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

Viktor V. Brygadyrenko, Daria Y. Reshetniak

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; Irmler 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_ has 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; Sasakawa 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 & Sask 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 sedg, 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 Zabrin 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 sug-
gests that any particular species of food object
will be consumed at different intensities in differ-
ent ecosystems, depending on the composition
of the other food species present.

With these three observations in mind we formu-
lated and tested the following hypotheses in our
experiments: (1) in the conditions of a single spe-
cies 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 us-
ing 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 develop-
ment of sexual characteristics. During the sec-
ond half of summer the area researched is af-
fected 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 ac-
cess to water could be considered as correspond-

ing 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 ana-
lytical 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 replen-
ished every day, and were provided with differ-
ent types of food of animal (litter invertebrates
cought 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 con-
ducted, 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 ex-
crement 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 micro-
scope MBC-10 and divided into different catego-
ries. 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 pro-
vided 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 $62.4 \pm 9.1$ 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 $1.9 \pm 1.7$ 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

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

there was access to water, the *H. rufipes* beetles lost $2.5 \pm 7.9$ 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 CO$_2$ and H$_2$O (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 $7.1 \pm 2.6$ 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* ($-1.9 \pm 4.8$) and *B. vulgaris* ($-1.8 \pm 6.4$) 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 (x ± S, n = 12)

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

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)
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. miliaceum* (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. 1a), buckwheat, 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.
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, *p* < 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, *p* < 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 & Fadl 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-
allowed, 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 intensivity 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.

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