times 10^{-5}$  g, maximum  $2.15 \times 10^{-2}$  g, variance  $2.0 \times 10^{-6}$ , standard deviation  $1.559 \times 10^{-3}$ , skewness coefficient 3.403.



**Fig. 3.** Weight distribution of all 590 fillings made by the larvae that gave rise to adults with the weights shown in the Fig. 2. The fillings were made of a dental material with a specific weight different from that of the bean seed. Average weight  $5.076 \times 10^{-3}$  g, minimum  $1.0 \times 10^{-3}$  g, maximum  $1.075 \times 10^{-2}$  g, variance  $2.0 \times 10^{-6}$ , standard deviation  $1.512 \times 10^{-3}$ , skewness coefficient -0.097.



**Fig. 4.** Cumulative data for all 590 individuals. Linear regression illustrating the relationship between adult weight and the weight of the filling of the corridor made by a larva that later developed into an adult. The relationship is statistically significant at the significance level of 0.05.  $R^2 = 0.273$ , and the  $p$ -value of the probability of making a type 1 error in the significance test for the slope of the regression line is less than 0.001.

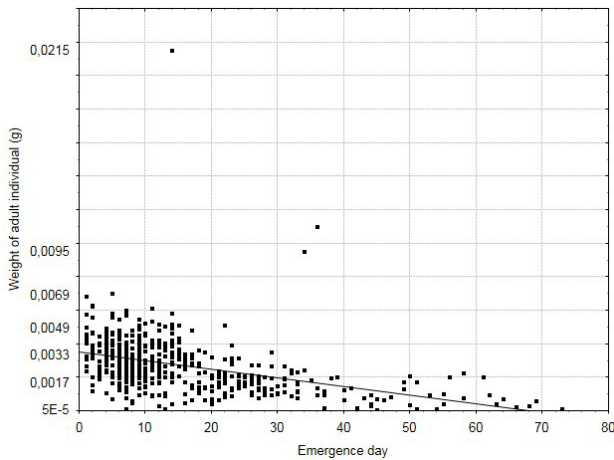


**Fig. 5.** Cumulative data for all 590 larvae. Linear regression illustrating the relationship between the weight of the filling and the development time of the larva. The horizontal axis shows the days that have elapsed since the first adult appeared on November 1. The relationship is statistically significant at the significance level of 0.05.  $R^2 = 0.167$ , and the  $p$ -value for the slope of the straight line is less than 0.001.

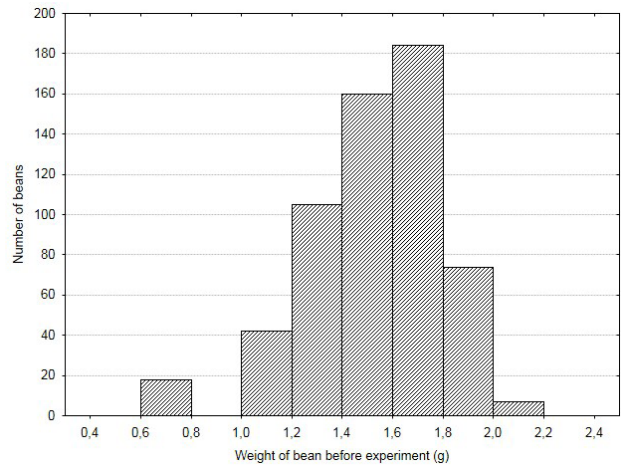
$p = 0.8 \times 10^{-5}$ ). Totally, 590 adult individuals emerged from bean seeds.

The weight distribution of all adult animals obtained in the experiment (Fig. 2) was clearly positively skewed with a predominance of individuals with low weights and few individuals with high weight. It also showed a large variability of the weights of adult individuals as the lightest individual had a weight of

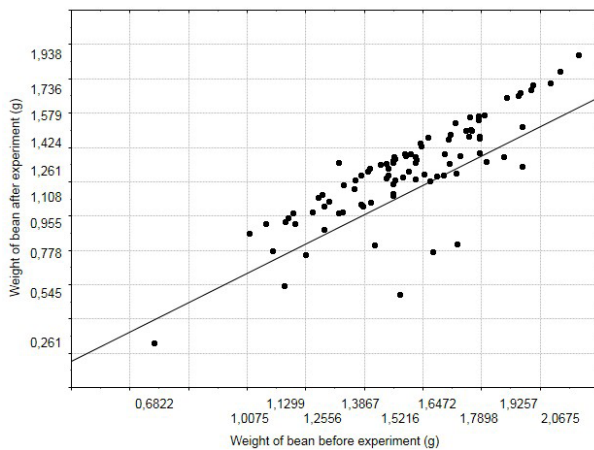
$5.0 \times 10^{-5}$  g and the heaviest one was  $2.15 \times 10^{-2}$  g. The distribution of weights of all fillings obtained (Fig. 3) was almost symmetrical (characterised by a slightly marked negative skewness) and with much lower variability; the smallest filling had a weight of  $1 \times 10^{-3}$  g and the heaviest was  $1.075 \times 10^{-3}$  g). There was a statistically significant positive correlation between the weight of the adult and the weight of



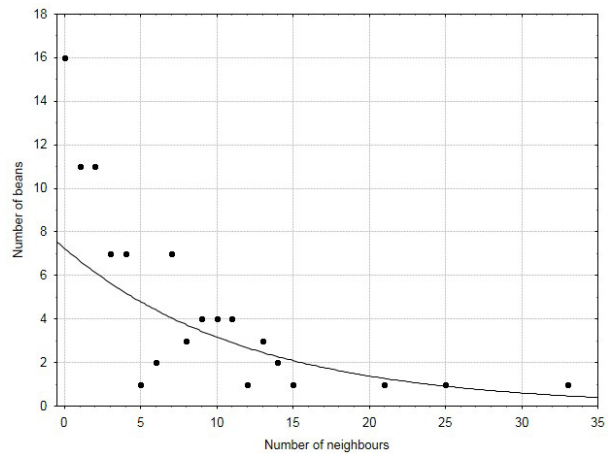
**Fig. 6.** Cumulative data for all 590 individuals. Linear regression illustrating the relationship between adult weight and development time of the larva. The horizontal axis shows the days that have elapsed since the first adult appeared on November 1. The relationship is statistically significant at the significance level of 0.05.  $R^2 = 0.181$ , and the  $p$ -value for the slope of the straight line is less than 0.001.



**Fig. 7.** Bean seed weight distribution before the experiment, illustrating one of the components of the variability in the conditions under which the larvae were foraging.



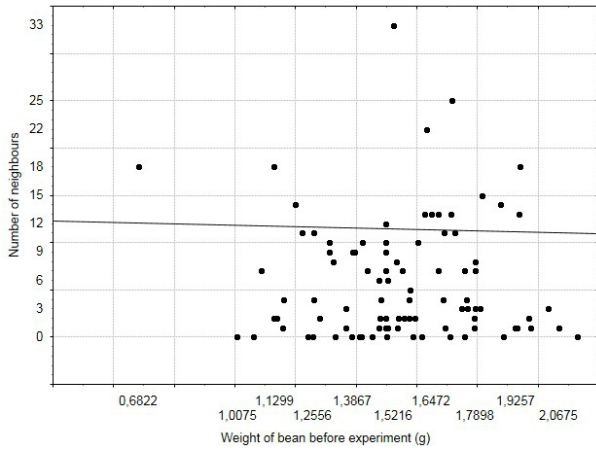
**Fig. 8.** Cumulative data for all bean seeds used in the experiment. Linear regression illustrating the relationship between the weight of the beans after the experiment and before the experiment. The relationship is statistically significant at the significance level of 0.05.  $R^2 = 0.532$ , and the  $p$ -value for the slope of the straight line is less than 0.0001.



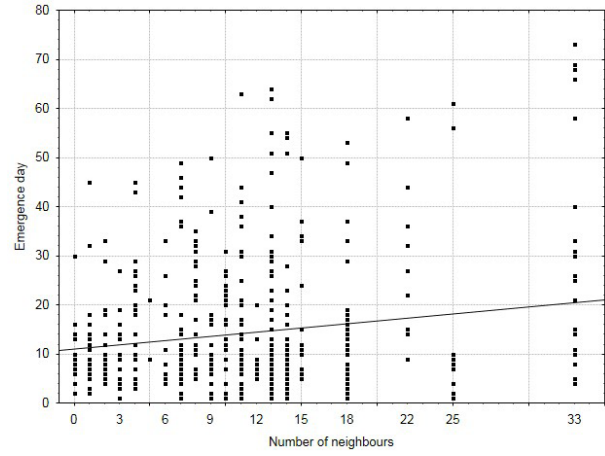
**Fig. 9.** Illustration of the relationship between the number of larvae foraging in a bean seed and the number of seeds with a given number of larvae. As explained in Tab. 1 the number of neighbours equal to, for example, 0 means that the seed is inhabited by only one larva that has no neighbours. To illustrate that in the experiment, a decreasing number of seeds was observed with an increased number of neighbours, a decreasing exponential function was fitted to the experimental points.

the filling of the corridor of its larva (Fig. 4). On the other hand, the longer the development of the larva (the longer stay in the bean seed) was associated with a smaller corridor left by it (Fig. 5). This, in combination with the relationship shown in Fig. 4, implied that a similar decreasing relationship was observed between the weight of the adult individual and the development time of the larvae (Fig. 6).

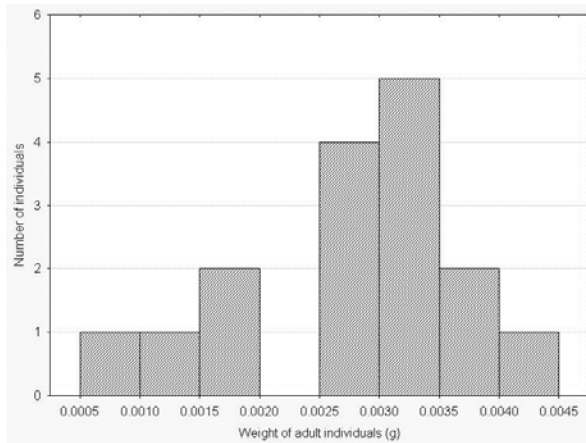
Contrary to the adult lifestyle, the interactions between the larvae were local. Competition between larvae was limited to neighbours foraging together in the same bean seed. Since the bean seeds had different weights before the experiment and different numbers of larvae could be found in a single seed, this allowed concluding that the living conditions of larvae were differing in this experiment.



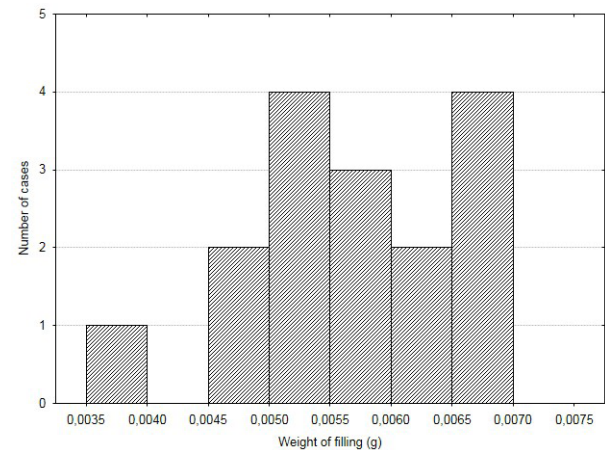
**Fig. 10.** Cumulative data for all bean seeds used in the experiment. Linear regression illustrating the relationship between the number of neighbours and the weight of the bean seed prior to the experiment. The relationship is not statistically significant at the significance level of 0.05.  $R^2 = 0.00066$ , and the  $p$ -value for the slope of the straight line is equal to 0.533.



**Fig. 11.** Cumulative data for all 590 larvae. Linear regression illustrating the relationship between larval development time and the number of neighbours feeding together in bean seeds. The relationship is statistically significant at the significance level of 0.05.  $R^2 = 0.011$ , and the  $p$ -value for the slope of the straight line is 0.011.



**Fig. 12.** Distribution of weights of adult individuals emerged from larvae that foraged individually in bean seeds. Average weight  $2.819 \times 10^{-3}$  g, minimum  $1.0 \times 10^{-3}$  g, maximum  $4.05 \times 10^{-3}$  g, variance  $1.0 \times 10^{-6}$ , standard deviation  $9.28 \times 10^{-4}$ , skewness coefficient  $-0.653$ .

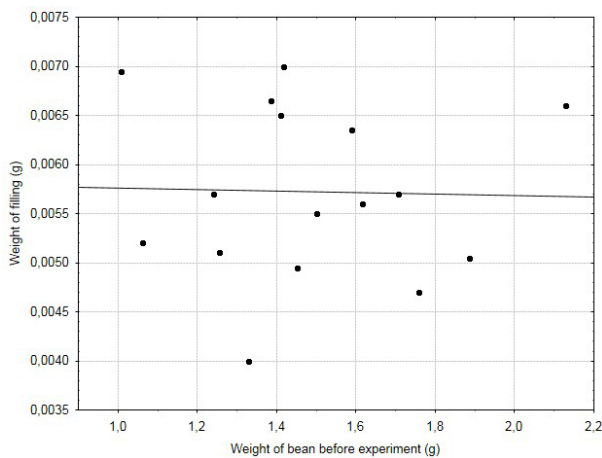


**Fig. 13.** Distribution of filling weights from bean seed inhabited by single larvae. Average weight  $5.722 \times 10^{-3}$  g, minimum  $4.0 \times 10^{-3}$  g, maximum  $7.00 \times 10^{-3}$  g, variance  $1.0 \times 10^{-6}$ , standard deviation  $8.78 \times 10^{-4}$ , skewness coefficient  $-0.135$ .

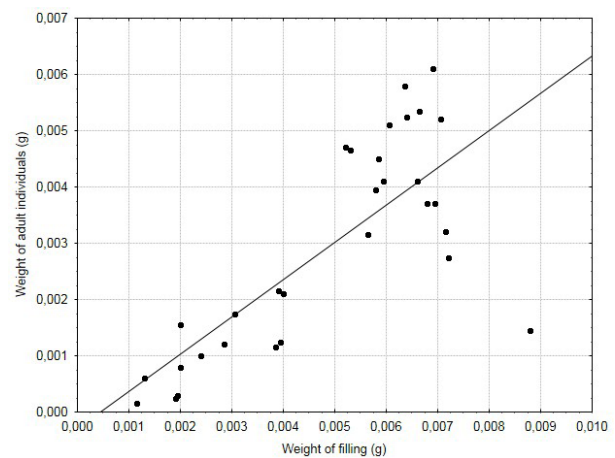
The weight of bean seeds to be used in the experiment varied (Fig. 7) There was a statistically significant increasing linear regression between the weight of the beans after the experiment (i.e., when all larvae foraging inside left them) and their weight before the experiment (Fig. 8). Table 1 and Fig. 9 (based on the data from Table 1), showing the relationship between the number of larvae foraging in the bean seed and the number of seeds with this number of larvae, demonstrated that most often only one larva foraged in a seed. Number of seeds quick-

ly decreased with increasing the number of larvae living inside. The greatest number of larvae living together in the seed was 34 and there was only one seed with this number of larvae.

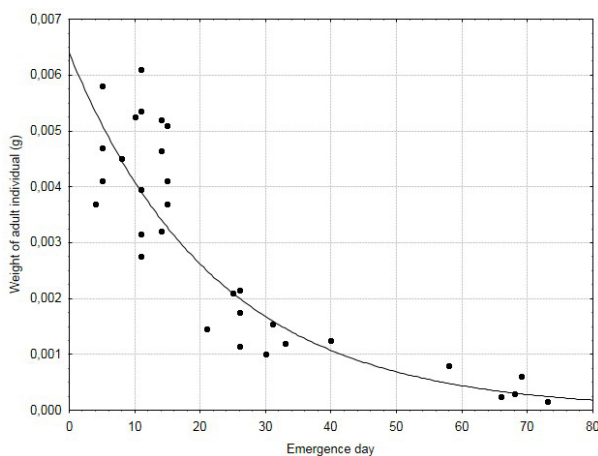
There was no statistically significant correlation between the number of larvae feeding in the bean seed and its weight before the experiment (Fig. 10). However, there was, although quite weak, a statistically significant positive relationship between the duration of the larvae stage and the number of larvae feeding together in the bean seed (Fig. 11).



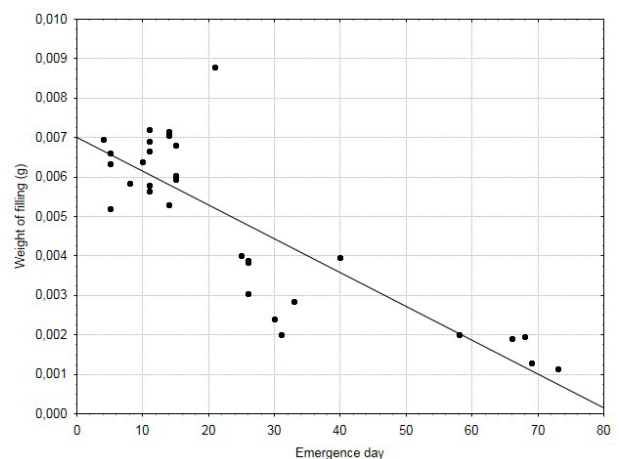
**Fig. 14.** Illustration of no statistically significant correlation between filling weight and bean seed weight prior to the experiment for seeds inhabited by single larvae. The relationship is not statistically significant at the significance level of 0.05.  $R^2 = 0.00069$ , and the  $p$ -value for the slope of the line is 0.923.



**Fig. 15.** The seed with 34 together foraging larvae. Illustration of the linear relationship between the weight of the adult individual and the weight of the filling. The relationship is statistically significant at the significance level of 0.05.  $R^2 = 0.574$ , and the  $p$ -value for the slope of the straight line is less than 0.001.



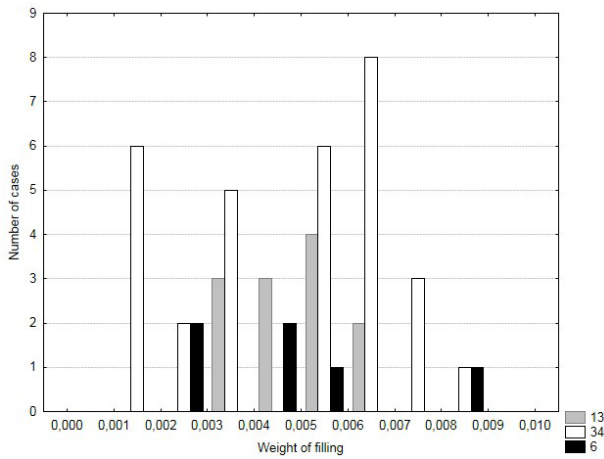
**Fig. 16.** The seed with 34 together foraging larvae. Illustration of the decreasing, exponential relationship between adult weight and length of the larval stage. The horizontal axis shows the days that have elapsed since the first adult appeared on November 1.



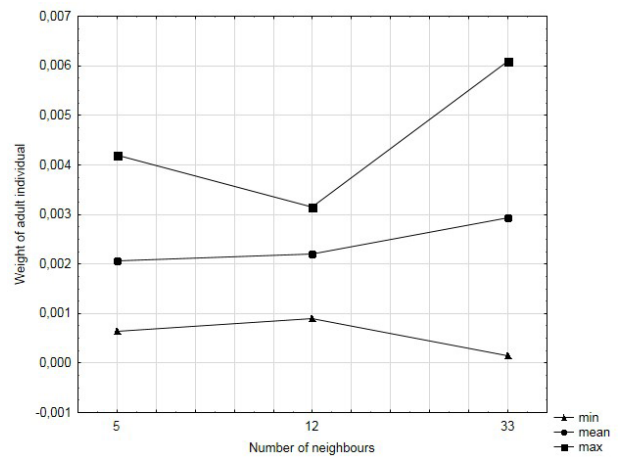
**Fig. 17.** The seed with 34 together foraging larvae. Illustration of the linear relationship between the weight of the filling and the duration of the larval stage. The horizontal axis shows the days that have elapsed since the first adult appeared on November 1. The relationship is statistically significant at the significance level of 0.05.  $R^2 = 0.701$ , and the  $p$ -value for the slope of the straight line is less than 0.001.

In the experiment, 16 bean seeds were found with one larva living inside (number of neighbours equal to 0). The distribution of adult weights in this case (Fig. 12) and the distribution of weights of fillings derived from seeds where only one larva was feeding (Fig. 13) demonstrated that both distributions proved that in the case where there is no interactions from the side of other individual weights of adult individuals and weights of fillings are variable. However, there were no statistically significant relationships, which were observed earlier in the

case of collective presentation of all data obtained in the experiment (see above). In particular, there was no statistically significant relationship between the filling weight and the bean seed weight before the experiment (Fig. 14), the adult weight and the filling weight, the weight of the filling or weight of adult individual and the duration of the larval stage (the latter relationships are not shown in the figures). The only statistically significant linear relationship was, as before, between the bean seed weight before and after the experiment (also not illustrated).



**Fig. 18.** Distributions of fillings from single bean seeds inhabited by a different number of larvae. Empty bars – 34 foraging together larvae (33 neighbours in the seed), the seed weight before the experiment was 1.5216 g. Black bars – 6 together foraging larvae (5 neighbours in the seed), the seed weight before the experiment was 1.5785 g. Grey bars – 13 together foraging larvae (12 neighbours in the seed), the seed weight before the experiment was 1.4978 g.



**Fig. 19.** Maximal (squares), mean (circles) and minimal (triangles) weights of adults emerging from single seeds in which 6, 13 and 34 larvae (5, 12 and 33 neighbours in one bean, respectively) foraged. The weight distributions of the fillings derived from these beans are shown in Fig. 18.

**Table 1.** Number of seeds inhabited by a given number of larvae. A number of neighbours equal to 0 means that the bean seed is being inhabited by one larva that has no neighbours, while the number of neighbours of 33 means that the seed is being inhabited by 34 larvae with 33 neighbours each.

| Number of neighbours | Number of bean seeds | Number of neighbours | Number of bean seeds |
|----------------------|----------------------|----------------------|----------------------|
| 0                    | 16                   | 17                   | -                    |
| 1                    | 11                   | 18                   | 3                    |
| 2                    | 11                   | 19                   | -                    |
| 3                    | 7                    | 20                   | -                    |
| 4                    | 7                    | 21                   | -                    |
| 5                    | 1                    | 22                   | 1                    |
| 6                    | 2                    | 23                   | -                    |
| 7                    | 7                    | 24                   | -                    |
| 8                    | 3                    | 25                   | 1                    |
| 9                    | 4                    | 26                   | -                    |
| 10                   | 4                    | 27                   | -                    |
| 11                   | 4                    | 28                   | -                    |
| 12                   | 1                    | 29                   | -                    |
| 13                   | 3                    | 30                   | -                    |
| 14                   | 2                    | 31                   | -                    |
| 15                   | 1                    | 32                   | -                    |
| 16                   | -                    | 33                   | 1                    |

Six single seeds were obtained in the experiment, inside which in each case a different number of larvae were foraging, from six to thirty-four; in other words, each larva had from five to thirty-three neighbours. The numbers of larvae in each seed were relatively small (Table 1) and, additionally, there were uninhabited seeds. In order not to be influenced by results burdened by chance, only very simple statistical indices were calculated and the case

with the largest number of larvae foraging together in a seed (34 larvae) was analysed primarily.

The results characterising the weights of adults derived from the bean seed with 34 larvae (Table 2) and the corresponding weights of fillings (Table 3) showed a statistically significant increasing relationship between adult weight and filling weight (Fig. 15). There was a statistically significant decreasing relationship between adult weight or filling weight and the

**Table 2.** Weights of adult individuals that emerged from larvae feeding in single bean seeds with a different number of larvae. For comparison, the first row of the table shows the values for those seeds where single larvae were foraging. Legend: 1. Number of neighbours. 2. Average adult weight (g). 3. Minimum adult weight (g). 4. Maximum adult weight (g). 5. Difference in values from the column 4 and 3 (g). 6. Bean seed weight before the experiment (g). 7. Bean seed weight after the experiment (g). 8. Difference of values from columns 6 and 7 (g). 9. Value from column 8 divided by the number of larvae foraging together (g).

| 1  | 2        | 3        | 4        | 5       | 6      | 7     | 8      | 9       |
|----|----------|----------|----------|---------|--------|-------|--------|---------|
| 0  | 0.002819 | 0.00100  | 0.00405  | 0.00305 |        |       |        |         |
| 5  | 0.002067 | 0.00065  | 0.0042   | 0.00355 | 1.5785 | 1.331 | 0.2475 | 0.0495  |
| 12 | 0.002204 | 0.00090  | 0.00315  | 0.00225 | 1.4978 | 1.12  | 0.3778 | 0.02815 |
| 15 | 0.002273 | 0.00035  | 0.003650 | 0.0033  | 1.8145 | 1.317 | 0.4975 | 0.03317 |
| 22 | 0.002589 | 0.00035  | 0.004950 | 0.0046  | 1.6335 | 1.353 | 0.2805 | 0.01275 |
| 25 | 0.003016 | 0.001950 | 0.004300 | 0.00235 | 1.7151 | 0.836 | 0.8791 | 0.03516 |
| 33 | 0.002935 | 0.000150 | 0.006100 | 0.00595 | 1.5216 | 0.545 | 0.9766 | 0.02959 |

**Table 3.** Weights of fillings, which were created by larvae foraging in single bean seeds with different number of neighbours. For comparison, the first row of the table shows the values for those seeds where single larvae were foraging. Legend: 1. Number of neighbours. 2. Average filling weight (g). 3. Minimum filling weight (g). 4. Maximum filling weight (g). 5. Difference of values from columns 4 and 3 (g). 6. Bean seed weight before the experiment (g). 7. Bean seed weight after the experiment (g). 8. Difference of values from columns 6 and 7 (g); 9. Value from column 8 divided by the number of larvae foraging together (g).

| 1  | 2        | 3        | 4        | 5       | 6      | 7     | 8      | 9       |
|----|----------|----------|----------|---------|--------|-------|--------|---------|
| 0  | 0.005722 | 0.00400  | 0.00700  | 0.003   |        |       |        |         |
| 5  | 0.004683 | 0.002750 | 0.008150 | 0.0054  | 1.5785 | 1.331 | 0.2475 | 0.0495  |
| 12 | 0.004879 | 0.003100 | 0.006500 | 0.0034  | 1.4978 | 1.12  | 0.3778 | 0.02815 |
| 15 | 0.005063 | 0.003050 | 0.009200 | 0.0062  | 1.8145 | 1.317 | 0.4975 | 0.03317 |
| 22 | 0.004471 | 0.001000 | 0.007150 | 0.00615 | 1.6335 | 1.353 | 0.2805 | 0.01275 |
| 25 | 0.005220 | 0.002900 | 0.008600 | 0.0057  | 1.7151 | 0.836 | 0.8791 | 0.03516 |
| 33 | 0.004869 | 0.001150 | 0.008800 | 0.00765 | 1.5216 | 0.545 | 0.9766 | 0.02959 |

duration of the larval stage for the same seed (Figs. 16 and 17). Fig. 18 compares the weight distributions of the fillings from the corridors hollowed in the three seeds with different numbers of foraging together larvae: 6, 13 and 34 individuals. Cases with 6 and 13 foraging together larvae were represented by single seeds, similarly to the single seed with 34 larvae.

Apart from the six cases represented by single seeds with different numbers of larvae feeding in them, there were also cases of other numbers of larvae feeding together but represented by a greater number of seeds and different in each case. In order not to introduce an additional source of variability in the results in the form of varying seed weights and varying number of seeds, the analysis presented here is limited to the above-mentioned six cases represented by a single seeds.

## Discussion

The way of life of the bean weevil larvae, i.e. the traces of foraging left by them as corridors inside bean seeds, provides a unique opportunity to estimate the amount of food obtained by individual

larvae. Before starting the experiment, it has been assumed that the presence of other foraging larvae in bean seeds limits their possibilities of obtaining food and, as a consequence, leads not only to lowering the average values of the parameters measured in the experiment but also to individual variability in their values. The aim of the experiment was therefore to search for traces of interaction (intraspecific competition) between bean weevil larvae foraging together in bean seeds, bearing in mind the results of previous studies on the ecological effects of intraspecific competition in even-aged populations of animals and plants. We judge primarily not on the changes in the mean values of the parameters measured but on the changes in the range of variability of these values when comparing the results of experiments where such interactions took place with the control. As it has turned out after the experiment, the number of larvae feeding together in a single bean seed was usually small. Therefore, the analysis of the results has been limited to the simplest parameters and the simplest statistical methods.

Summarising the experimental results, we can conclude that the presence of interactions between

individuals determines the obtained results and leads to the emergence of statistically significant relationships between the measured parameters. On the other hand, the lack of interaction between individuals leads to chaos and the lack of this type of relationships.

Looking at the cumulative data from the experiment, we can easily see a large individual variability in the amount of food obtained by the larvae (the weight of the fillings, which is a measure of the cumulative consumption of the larvae throughout their development) (Fig. 3). In the case of pooled data, there is a strong correlation between the amount of food obtained by the larvae and the weight of the adult animal (Fig. 4). Consequently, individual variability has also been observed in the weights of adults produced from larvae with varying food consumption (Fig. 2). While the size distribution of fillings is almost symmetrical, the distribution of weights of adults is negatively skewed. The latter distribution remains skewed if we remove from the analysis the three heaviest individuals, which are not those with the highest cumulative food consumption (Fig. 4). This difference in the shapes of the two distributions can be explained having in view that the weight of the larva is due to the difference in cumulative food consumption (or assimilation, assuming a constant assimilation efficiency coefficient) and the cumulative energy cost of life measured by the organism's respiration. Furthermore, we can postulate that larvae with low weight and low food consumption bear increased energy costs of living compared to larvae with high weight and high food consumption. It is difficult to explain the nature of these disproportions in the cost of living. This could be estimated by constructing mathematical models of larval growth using the so-called balance growth equation (MAJKOWSKI & UCHMAŃSKI 1980). However, it can probably be assumed that these disproportions in the energy costs of living are the result of the difficulties in life faced by larvae with low weights. This could be due to the nature of the resources the larvae use but it could also be the presence of other larvae in the bean seed. Due to the lack of correlation between the number of neighbours foraging together in bean seeds and the bean seed weights (Fig. 10), it follows that bean weevil larvae cannot estimate bean seed size. On the other hand, having in view that there is a negative relationship between the number of seeds encountered in the experiment and the number of larvae feeding in them (Fig. 9), it can be concluded that the larvae can assess whether other larvae have already attacked the seeds and prefer seeds not inhabited by other indi-

viduals. This may indicate that the presence of other larvae is an obstacle in the life of the bean weevil larvae. Another clearer indicator of the existence of interactions between larvae feeding together in bean seed is the development time of the larvae in seeds with different numbers of neighbours. The mean development time of the larvae increases slightly (however, statistically significantly) with increasing number of neighbours in the seed (Fig. 11). The prolongation of the development time of the larvae is supposed to increase their foraging period and, thus, increasing the weight of an adult individual. However, the later appearing adults, i.e. those that transform from longer-developing larvae, have lower weights (Fig. 7) and leave behind smaller corridors in the seed (Fig. 6) than those arising from faster developing larvae.

In the case when larvae foraging individually in the bean seed, the consumption rate of the larva was not influenced by the interaction of other larvae but only by the individual larva abilities in this regard and the quality and quantity of resources contained in the seed. A very distinctive feature of the data from seeds invaded by a single larva is the lack of relationships among measured parameters. These data are random. E.g., one would expect that, in the absence of interaction, single larvae would have similar and the maximum possible weights. However, despite the lack of interaction between the foraging larvae, the adult individuals differed quite significantly in their weights (Fig. 13) and the larvae from which these adults were formed differed in the amount of resources obtained from seeds (Fig. 14). The lack of relationship between the size of the filling and the weight of the bean (Fig. 15) indicates that the consumption rate of the larvae was not influenced by the bean seed weight. The absence of significant relationships between the weight of adults (or the weight of the filling) and the length of the larval period (i.e., the length of time the larva forages inside the bean) confirms that, in the case when there is no interactions between individuals, the data are random and quite variable. It may be the result of the natural variability of the bean weevil larvae in this regard.

In the experiment, single bean seeds were also obtained, in which a different number of larvae were foraging, i.e. 6, 13, 16, 23, 26 and 34. These seeds differed in their weight before the experiment, so it can be assumed that the obtained results were influenced not only by the number of foraging together larvae but also by the size of the seeds.

It is interesting to compare adults that emerged from the seed infested with the highest number of

larvae (34) and those from seeds inhabited by a single larva. The smallest weight of an adult individual foraging together with 33 neighbours was almost the same as the smallest weight of an adult individual foraging alone in bean seed (Table 2). On the other hand, the highest weight of an adult individual emerging from the larva foraging together with 33 other larvae was much greater than the highest weight of an adult emerging from larva foraging alone. Thus, it seems that interactions between larvae increase larvae differentiation. A characteristic effect is also an asymmetry of this differentiation. This effect is even more evident in the case of filling weights (Table 3) – not only the heaviest filling from seed with 34 larvae was heavier than the heaviest filling from seeds with a single larva but also the lightest filling from the seed with 34 larvae was much smaller than the lightest filling from seeds with a single larva. Thus, the individual variability caused by interactions between the larvae was more strongly expressed in the amounts of resources obtained by the larvae from the environment than in the weight of adult individuals. It is worth noting that the weight of the seed prior to the experiment, where 34 larvae were foraging, was one of the smaller in comparison to the other seeds in the experiment. This seed had the lowest weight after the experiment, which means that larvae ate most of it, but on average larvae obtained the fewest resources per head in this case (Table 2).

In the cases of a single larva foraging in a bean seed, the lack of dependence of the weight of adults on the weight of the filling and the weight of adults or the weight of the filling on the duration of the larval stage was characteristic. Interactions between foraging individuals cause such relationships. In the case of the seed where 34 larvae were foraging together, all the above-mentioned relationships were significant (Figs. 15–17). This indicates the activation of a mechanism to extend the development time of the larva (and, thus, also the feeding time in the seed) to compensate for the loss in body weight resulting from interactions between the larvae.

As for other single seeds, in which a smaller than 34 number of larvae were foraging, the results were more or less in line with the above-presented pattern. Due to the smaller sample sizes, they turned out to be less clear, especially for seeds with the lowest number of foraging larvae (6 and 13). However, the results became similar to those described above when the number of larvae feeding together in the seed became 16, 23 or 26. Fig. 18 compares the distribution of filling weights from single seeds, in which 6, 13 and 34 larvae foraged together. As

seen, even the strongest competition, i.e. the presence of 34 larvae foraging in the same seed, did not prevent the best competitor from obtaining the same amount of resources as the larva with the highest consumption under much weaker competition (6 larvae feeding together). We are dealing here, in a sense, if we compare it with the results for the foraging larvae without the presence of competitors, with the overconsumption of resources manifested by the strongest competitor in the presence of strong competition. However, the weakest competition in the conditions of strong competition obtained much less resources than in the conditions of weaker competition. In the case of these two seeds, the effect of seed size was probably insignificant as they differed slightly in weight. On the other hand, the distribution of weights of fillings for 13 larvae foraging together in the seed is clearly shifted towards lower values in relation to the distribution for the weakest competition. This is probably because 13 larvae were feeding together in a seed smaller than the other two. This created worse conditions for all feeding larvae, even for the strongest competitors. The seed with 13 larvae is also one from which the larvae did not manage to eat much, and on average there was relatively little loss in seed weight per head before and after the experiment (Table 3).

The variability of the size of the fillings (being, in fact, the size of the cumulative consumption of the larvae, Fig. 18) is reflected in the variability in the weights of adults emerging from these larvae (Fig. 19). The results show how erroneous it can be to use the average weight value when assessing the impact of competition on competing individuals. Contrary to intuition, in conditions of strong competition, the average weight may be higher than in the case of weaker competition. This is because the strongest competitors are able to gain enough heavy weights for this effect to arise. This is not hindered by the fact that the weight gain is in fact the difference between resource consumption and the energy cost of living, which in this case, although not directly measured, could not be high in the case of the best competitors.

The results discussed in the last two paragraphs lead to the conclusion that in conditions where there are interactions between individuals (and such situations we most often meet when studying ecological systems), it is very important to pay attention to the individual variability of the measured parameters and not to focus only on the average values.

The last category of seeds were those in which from two to nineteen larvae were foraging together (2, 3, 4, 5, 7, 8, 9, 10, 11, 12, 14, 15 or 19 larvae)

and which were represented by several seeds with the same number of larvae foraging in them. Unfortunately, the sample sizes in this case were too small and number of seeds and their weights to variable to make it possible to indicate any clear pattern in variability of measured parameters. If a greater number of seeds had the same number of larvae foraging in them, then these were the cases when these numbers of larvae were small. On the other hand, if a greater number of larvae were foraging in bean seeds, then there were very few such seeds. In both cases, it made it impossible to obtain interesting and unambiguous results that would be able to supplement the previously presented results with interesting facts.

Why in the results of the experiment presented here it is difficult to find traces of such intense intraspecific competition, which would lead to a reduction in the value of parameters also in the strongest competitor? In this experiment, bean weevil larvae probably had access to excess bean seeds. According to the literature (ROMANKOW 1958, FILIPEK 1962, NAWROT 2001), the larvae of this species, after hatching from eggs, tend to disperse and enter distant seeds. Possibly, this mechanism prevents intense intraspecific competition. Under the conditions that were created for the larvae in this experiment, the dominant situation was when the larvae interacted locally in small local groups of a few individuals. Only in a few cases, when several dozen larvae were in one seed, it was possible to notice symptoms of competition for resources, which were expressed in a relatively high variability of the parameters characterizing the interacting individuals. The fact that there were few such situations with a large number of larvae foraging together in one bean seed indicates that competition between larvae takes place if their local number is sufficiently large. The results obtained in the experiment illustrate the conditions prevailing in the population in the first generation. In subsequent generations, if the bean seed stock were not renewed or replenished, the next generations would face increasingly difficult nutritional conditions. There would be fewer and fewer seeds that had not been settled or previously exploited, which would lead to an increase in the number of larvae feeding together in the seeds, a greater intensity of competition and a more pronounced effect of it. This can be seen not only in greater individual variability but also in decreasing average values of measured parameters. A week symptoms of such situation can be seen in the case of single seed with 13 larvae foraging inside (see above).

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