

Trophic preferences of *Harpalus rufipes* (Coleoptera, Carabidae) with regard to seeds of agricultural crops in conditions of laboratory experiment

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Our research fills an important gap by making a quantitative assessment of the trophic preferences of a widespread, abundant species, *Harpalus rufipes* (De Geer, 1774) in laboratory conditions. We conducted three types of 5-day laboratory experiment in which 1, 5 and 15 species of seeds of agricultural crops commonly consumed by the beetle within the Ukrainian part of its range were offered. The *H. rufipes* imagines were kept in plastic containers and the changes in weight of the food and changes in weight of the imagines were measured. When beetles were offered only one type of food the average consumption was 52.9 ± 24.9 mg/day per specimen for the seeds of *Fagopyrum esculentum* Moench, 40.6 ± 2.9 for *Beta vulgaris* L. and 40.8 ± 24.8 mg/day per specimen for *Helianthus annuus* L. Significant amounts (19.1 – 34.0 mg/day per specimen) of other seeds offered were consumed. The least consumed were *Hordeum vulgare* L. (10.0 ± 4.5 mg/day per specimen), *Secale cereale* L. (9.6 ± 4.0), *Sorghum drummondii* (Steud.) Millsp. & Chase (11.8 ± 4.1) and *Papaver somniferum* L. (16.0 ± 7.9). On average with a choice of seeds of 15 agricultural crops, a single *H. rufipes* beetle consumed 62.4 ± 9.1 mg per day, that is 2.46 times more than average consumption across seeds in the experiment with only one species of food plant. In free choice conditions the average weight of beetles rose only by 1.9 ± 1.7 times in 24 hours. The consumption by *H. rufipes* imagines of agricultural seeds in free choice conditions is presented as follows in declining order of preference, measured as mg/day per specimen: *Avena sativa* (7.1 ± 3.5), *Triticum aestivum* (6.9 ± 2.9), *Panicum miliaceum* (6.3 ± 2.4), *F. esculentum* (5.9 ± 2.7), *S. cereale* (5.1 ± 2.8), *S. drummondii* (5.0 ± 3.0), *Cannabis sativa* (4.2 ± 3.2), *Brassica napus* (3.5 ± 2.7), *Sinapis arvensis* (3.4 ± 1.7), *Beta vulgaris* (3.3 ± 1.4), *Juglans regia* (3.0 ± 1.5), *Hordeum vulgare* (2.9 ± 2.3), *Papaver somniferum* (2.7 ± 2.3), *Helianthus annuus* (2.3 ± 0.4) and *Arachis hypogaea* (0.9 ± 0.5). For keeping *H. rufipes* in laboratory conditions 5 variants of mixed diet, each consisting of 5 plant species, were tested: the first mostly carbohydrate, the others with average and high content of fat. Out of these diets only the carbohydrate diet involved a significantly higher level of food consumption. It contained seeds of *T. aestivum*, *A. sativa*, *S. cereale*, *F. esculentum*, *B. vulgaris*. When different multicomponent diets were offered the consumption of different types of food varied by 1.5 to 2.0 times.

Key words: food consumption, body mass, phytophage, polyphage

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INTRODUCTION

Harpalus rufipes (De Geer, 1774) – is an abundant, ubiquitous species, living in an extremely wide range of terrestrial ecosystems, with especially high populations inhabiting anthropogenically transformed environments: ploughed land, parks, fallow fields, industrial areas, populated areas etc. This species is distributed in Central and Eastern Europe, introduced to North America (Dunn 1981; Lindroth 1985; Frampton et al. 1995; Kromp 1999; Irmiler 2003; Porhajašova et al. 2009). The beetles feed on the pests of agricultural crops (mostly Lepidoptera and Coleoptera) and also cause great damage to certain weed species (Lang et al. 1999; Harrison & Gallandt 2012). *H. rufipes* can migrate both by ground and by air, enabling large aggregations to form in areas with an optimal hydrothermal regime and high aggregations of food objects (plants and animals). Under the impact of many factors ground beetles of this species can form aggregations up to tens and hundreds of beetles per square meter (Currie et al. 1996, Midtgaard 1999). In areas where the species is abundant they can have a considerable negative influence on various agricultural crops (Petrusenko & Petrusenko 1973). Unfortunately, until now the trophic preferences of many species of ground beetles have not undergone quantitative study in laboratory experiments (Currie et al. 1996, Brygadyrenko & Korolev 2006, Sasakawa 2009, Korolev & Brygadyrenko 2012), *H. rufipes* having only been studied in qualitative terms in laboratory experiments (Thiele 1977; Hengeveld 1980; Monzo et al. 2011; Reshetniak & Brygadyrenko 2013). The study of the trophic connections of this species with the seeds of various species of plants is very significant for agriculture and science (for inventing methods of population censusing for certain species in agricultural environments). By consuming seeds selectively, the beetle can exert a stronger influence upon the structure of a phytocenosis than when eating vegetative parts of a plant (Honek et al. 2003; Saska et al. 2010).

A capacity to feed on seeds is typical for many species of ground beetles which have a varied diet (Honek et al. 2003; Fawki & Toft 2005; Honek et al. 2009; Klimeš & Saska 2010). The consumption of seeds by *H. rufipes* allows us to define the general food preferences of the species, but experiments have not yet been designed for a sufficiently wide variety of agricultural crops (Jorgensen & Toft 1997; Hartke et al. 1998; Shearin et al. 2008). According to information from various authors the species feeds on grain crops (wheat, rye, millet, barley, oats, rice, sorghum, corn, buckwheat), leguminous plants (pea, haricot, soy-beans, beans), industrial crops (beet, potatoes, sunflower, pea-nut, mustard, rape, chufa sedge, tanacetum, plantain) and food crops (Sudan grass, timothy-grass, vetch, lupin, clover, sainfoin) (Petrusenko & Petrusenko 1973).

The Harpalini species consumed a wider variety of seed species than their equivalents Zabrinii in the same size groups (Honek et al. 2007). Harpalini species more intensively consumed the seeds of *Cirsium arvense* and *Viola arvensis* (Petrusenko & Petrusenko 1973; Honek et al. 2007). The seeds of plants are one of the main sources of energy for ground beetles of this particular species, i.e. the beetles intensively search for them. For example *H. rufipes* selectively eats wild and cultivated strawberry seeds (Briggs 1965), causing only slight damage to the fruit (more often in the conditions of insufficient moisture). The species is very significant as a model-object for the estimation of peculiarities of choice of dietary components measured by the amount of food consumed.

For *H. rufipes*, as with any polyphage species, a varied diet when a wide range of food items is available at any moment ensures an optimal consumption of amino acids, vitamins, microelements and other dietary components (Thiele 1977; Currie et al. 1996). The natural diet of this species includes a significant proportion of insect larvae with a high fat content (Lang et al. 1999). Our studies of the diet of Carabidae in different ecosystems in Ukraine (Brygadyrenko & Korolev 2006; Korolev & Brygadyrenko 2012) have shown a high variability of potential food objects in sepa-

rate, ecologically differentiated plots, which suggests that any particular species of food object will be consumed at different intensities in different ecosystems, depending on the composition of the other food species present.

With these three observations in mind we formulated and tested the following hypotheses in our experiments: (1) in the conditions of a single species of food plant *H. rufipes* will consume less food, than when offered a variety of food items; (2) a high calorie diet (with high concentration of fat) will cause a greater gain in the beetles' weight; (3) with different combinations of plant seeds offered, the level of consumption of some of these components will noticeably vary.

MATERIAL AND METHODS

H. rufipes imagines were collected in July 2013 on the outskirts of Dnipropetrovsk from land cultivated with *Hordeum vulgare* and maize using pitfall traps. The collection of beetles was carried out before their season of reproduction (in the steppe zone this takes place from early August to mid September) in order to minimize the influence of moisture loss and the development of sexual characteristics. During the second half of summer the area researched is affected by annual droughts lasting from 20 to 40 days when dew is almost completely absent from agricultural fields. For this reason experiments on beetles conducted without giving them access to water could be considered as corresponding well to the microclimatic conditions at this season in the steppe zone of Ukraine.

The influence of diet upon the weight of *H. rufipes* imagines was studied in the laboratory of Zoology and Ecology Department of Oles Honchar Dnipropetrovsk National University. The weight was defined using laboratory analytical scales ID-100 (accuracy – 1 mg). Before the beginning of experiment all ground beetle specimens were kept in one common container. They had free access to water, which was replenished every day, and were provided with different types of food of animal (litter invertebrates

caught in the pitfall traps together with *H. rufipes* in the course of the collection for the experiments) and of plant (moistened seeds of wheat) origin.

A series of three types of experiments was conducted, in which 1, 5 and 15 types of food were offered respectively. In each experiment a single *H. rufipes* imago was kept in a separate container (8 x 12 cm) over a period of five days. The weight of each food item and each beetle was determined at the beginning and end of each experiment. The average weight of the beetles in the experiment was 157.1 ± 29.9 mg. Only a small amount of excrement was observed and not in all containers. The excrement was scattered at the bottom of the containers and was impossible to weigh. At the end of the experiment the food remaining was examined using a binocular stereoscopic microscope MBC-10 and divided into different categories. Before the beginning of the experiment the food was desiccated over five days using a room heater at a temperature of +55 °C, at the end of the experiment the food remaining was desiccated by the heater for one day and then weighed. The desiccation was necessary in order to eliminate the complication of fluctuation in the seeds' weight, which could occur as a result of the seeds' adsorption of atmospheric moisture (David 1998).

The seeds of 15 food plants (Table 1) were provided for the *H. rufipes* beetles in this experiment. The seeds with the high fat content (more than 6%) were sunflower, Persian walnut, industrial cannabis, field mustard, peanut, rape seed, opium poppy. The seed with a moderate fat content (3–6%) was oat. The seeds with low fat content (0.5–3%) were Sudan grass, proso millet, bread wheat, buckwheat, barley, sea beet, rye (Robinson, 1987). The largest seeds (average diameter 3 mm and over) were Persian walnut, peanut, sea beet, the middle size group of seeds (average diameter 1–3 mm) was sunflower, industrial cannabis, field mustard, rape seed, oat, proso millet, bread wheat, buckwheat, barley, rye. The smallest size group (under 1 mm) was opium poppy and Sudan grass.

Three different feeding regimes were used in the experiment: no-choice experiment (amount of food offered 2,000 mg), choice experiment with

five components (total amount 2,500 mg, 500 mg of each component), and choice experiment with 15 components (total amount 7,500 mg, 500 mg of each component) (Table 2). The weight of each food component in a container at the beginning of the experiment could vary from 490–510 mg when a mixed ration was provided and from 1,990–2,010 mg, when a single type of food was provided. At the end of the experiment the weight of the unconsumed food in each container was subtracted from the initial weight of the food provided. To eliminate the influence of adsorption of atmospheric moisture upon the weight of the beetles and the food in the containers with beetles, no water was provided nor was any substrate placed at the bottom of the containers. The only element at the bottom of the containers was a sheet of plastic, which was used by the beetles for shelter during the brightest part of the day. The containers were numbered and placed in random order out of direct sunlight on the laboratory table. The temperature in the laboratory varied from +22 °C at night to +28 °C during the day and the relative air humidity ranged from 38 to 54%.

The entire laboratory part of the experiment was conducted in 15 days between 10 and 25 July 2013 (three series of experiments each lasting five days). All beetles were used only once. In each type of experiment an equal ratio of males and females were used. For the 15 experiments when a single food plant species was offered $n = 8$ (involving a total of 120 imagines), for the five experiments offering 5 food plant species $n = 12$ (involving a total of 60 imagines), for experiments with 15 food plant species $n = 12$, for the experiments without provision of food (control group 1) $n = 12$, for the experiments without provision of food and water (control group 2) $n = 12$. Overall 216 beetles were involved in the experiments. No deaths of beetles occurred during the experiments. This can be explained by the fact that in a previous series of experiments we found that *H. rufipes* imagines can easily tolerate the above-mentioned microclimatic conditions in the containers without access to food and water for over 10 days.

The analysis of the data was conducted by statistical calculations (ANOVA, Advanced PCA factor analysis) – using Statistica software (StatSoft Inc. 2004). The reliability of differences between samples was assessed using one-way ANOVA, for multivariate comparison the Tukey test was used StatGraphics Plus v5.1 (StatPoint Inc. 2006). The text and tabular data is presented in the form $x \pm SD$. The diagrams show median, 25–75% quartiles (box) and selected outlier data points.

RESULTS

Consumption of crop seeds in no-choice conditions

In the laboratory experiments where the beetles were denied choice of different plants *H. rufipes* on average consumed more than 52.9 ± 24.9 mg/specimen of *F. esculentum* seeds, 40.6 ± 2.9 of *B. vulgaris* seeds and 40.8 ± 24.8 mg of *H. annuus* seeds daily. Also they consumed large amounts (average values vary between 19.1 or 34.0 mg daily for a single beetle) of other seeds offered (Fig. 1). The least consumed were *H. vulgare* (10.0 ± 4.5 mg daily), *S. cereale* (9.6 ± 4.0) and *S. drummondii* (11.8 ± 4.1) seeds, which were firm and dry, and *P. somniferum* (16.0 ± 7.9), the seeds of which contain highly active morphine alkaloids.

As a result of being kept in a container with an abundant supply of food, the average daily weight gain of the *H. rufipes* imagines was greatest in the variants with *F. esculentum* (with a gain of 33.5 ± 13.1 mg with the beetles' initial weight 157.1 ± 29.9 mg, i.e. by 21.3% daily average). When fed on *T. aestivum* the beetles gained 15.9 ± 13.3 mg. In the experiment with *H. vulgare* (-4.6 ± 7.9 mg daily), *S. arvensis* (-4.9 ± 8.2), *B. vulgaris* (-5.4 ± 13.7) and *S. cereale* (-1.3 ± 9.6) the weight decreased. In the other variants tested the weight of ground beetles was maintained or slightly increased (on average for certain food plants by 0.5–9.5 mg). In the control experiment without any access to food and water the beetles lost 28.0 ± 7.8 mg. When no food was provided but

Consumption of crop seeds in choice conditions

On average when a choice of seeds of 15 agricultural crops was offered, a single *H. rufipes* beetle consumed 62.4 ± 9.1 mg/day, which is 2.46 times more than in the experiment with only one kind of food (Fig. 3). It is interesting to note that the average weight of beetles rose only by 1.9 ± 1.7

mg/day per specimen (11 out of 12 beetles in the experiment gained from 1 to 28 mg during 5 days of the experiment and only 1 beetle lost 1 mg). In conditions of free choice of food in contrast to a single plant diet there was a smaller difference in weight between individual beetles. When a single plant species was offered some of the beetles gained weight while others lost weight.

Table 1. Brief characteristics of the food species offered to *H. rufipes* in the laboratory experiment

Family	Species	English name	Method of preparation
Poaceae	<i>Avena sativa</i> L.	Oat	intact
Polygonaceae	<i>Fagopyrum esculentum</i> Moench	Buckwheat	husk removed
Poaceae	<i>Hordeum vulgare</i> L.	Barley	intact
Brassicaceae	<i>Sinapis arvensis</i> L.	Field mustard	intact
Chenopodiaceae	<i>Beta vulgaris</i> L.	Sea beet	intact
Poaceae	<i>Secale cereale</i> L.	Rye	intact
Asteraceae	<i>Helianthus annuus</i> L.	Sunflower	husk removed
Juglandaceae	<i>Juglans regia</i> L.	Persian walnut	husk removed
Fabaceae	<i>Arachis hypogaea</i> L.	Peanut	husk removed
Poaceae	<i>Sorghum drummondii</i> (Steud.) Millsp. & Chase	Sudan grass	intact
Brassicaceae	<i>Brassica napus</i> L.	Rapeseed	intact
Cannabaceae	<i>Cannabis sativa</i> L.	Industrial cannabis	intact
Poaceae	<i>Panicum miliaceum</i> L.	Proso millet	husk removed
Papaveraceae	<i>Papaver somniferum</i> L.	Opium poppy	intact
Poaceae	<i>Triticum aestivum</i> L.	Bread wheat	intact

there was access to water, the *H. rufipes* beetles lost 2.5 ± 7.9 mg. Thus, seeds of all the plant species consumed in the experiments could be important components of the diet of *H. rufipes* which promotes the maintenance of their weight and increases the survival chances of the species in the extreme dry climatic conditions of the steppe zone.

In most cases the ratio of the weight of food consumed to the alterations of the beetles' weight in the course of a 1 day experiment is close to 1. This is the evidence of practically complete retention of food in the body (Fig. 2). If the coefficient is significantly greater than 2, it means the food is either assimilated quickly: partly through the conversion of beetles' weight into CO₂ and H₂O (loss when breathing through the tracheal system and evaporation through cuticles) or lost through rapid excretion of undigested remains as faeces during the first day. The maximum loss

through excretion and respiration of *H. rufipes* was observed when eating seeds of *H. annuus*: when 7.1 ± 2.6 times more food was expended on these processes than was converted into weight gain. Negative values of the coefficients for most beetle specimens were received with consumption of seeds of *S. arvensis* (-1.9 ± 4.8) and *B. vulgaris* (-1.8 ± 6.4) and here a laxative effect was observed – a loss of weight through voiding of excrement. In the rest of the experiments the average coefficients for different species of plant varied from 0.5 to 2.5. It should be mentioned that the variation in coefficients between certain beetle specimens were quite significant. This is connected with the pronounced laxative effect the food consumed had on some *H. rufipes* individuals while the majority of specimens remained free of diarrhoea. The diarrhoea was caused by infections and parasitic infections, and by the beetles' failure to evacuate the intestine every day, which is typical for this species.

Table 2. Increase in the body weight of *H. rufipes* when offered a multi-component mix ($\bar{x} \pm S_x, n = 12$)

No	Composition of the ration	Weight of food consumed, mg/day per specimen	Increase in <i>H. rufipes</i> weight, mg/day
1	<i>T. aestivum</i> , <i>A. sativa</i> , <i>S. cereale</i> , <i>F. esculentum</i> , <i>B. vulgaris</i>	39.8 ± 7.6^a	2.1 ± 3.1^d
2	<i>T. aestivum</i> , <i>H. vulgare</i> , <i>C. sativa</i> , <i>H. annuus</i> , <i>B. vulgaris</i>	26.7 ± 4.5^b	2.3 ± 2.1^d
3	<i>F. esculentum</i> , <i>A. sativa</i> , <i>S. arvensis</i> , <i>J. regia</i> , <i>S. drummondii</i>	29.3 ± 7.9^b	2.9 ± 2.3^d
4	<i>P. miliaceum</i> , <i>S. cereale</i> , <i>P. somniferum</i> , <i>B. napus</i> , <i>A. hypogaea</i>	26.6 ± 3.6^b	2.5 ± 2.5^d
5	<i>C. sativa</i> , <i>H. annuus</i> , <i>S. arvensis</i> , <i>P. somniferum</i> , <i>A. hypogaea</i>	24.5 ± 5.3^b	2.2 ± 2.1^d
6	<i>T. aestivum</i> , <i>F. esculentum</i> , <i>S. cereale</i> , <i>A. sativa</i> , <i>H. vulgare</i> , <i>B. napus</i> , <i>S. arvensis</i> , <i>H. annuus</i> , <i>A. hypogaea</i> , <i>P. miliaceum</i> , <i>B. vulgaris</i> , <i>S. drummondii</i> , <i>J. regia</i> , <i>C. sativa</i> , <i>P. somniferum</i>	62.4 ± 9.1^c	1.9 ± 1.7^d

Note: Differences between the statistics shown in the table are marked by letters indicating statistical reliability ($p < 0.05$, Tukey test).

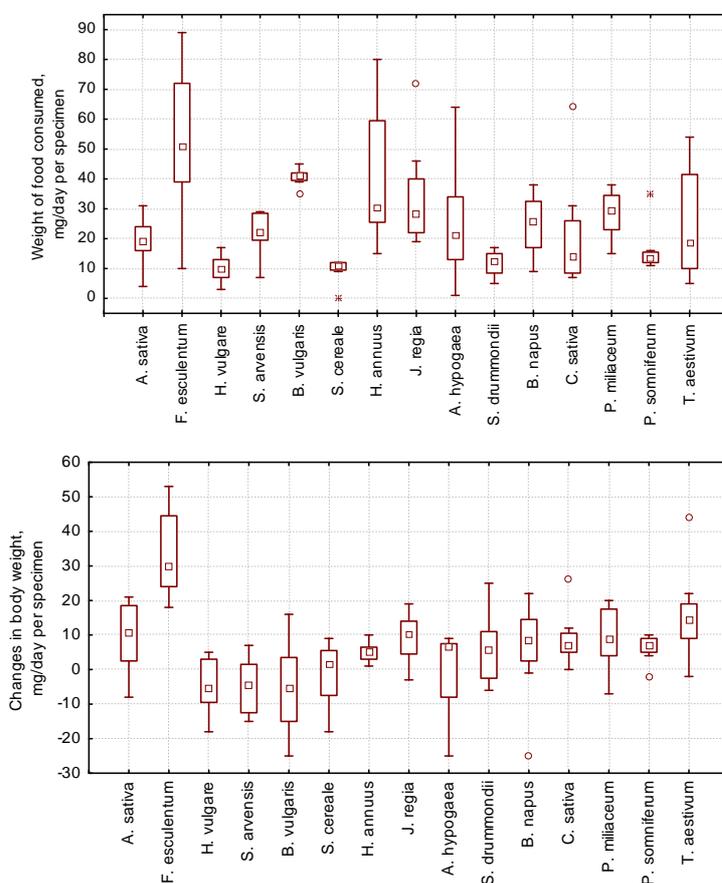


Fig. 1. Weight of food consumed (*a*, mg/day per specimen) and changes in body weight (*b*, mg/day per specimen) of the beetle *H. rufipes* as the result of a single food experiment ($n = 8$)

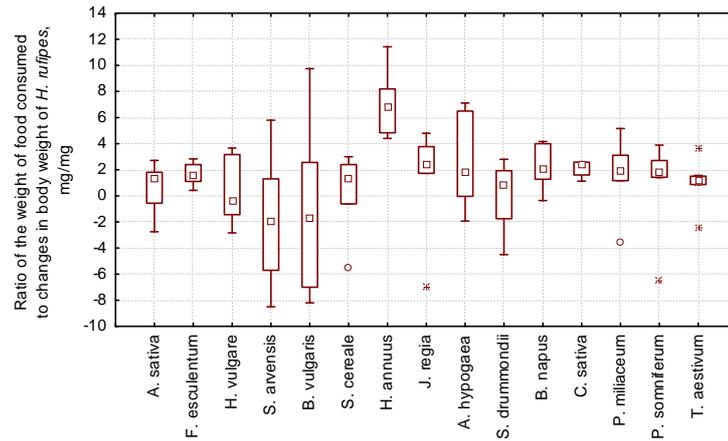


Fig. 2. Ratio of the weight of food consumed to changes in body weight of *H. rufipes* (mg/mg) as a result of a single day experiment ($n = 8$)

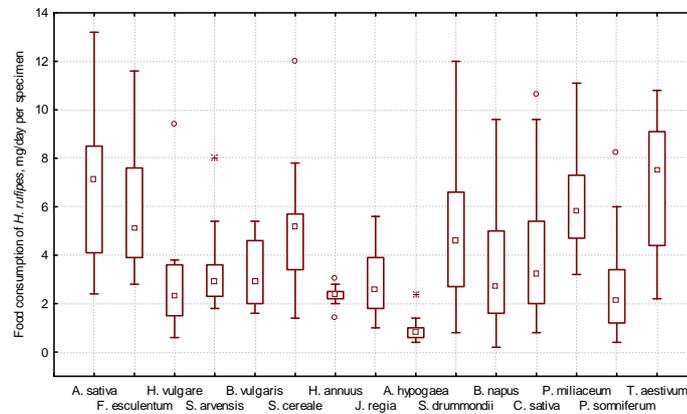


Fig. 3. Food consumption of *H. rufipes* (mg/day per specimen) when offered free choice of 15 food components ($n = 12$).

The seeds consumed in free choice of food conditions rated according to diminishing order of preference is as follows, measured as mg/day per specimen: *A. sativa* (7.1 ± 3.5), *T. aestivum* (6.9 ± 2.9), *P. miliaecum* (6.3 ± 2.4), *F. esculentum* (5.9 ± 2.7), *S. cereale* (5.1 ± 2.8), *S. drummondii* (5.0 ± 3.0), *C. sativa* (4.2 ± 3.2), *B. napus* (3.5 ± 2.7), *S. arvensis* (3.4 ± 1.7), *B. vulgaris* (3.3 ± 1.4), *J. regia* (3.0 ± 1.5), *H. vulgare* (2.9 ± 2.3), *P. somniferum* (2.7 ± 2.3), *H. annuus* (2.3 ± 0.4), *A. hypogaea* (0.9 ± 0.5).

It is interesting that the most highly consumed item in the no-choice experiment (Fig. 1 a), buck-

wheat, was only the 4th most consumed in the choice experiment (Fig. 3), while oats, the 11th on the list in the no-choice experiment, was the most consumed in choice experiments ahead of wheat.

The results of Principal Component Analysis of the diet of *H. rufipes* in conditions of free choice of 15 types of food (Fig. 4) show that more than quarter of dispersion is shown as Factor 1, which we interpret as mechanical solidity of seeds of food plants, about 15% of dispersion is shown as Factor 2 – the sizes of food components offered in the experiment.

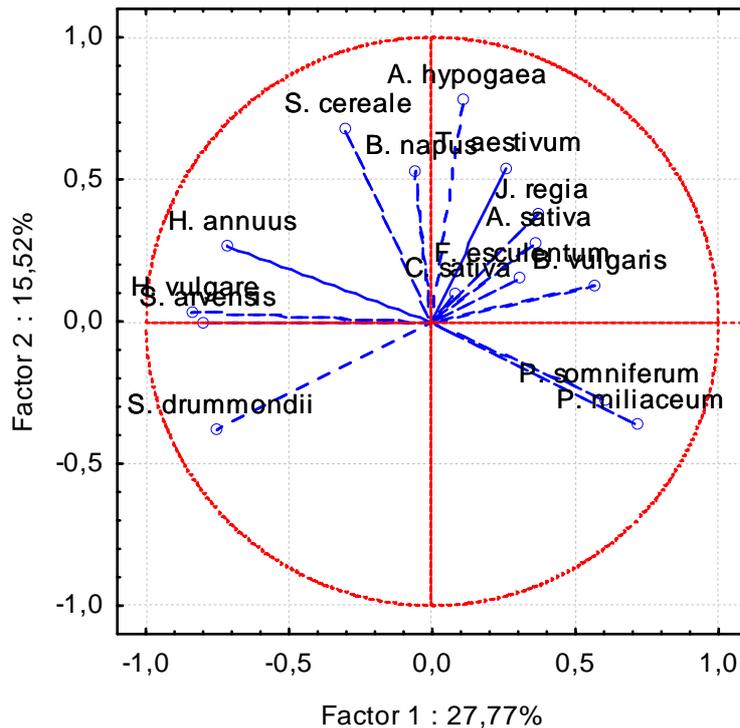


Fig. 4. Projection of the variables (species of food plant) on the factor plane in Advanced PCA factor analysis: Factor 1 – mechanical hardness of the seed offered in the experiment (positive values indicate rising degrees of softness of the food object, negative values rising degrees of hardness), Factor 2 – size of the food objects offered in the experiment (positive values indicate larger sizes of food objects, negative values – smaller sizes)

Optimal crop seed mixture for *H. rufipes*

For keeping *H. rufipes* in laboratory conditions on a regulated diet that consists of seeds of 5 species of plants, we chose 5 variants (table 2): mostly carbohydrate (1), with average (2, 3, 4) and high (5) fat contents. Out of the 5 diets we selected ($F = 12.33$, $F_{0.05} = 2.54$, $\mathcal{D} < 0.001$) only the carbohydrate variant involved a higher level of food consumed. It contains seeds of *T. aestivum*, *A. sativa*, *S. cereale*, *F. esculentum*, *B. vulgaris*.

The diets with average (2, 3, 4) and high (5) fat contents ($F = 74.18$, $F_{0.05} = 2.54$, $\mathcal{D} < 0.001$) were less intensively consumed by the beetles than the diets that contain 15 types of food. Thus, an optimal diet for keeping *H. rufipes* imagines in

laboratory conditions based on price and availability is the seed mixture that contains equal weights of *T. aestivum*, *A. sativa*, *S. cereale*, *F. esculentum* and *B. vulgaris*.

DISCUSSION

The research we performed on consumption in laboratory conditions of the generative parts of all the plant species offered in our experiments with the aim of forming a quantitative assessment of the consumption of seeds of agricultural plants by *H. rufipes* imagines supplements earlier research on this topic (Thiele 1977; Zhang et al. 1997; Shearin et al. 2008; Harrison & Gallant 2012). Our experiment confirmed our first hypothesis, establishing that when the seeds of a single

plant species were offered *H. rufipes* consumed less food than when a varied diet was offered. An optimal gain in weight was observed with the seeds of three species of *Poaceae* (*T. aestivum*, *A. sativa*, *S. cereale*), one species of *Polygonaceae* (*F. esculentum*), and one species of *Chenopodiaceae* (*B. vulgaris*). A further increase in variety of diet, offering the seeds of 15 species, increases the food consumption by the beetles by only one and a half times (on average from 39.8 to 62.4 mg/day per specimen), although this does not lead to a reliable increase in weight (2.1 and 1.9 mg/day per specimen respectively). This means that a five component diet can be considered acceptable for the maintenance of *H. rufipes* imagines in laboratory conditions.

The absence of differences in gain in body weight with high fat, high carbohydrate and mixed diets when there was a reliably high consumption of the high carbohydrate diet in comparison to the high fat and mixed diets indicates that the second hypothesis we held before the experiment, that a high fat diet would facilitate a more rapid increase in the beetles' body weight, was erroneous. The high fat diet is characterised by a minimum level of consumption compared with the other variants of beetles' diet tested (Table 2).

The third hypothesis that with multicomponent diets the level of consumption of some of the components will significantly vary was upheld. Thus the seeds of *B. vulgaris* when part of a mixed and mostly carbohydrate diet (Fig. 5a) were consumed one and a half times more intensively than when part of the mixed diet of average fat content (Fig. 5b). *H. annuus* as part of a seed mix from fat-oil cultivation was consumed over two times more intensively (Fig. 5e) than in a mix of average fat components (Fig. 5b). This means that when provided with food with an extra high fat content the beetle chooses the components with the lowest fat content. An equivalent situation also applies when we analyzed the consumption of *C. sativa*: in a high fat content mix (Fig. 5e) there is a one and a half times higher intensity of consumption of this food component than with a low fat diet.

Our laboratory experiments allowed us to make only an approximate estimate of the variations in the relative contributions of the plant species studied to the natural diet of *H. rufipes*, which can vary fundamentally depending on the physical ecosystem it inhabits (Pollet & Desender 1987; Magura 2002). The damage inflicted by this species on grain cultures can vary greatly depending on the presence of additional sources of food plants in a field, which can be close relatives of the plant species under cultivation and tested in this experiment (Davies 1953; Collins et al. 2002; White et al. 2007). It is interesting to note that under absence of choice conditions *H. rufipes* consumed *Taraxacum* agg. (dandelion) seeds 25.9 times more intensively than in the experiment with free choice of food (Honek et al. 2009). It is well known that the damage caused by the beetles is compensated for by their destruction of pest insects and weed seeds (Kabacik-Wasilik & Jaworska 1973; Kabacik-Wasilik & Kmitowa 1973).

In any given ecosystem the competitor species of ground beetle may in their turn influence the content of the diet of *H. rufipes*, being able in most cases to consume a variety of food species (Traugott 1988; Snyder & Wise 1999). Thus in conditions of specific crop rotation regimes, communities of polyphage ground beetles gradually form, which are gradually supplemented by individuals of other species which migrate in from nearby plots (Niemela 1993; Purvis & Fadd 2002). *H. rufipes* is one of the most persistent (in many aspects) dominant species in this process because of the breadth of its trophic niche, not only in conditions of crop rotation but also in gardens, parks and other types of forest plantation on account of their ability to find sufficient seeds of crops in the intervals between the trees (Kutasi et al. 2004).

When keeping *H. rufipes* imagines in laboratories with the aim of developing new techniques of chemical, biological and integrated methods of control with this species it is necessary to use a maximally full set of food components. When a suboptimal laboratory maintenance regime is fol-

lowed, using just a single type of food, there is a risk of obtaining unreliable data about the effectiveness of a specific method of control of this species of ground beetle. The experiment described in this article allows us to recommend the following seed mixture as being one of the closest diets to the natural diet of *H. rufipes* for the maintenance of imagines of the species in laboratories: *T. aestivum*, *A. sativa*, *S. cereale*, *F. esculentum* and *B. vulgaris*.

CONCLUSIONS

Defining the food preferences of polyphage species is a potentially rewarding task for applied ecology, which allows one to estimate the effect of a certain insect population upon its environment. It is particularly interesting to investigate why certain food items are more intensively consumed than others. Our first hypothesis was upheld, the beetles intensity of consumption was greater when offered a multicomponent diet than with a single component diet. The second hypothesis that the beetles would feed more intensively when offered a high fat diet was not upheld. The third hypothesis that when different multicomponent diets are offered the intensity of consumption of some of the components will significantly vary. Further studies are needed for the physiological peculiarities of digestion for certain food types, and also the effect upon them of the intestinal microbial environments of individual beetles.

REFERENCES

- Briggs J.B. 1965. Biology of some ground beetles (Coleoptera, Carabidae) injurious to strawberries. Bull. Entomol. Res. 56 (1): 79-93.
- Brygadyrenko V.V., Korolev O.V. 2006. Osoblyvosti spektra zhyvlennja *Pterostichus melanarius* (Coleoptera Carabidae) u laboratornyh umovah (Range feeding characteristics of *Pterostichus melanarius* (Coleoptera, Carabidae) in laboratory conditions). Bulletin of Bilocerkiivskiy State Agrarian University 43: 67–71. (In Ukrainian; abstract in English).
- Collins K.L., Boatman N.D., Wilcox A., Holland J.M., Chaney K. 2002. Influence of beetle banks on cereal aphid predation in winter wheat. Agric. Ecosyst. Environ. 93 (1–3): 337-350.
- Currie C.R., Spence J.R., Niemela J. 1996. Competition, cannibalism and intraguild predation among ground beetles (Coleoptera: Carabidae): A laboratory study. Coleopt. Bull. 50(2): 135-148.
- David J.-F. 1998. How to calculate leaf litter consumption by saprophagous macrofauna? Eur. J. Soil Biol. 34: 111-115.
- Davies M.I. 1953. The contents of the crops of some British carabid beetles. Entomol. Mon. Mag. 89: 18-23.
- Dunn G.A. 1981. Distribution of *Harpalus rufipes* De Geer in Canada and United States (Coleoptera: Carabidae). Entomol. News 92 (5): 186-188.
- Fawki S., Toft S. 2005. Food preferences and the value of animal food for the carabid beetle *Amara similata* (Gyll.) (Col., Carabidae). J. Appl. Entomol. 129 (9–10): 551-556.
- Frampton G.K., Cilgi T., Fry G.L.A., Wratten S.D. 1995. Effects of grassy banks on the dispersal of some carabid beetles (Coleoptera: Carabidae) on farmland. Biol. Cons. 71 (3): 347-355.
- Harrison S., Gallandt E.R. 2012. Behavioural studies of *Harpalus rufipes* De Geer: An important weed seed predator in Northeastern US agroecosystems. Int. J. Ecol. DOI: 10.1155/2012/846546.
- Hartke A., Drummond F.A., Liebman M. 1998. Seed feeding, seed caching, and burrowing behaviors of *Harpalus rufipes* De Geer larvae

- (Coleoptera: Carabidae) in the main potato agroecosystem. *Biol. Control*. 13 (2): 91-100.
- Hengeveld R. 1980. Qualitative and quantitative aspects of the food of ground beetles (Coleoptera, Carabidae): A review. *Neth. J. Zool.* 30(4): 555-563.
- Honek A., Martinkova Z., Jarosik V. 2003. Ground beetles (Carabidae) as seed predators. *Eur. J. Entomol.* 100(4): 531-544.
- Honek A., Martinkova Z., Saska P., Koprdoва S. 2009. Role of post-dispersal seed and seedling predation in establishment of dandelion (*Taraxacum* agg.) plants. *Agric. Ecosyst. Environ.* 134: 126-135.
- Honek A., Martinkova Z., Saska P., Pekar S. 2007. Size and taxonomic constraints determine the seed preferences of Carabidae (Coleoptera). *Basic Appl. Ecol.* 8: 343-353.
- Irmeler U. 2003. The spatial and temporal pattern of carabid beetles on arable fields in northern Germany (Schleswig-Holstein) and their value as ecological indicators. *Agric. Ecosyst. Environ.* 98 (1-3): 141-151.
- Jørgensen H. B., Toft S. 1997. Food preference, diet dependent fecundity and larval development in *Harpalus rufipes* (Coleoptera: Carabidae). *Pedobiologia* 41(4): 307-315.
- Kabacik-Wasilik D., Jaworska M. 1973. The effect of pesticides used to control the Colorado beetle on the Carabidae. *Ekol. Pol. Seria A*, 21: 369-375.
- Kabacik-Wasilik D., Kmitowa K. 1973. The effect of single and mixed infections of entomopathogenic fungi on the mortality of the Carabidae (Coleoptera). *Ekol. Pol. Seria A*, 41: 645-655.
- Klimeš P., Saska P. 2010. Larval and adult seed consumption affected by the degree of food specialization in *Amara* (Coleoptera: Carabidae). *J. Appl. Entomol.* 134(8): 659-666.
- Korolev O.V., Brygadyrenko V.V. 2012. Trofichni зв'язки *Pterostichus melanarius* (Coleoptera, Carabidae) iz dominantnykh vydamy bezhrebetnykh lisovykh ekosystem stepovogo Prydniprov'ja (Trophic connections of *Pterostichus melanarius* (Coleoptera, Carabidae) with dominant species of invertebrates in forest ecosystems of the Steppe Dnieper basin). *Visn. Dnipropetr. Univ. Ser. Biol. Ekol.* 20(1): 48-54. (In Ukrainian; abstract in English).
- Kromp B. 1999. Carabid beetles in sustainable agriculture: A review on pest control efficacy, cultivation impacts and enhancement. *Agric. Ecosyst. Environ.* 74(1-3): 187-228.
- Kutasi C., Markó V., Balog A. 2004. Species composition of carabid (Coleoptera: Carabidae) communities in apple and pear orchards in Hungary. *Acta Phytopathol. Hung.* 39 (1-3): 71-89.
- Lang A., Filser J., Henschel J.R. 1999. Predation by ground beetles and wolf spiders on herbivorous insects in a maize crop. *Agric. Ecosyst. Environ.* 72(2): 189-199.
- Lindroth C.H. 1985. The Carabidae (Coleoptera) of Fennoscandia and Denmark. No. 1. Brill Academic Pub.
- Magura T. 2002. Carabids and forest edge: Spatial pattern and edge effect. *Forest Ecol. Manag.* 157 (1-3): 23-37.
- Midtgaard F. 1999. Is dispersal density-dependent in carabid beetles? A field experiment with *Harpalus rufipes* (Degeer) and *Pterostichus niger* (Schaller) (Col., Carabidae). *J. Appl. Entomol.* 123 (1): 9-12.
- Monzó C., Sabater-Muñoz B., Urbaneja A., Castañera P. 2011. The ground beetle *Pseudophonus rufipes* revealed as predator of *Ceratitis capitata* in citrus orchards. *Biol. Control.* 56 (1): 17-21.

- Niemelä J. 1993. Interspecific competition in ground-beetle assemblages (Carabidae): What have we learned? *Oikos* 66 (2): 325-335.
- Petrusenko A.A., Petrusenko S.V. 1973. Semejstvo zhuzhelicy (Carabidae) (The family of ground beetles (Carabidae)) In: Vasil'ev V.P. (Ed.). *Vrediteli Sel'skohozhajstvennyh Kul'tur i Lesnyh Nasazhdenij* (Pests of Agricultural Crops and Forest Plantations). Kiev, Urozhaj. 1: 363-387. (In Russian).
- Pollet M., Desender K. 1987. Feeding ecology of grassland inhabiting carabid beetles (Coleoptera, Carabidae) in relation to the availability of some prey groups. *Acta Phytopathol. Entomol. Hung.* 22 (1-4): 223-246.
- Porhajašova J., Petřvalsky V., Macak M., Urmínska J. 2009. Occurrence of species family Carabidae (Coleoptera) independence on the input of organic matter into soil. *J. Cent. Eur. Agr.* 9(3): 557-565.
- Purvis G., Fadl A. 2002. The influence of cropping rotations and soil cultivation practice on the population ecology of carabids (Coleoptera: Carabidae) in arable land. *Pedobiologia* 46(5): 452-474.
- Reshetniak D.Y., Brygadyrenko V.V. 2013. Optimizacija racionala *Harpalus rufipes* (Coleoptera, Carabidae) v uslovijah laboratornogo sodержanija (Optimizing of *Harpalus rufipes* (Coleoptera, Carabidae) diet under laboratory conditions). *Visn. Dnìpropetr. Univ. Ser. Biol. Ekol.* 21 (1): 38-42. (In Russian; abstract in English).
- Robinson D.S. 1987. Food – biochemistry and nutritional value. Leeds, UK, Univ. Leeds. 554 pp.
- Sasakawa K. 2009. Diet affects male gonad maturation, female fecundity, and larval development in the granivorous ground beetle *Anisodactylus punctatipennis*. *Ecol. Entomol.* 34(3): 406-411.
- Saska P., Martinkova Z., Honek A. 2010. Temperature and rate of seed consumption by ground beetles (Carabidae). *Biol. Control* 52 (2): 91-95.
- Shearin A.F., Reberg-Horton S.C., Gallandt E.R. 2008. Cover crop effects on the activity-density of the weed seed predator *Harpalus rufipes* (Coleoptera: Carabidae). *Weed Sci.* 56(3): 442-450.
- Snyder W.E., Wise D.H. 1999. Predator interference and the establishment of generalist predator populations for biocontrol. *Biol. Control.* 15 (3): 283-292.
- StatPoint Inc. 2006. Statgraphics Centurion XV, version 15.1.02. www.statgraphics.com.
- StatSoft Inc. 2004. Statistica (data analysis software system), version 7. www.statsoft.com.
- Thiele H.U. 1977. *Carabid beetles in their environments*. Berlin, Springer-Verlag, 369 pp.
- Traugott M. 1998. Larval and adult species composition, phenology and life cycles of carabid beetles (Coleoptera: Carabidae) in an organic potato field. *Eur. J. Soil Biol.* 34 (4): 189-197.
- White S.S., Renner K.A., Menalled F.D., Landis D.A. 2007. Feeding preferences of weed seed predators and effect on weed emergence. *Weed Sci.* 55 (6): 606-612.
- Zhang J., Drummond F.A., Liebman M., Hartke A. 1997. Phenology and dispersal of *Harpalus rufipes* DeGeer (Coleoptera: Carabidae) in agroecosystems in Maine. *J. Agr. Urban Entomol.* 14 (2): 171-186.

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