Nutrition of *Opatrum sabulosum* (Coleoptera, Tenebrionidae) when fed on leaves of trees, shrubs and liana plants in the conditions of a laboratory experiment

Viktor V. Brygadyrenko, Sergii S. Nazimov

Brygadyrenko V.V., Nazimov S.S. 2014. Nutrition of *Opatrum sabulosum* (Coleoptera, Tenebrionidae) when fed on leaves of trees, shrubs and liana plants in the conditions of a laboratory experiment. *Baltic J. Coleopterol., 14(1): 59 – 72.*

This paper provides data of the analysis of the role of the dried leaves of 33 plant species (21 trees, 10 shrubs and 2 perennial liana plants) in the nutrition of *Opatrum sabulosum* (L.), a mass pest of field crops in the Eurasia steppe zone. Imagines of darkling beetles were maintained during 5 days ($n = 32$) in plastic containers with an equal weight of leaves of each plant species offered. None of three parameters under study (mass of food consumed, change in body weight, faecal mass) taken individually can be sufficient for evaluation of the metabolic value of each trophic object for the beetle. To evaluate the metabolic value of each plant species for the beetle a normative rating was assigned for each of the above three parameters. The plants which provided the maximum metabolic value for *O. sabulosum* were *Mîrus nigra* L., *Ulmus laevis* Pall., *Armeniaca vulgaris* Lam., *Tilia cordata* Mill., *Prunus cerasifera* Ehrh. and *Quercus robur* L. The metabolic value of *Cornus mas* L., *Acer platanoides* L., *Prunus nigra* L., *P. spinosa* L., *Ribes nigrum* L. was less pronounced. The metabolic value of *Vitis vinifera* L., *Crataegus monogyna* Jacq., *Rhamnus cathartica* L., *Acer negundo* L. and *Armeniaca vulgaris* Lam. featured medium intensity. Practically no metabolic value was found for *Malus domestica* Borkh., *Paeonia suffruticosa* Andrews., *Viburnum opulus* L., *Morus alba* L., *Sambucus nigra* L., *Caragana arborescens* Lam., *Salix alba* L., *Rubus idaeus* L., *Elaeagnus angustifolia* L., *Juglans regia* L., *Populus alba* L. and *Ulmus minor* Mill.

Keywords: *Opatrum sabulosum*; Tenebrionidae; food preferences; laboratory experiments; phytophagous insects

V. V. Brygadyrenko & S. S. Nazimov, Department of Zoology & Ecology, Oles Honchar Dnipropetrovsk National University, Gagarin ave., 72, Dnipropetrovsk, 49010, Ukraine; e-mail: brigad@ua.fm

INTRODUCTION

Many phytophagous insects are distinguished by the wide range of food items they take, allowing them to redistribute the trophic load to other food types whenever the supply of any particular component of their diet decreases. Nutrition of polyphages such as darkling beetles in natural conditions is of practical interest for limiting their nega-

tive impact on human economic activity, but it is also important from the point of view of fundamental ecology (Allsopp 1980, De Los Santos et al. 1988, Carpaneto & Fattorini 2001, Fattorini 2011). Investigation of a specific species in this regard comprises three successive steps: (1) determination of the potential width of its trophic niche (complete list of possible food items), (2) revealing of the effect of a specific food on the metabolism of the

organism and (3) evaluation of the occupied trophic niche (ratio of actual diet in the specific ecosystem to that potentially possible for the given species) (Chernyshev 1996). In natural conditions it is possible only to take account of budgets (expenditures) of time spent by any phytophage studied for nutrition on each food type (Rogers et al. 1988, Chen et al. 2004). The effect of a specific type of food on a species' metabolism *in vivo* cannot be determined even with state-of-the-art computer technologies because of the impact of numerous indeterminable factors (Knor 1975, Parmenter & Macmahon 1984, Whicker & Tracy 1987, Crawford 1988, Parmenter et al. 1989a, 1989b, Gehrken & Sømme 1994, Semida et al. 2001).

In laboratory experiments (Wise 1981, Miller & Redfern 1988, Nazimov & Brygadyrenko 2013), food consumption, mass of faeces and changing of body weight of the species under study during the experiment are usually taken into account when the availability of an appropriate method provides the opportunity. The mass of food intake consumed is expended on respiration (oxidation, constructive metabolism, breathing and catabolism), formation of body weight (anabolism) and excretion of undigested residues as faeces. Recording of food consumption alone, changes of body weight alone or amount of faeces alone will not give a complete picture of the effect of the given component of the diet on metabolism. Simultaneous integrated assessment of the three parameters as a whole is required. In our opinion, none of the three parameters of food consumption by *O. sabulosum* in our study when taken individually can be sufficient for evaluation of the metabolic value for the beetle of a certain plant species included in our experiments (Nazimov & Brygadyrenko 2013).

Our previous experiments on the metabolic value for this species of darkling beetle of leaves in various stages of decomposition show that the quantity of food taken varies significantly with the degree of the plants' moisture. Earlier work indicates that *O. sabulosum* utilises decaying organs of plants in order to obtain moisture (Rejnhardt 1936). Thus the influence of secondary metabolites rather than the degree of a plant's decay is of especial interest and this can be studied only on the basis of evalu-

ation of consumption of dry vegetational parts of plants.

It is worth noting that two agents take part in any trophic activity, the consumer and the consumed. For this reason it is necessary to make a clear distinction between the two aspects of the trophic connection. The question can be studied from the point of view of the object eaten as well as from that of the consuming organism. Most publications on the trophic relations of *O. sabulosum* are focussed on the damage suffered by the plants and not on the advantage accrued to the darkling beetle by the connection. Primary metabolites (for example glucose and its derivatives – starch, cellulose and pectin) have a weak effect on the feeding preferences of the beetle *O. sabulosum*. There is good reason to study the potential possibility of this darkling beetle's consumption of secondary metabolites in dry leaves, which can only be achieved through laboratory experiments.

The objective of this work is to evaluate the effect of consumption by the imago of *O. sabulosum* on dried leaves of various trees and shrubs on its body weight and the intensity of formation of its faeces. The chemical composition of plants changes with the vegetational process and also with the process of dying and decomposition, which begins with proteins, continuing with other higher molecular compounds. Bearing this in mind, the aim of this work is to assess the metabolic value for *O. sabolusum* of different species of green plants obtained at the peak of their vegetational cycle.

Opatrum sabulosum (Linnaeus, 1761) is distributed practically throughout Europe, its eastern range extending to Siberia and Central Asia (Dolin 1975). It is one of the commonest species in its genus (Leo et al. 2011, Jia et al. 2013). It is a polyphagous pest, having a highly significant impact on *Helianthus annuus* L., *Zea mays* L. and *Beta vulgaris* L. The number of this species on many agricultural fields in the south of Ukraine reaches several dozen specimens per square meter. The high mobility of this species allows the beetles to survive periods when the fields are out of crop (without vegetation food) by feeding on tree leaf litter in forest belts adjacent to the agro-ecosystems. How-

ever, no quantitative evaluation of the metabolic value of various tree species for this beetle has been attempted so far (Minoranskij 1978).

Among the food items consumed by this species over 40 plant species (predominantly, herbaceous plants) have been recorded in the literature (Dolin 1975, Kabanov 1977, 1981, Kabanov & Sedin 1981). Furthermore, the literature contains only fragmentary information on the feeding of beetles on tree species. Rejnhardt (1936) states that *O. sabulosum* beetles feeding on leaves of the natural steppe flora turn to weed plants (*Polygonum aviculare* L., *Atriplex spp.*, *Cirsium spp.*) on fields, and that sometimes they gnaw dry plant residues and dry horse manure.

According to the summary of Medvedev (1968), *O. sabulosum* beetles eat the bases of stems, roots and other underground parts of plants (underground stems of potatoes and beet-roots), making deep narrow passages in them. Beetles damage *Triticum durum* Desf., *Hordeum vulgare* L., Panicum miliaceum L., *Sorghum bicolor* Moench., *Cicer arietinum* L., *Beta vulgaris* L., *Solanum tuberosum* L., *Solanum lycopersicum* L., *Nicotiana tabacum* L., *Helianthus annuus* L., *Gossypium hirsutum* L., *Cucumis sativus* L., *Alium cepa* L., *Perilla nankinensis* (Lour.) Decne, gnaw out cotyledons of fruit crops, cause damage to *Vitis vinifera* L. (Medvedev 1968) and young pine trees (Chernej 2005). Until now, no special experiments have been carried out under laboratory conditions with regard to the feeding of this darkling beetle species on leaves of trees and shrubs.

MATERIAL AND METHODS

Imagines of *O. sabulosum* were caught manually in natural steppe ecosystems in the vicinity of Dnipropetrovsk (Ukraine) at the end of July 2013. Before the beginning of the experiment the beetles were kept in the laboratory for 10 days on a diet which was optimal for their laboratory maintenance (leaves of *Lactuca sativa* L., *Brassica oleracea* L. and *Vitis vinifera* L.) with access to water.

Each experiment on a particular plant species was carried out in 8 replicates. 4 specimens of *O. sabulosum* were put in each plastic container of $8 \times 12 \times 10$ cm by size, with equal proportions of males and females). 32 specimens of adult beetles (with four beetles in each of the eight containers) were subjected to the experiment with each food plant species, involving a total of 1,088 beetles in 272 containers for the 33 plant species involved in the study including the control group of beetles denied access to food . Daily temperature variations in the laboratory did not exceed 3 °C(+25…+28 °C). Access of laboratory animals to vegetation or animal food except for that offered by experimenters was completely excluded. The darkling beetles were fed on leaves taken in advance of the experiment from the twigs and branches of trees and shrubs at the peak of their vegetational cycle, and collected from natural ecosystems or artificial ecosystems not subjected to intensive man-made pollution. The green leaves were dried for two weeks on racks under an open sided garden shed until they were dessicated and fragile. A control group of 32 beetles was kept in 8 plastic containers without soil, litter or vegetation. All the containers involved in the experiment were randomly distributed in a single laboratory so neither the 8 replicates of a given plant species nor those of the control group were grouped together. In all variants of the experiment the animals had no access to water; dry leaves of plants in the containers were not moistened throughout the experiment. Based on the results of our preliminary experiments, even insignificant moistening of food or the appearance of water droplets on the beetles' bodies causes rapid death of beetles in the laboratory conditions from bacterial or fungal infections. In natural conditions a relatively high rate of mortality can be observed following atmospheric precipitation. However, in laboratory conditions even a minimal mortality is unacceptable because an intenstinal infection of even a small number of specimens leads to distortion of the results.

During determination of the mass of food consumed, microbial decay of the leaf weighed portion was taken into account. For that purpose, a weighed sample of leaves was put in similar con-

tainers ($n = 8$) without beetles, concurrently with the experiment, under similar conditions. Coefficient *D* – change of their mass in the control, was calculated:

$$D = (M'_0 - M'_n) / M'_0,$$

where M'_0 and M'_n – initial and final masses of control weighed portion of food not exposed to beetles. Consumption of food by the beetle for each variant of the experiment was calculated by the optimized formula proposed by David (1998):

$$\tilde{N} = (M_0 - M_0 D - M_n) / (1 - D)^{0.5},$$

where $\tilde{N}$ – food consumption by the beetle, M_0 and M_n – initial and final masses of weighed portion of food in the conditions of the experiment.

With a view to evaluating the metabolic value, we suggest the application of the rated value of each of the studied parameters. For that purpose the standard rating procedure is appropriate: from the specific value of the median of the characteristic its mean value was subtracted, and divided by the standard error. This being the case, the mean value of each characteristic is equal to zero, while the standard error on each of columns is 1. S_x of the metabolic value of each food item for *O. sabulosum* is calculated from three normalised medians (food consumption, formation of excrement and change in body weight).

All experiments were carried out at the same time, in the same lighting conditions, temperature and humidity, with a 5-day duration of each experiment. The mass of food, beetles and their faeces was determined on analytical scales JD-100 (with accuracy to 1 mg). During statistical data processing, $x \pm SD$, median and range of each characteristic's variation were calculated. Differences between samples were considered significant at $Đ < 0.05$ (estimated with the use of one-way analysis of variance). The data for all 33 tests in all three parameters was first combined and ranked from the smallest to the largest measurements for each plant species. The average rank was then computed for the data at each level. 33 tests were conducted for each parameter using a Tukey honest significant difference test. It was used in conjunction with an ANOVA to find the means that significantly varied from each other.

For the statistical analyses, we took the averages of the 4 beetles in each container (use the average) to end up with 8 replicates per plant species and control.

RESULTS

Average values for the complete series of experiments

The average daily intake of food by a single beetle for the entire series of experiments analyzed in this paper was found to be at a low level (0.20 ± 1.20 mg/day), differing significantly (df1 = 32, df2 = 259, F = 3.75, $F_{0.05}$ = 1.49, P = $1.49*10^{-9}$) for individual species of trees and shrubs (Table 1). On average, for all variants of the nutritional experiment offering a diet of different species of leaves of trees, shrubs and liana plants, the body weight of adult *O. sabulosum* decreased by 0.81 ± 0.51 mg on a daily basis (df1 = 32, df2 = 263, F = 2.41, $F_{0.05}$ = 1.49, P = $8.01*10^{-5}$). This confirms that feeding on dried leaves of trees, shrubs and liana plants is not typical for the given species on the whole in natural conditions. In the control experiment conditions, in the full absence of food during five days, average daily losses of live body weight for each specimen amounted to 1.02 ± 0.27 mg (Table 2).

The average daily formation of faeces (Table 3) was equal to 0.39 ± 0.44 mg/specimen (df1 = 32, df2 = 231, F = 5.33, $F_{0.05}$ = 1.49, P = $1.03*10^{-14}$), but in some variants of the experiment with sufficient significant replications (32 specimens were kept on each diet during 5 days) no faeces were obtained at all. The data for the relative distribution of the characteristics in the course of the experiment are of interest (Fig. 1). The beetles' body weight had a normal distribution (As = 0.16 ± 0.15, Ex = -0.19 ± 0.30; P > 0.05). The beetles' food consumption (As = 2.35 ± 0.15, Ex = 10.37 ± 0.30; P < 0.001) and the rate of excrement production (As = 1.79 ± 0.15, Ex = 5.44 ± 0.30; P < 0.001) showed a statistically significant variation from the normal distribution both in its high asymmetry and in its high excess. Changes in the beetles' body weight in the course of the experiment (As = 0.14 ± 0.15, Ex = 5.37 ± 0.30; P <

Table 1. Consumption of dried leaves (mg/specimen per day) of various trees, shrubs and lianas by imagines of *O. sabulosum* in laboratory conditions ($n = 8$)

Family	Plant species	Median	$x \pm SD$	Min – Max	Tukey's test
Vitaceae	*Parthenocissus quinquefolia* (L.) Planch.	0.99	2.31 ± 2.81	$0.00 - 6.50$	a
Ulmaceae	*Ulmus laevis* Pall.☐	1.11	1.55 ± 1.73	$0.31 - 5.51$	b
Vitaceae	*Vitis vinifera* L.	0.33	1.28 ± 1.80	$0.00 - 5.14$	b
Viburnaceae	*Viburnum opulus* L.	1.26	1.15 ± 0.45	$0.00 - 1.55$	b
Rosaceae	*Armeniaca vulgaris* Lam.	0.96	0.96 ± 0.57	$0.00 - 1.66$	c
Moraceae	*Morus nigra* L.	0.75	0.85 ± 0.34	$0.46 - 1.38$	c
Sambucaceae	*Sambucus nigra* L.	0.64	0.82 ± 0.49	$0.00 - 1.66$	c
Fagaceae	*Quercus robur* L	0.63	0.73 ± 0.62	$0.00 - 1.49$	c
Cornaceae	*Cornus mas* L.	0.73	0.67 ± 0.47	$0.00 - 1.32$	c
Rosaceae	*Prunus spinosa* L.	0.60	0.65 ± 0.35	$0.10 - 1.35$	c
Rosaceae	*Prunus cerasifera* Ehrh.	0.55	0.64 ± 0.50	$0.00 - 1.56$	c
Rhamnaceae	*Rhamnus cathartica* L.	0.55	0.55 ± 0.37	$0.00 - 1.13$	c
Rosaceae	*Cerasus vulgaris* Mill.	0.49	0.52 ± 0.39	$0.00 - 1.37$	c
Rosaceae	*Padus avium* Mill.	0.47	0.47 ± 0.26	$0.00 - 0.89$	c
Aceraceae	*Acer platanoides* L.	0.35	0.45 ± 0.51	$0.00 - 1.76$	c
Fagaceae	*Caragana arborescens* Lam.	0.43	0.43 ± 0.32	$0.00 - 1.00$	c
Paeoniaceae	*Paeonia suffruticosa* Andrews.	0.44	0.43 ± 0.16	$0.12 - 0.66$	c
Rosaceae	*Persica vulgaris* Mill.	0.31	0.34 ± 0.39	$0.00 - 1.29$	c
Rosaceae	*Rubus idaeus* L.	0.38	0.34 ± 0.18	$0.00 - 0.52$	c
Grossulariaceae	*Ribes nigrum* L.	0.27	0.32 ± 0.22	$0.07 - 0.77$	c
Elaeagnaceae	*Elaeagnus angustifolia* L.	0.29	0.31 ± 0.32	$0.00 - 1.03$	c
Ulmaceae	*Ulmus minor* Mill.	0.33	0.31 ± 0.13	$0.00 - 0.45$	c
Tiliaceae	*Tilia cordata* Mill.	0.26	0.26 ± 0.18	$0.05 - 0.65$	c
Rosaceae	*Malus domestica* Borkh.	0.25	0.25 ± 0.14	$0.08 - 0.44$	c
Juglandaceae	*Juglans regia* L.	0.28	0.25 ± 0.13	$0.00 - 0.44$	c
Aceraceae	*Acer negundo* L.	0.09	0.22 ± 0.37	$0.00 - 1.20$	c
Rosaceae	*Crataegus monogyna* Jacq.	0.17	0.21 ± 0.24	$0.00 - 0.77$	c
Moraceae	*Morus alba* L.	0.21	0.21 ± 0.11	$0.00 - 0.35$	c
Fabaceae	*Robinia pseudoacacia* L.	0.15	0.18 ± 0.14	$0.00 - 0.47$	c
Hydrangeaceae☐	*Philadelphus coronarius* L.	0.17	0.17 ± 0.16	$0.00 - 0.51$	c
Salicaceae	*Populus nigra* L.	0.12	0.12 ± 0.07	$0.00 - 0.24$	c
Salicaceae	*Populus alba* L.	0.11	0.10 ± 0.06	$0.00 - 0.19$	c
Salicaceae	*Salix alba* L.	0.08	0.18 ± 0.21	$0.00 - 0.59$	c
Without food resources		0.00	0.00 ± 0.00	$0.00 - 0.00$	c

Note: different letters in the last column indicate statistically significant differences among means (Tukey's test, $P < 0.05$).

0.001) significantly differed in distribution from the normal high value for excess.

Consumption of leaves of individual tree and shrub species

The maximum consumption of dried leaves (median is equal to 0.60–1.26 mg/specimen per day or 1.21–2.53% of body weight per day) of all the studied tree and shrub species was recorded for *V. opulus*, *U. laevis*, *P. quinquefolia*, *A. vulgaris*, *M. nigra*, *C. mas*, *S. nigra*, *Q. robur*, *P. spinosa*. Except for *S. nigra* and *V. opulus*, these species are typical representatives of artificial steppe plantations in

the greater part of the range of the beetle under study (Table 1).

A lower level of leaf consumption (median – 0.43– 0.55 mg/specimen per day or 0.86–1.11% of body weight per day) was recorded for *P. cerasifera*, *R. cathartica*, *C. vulgaris*, *P. avium*, *P. suffruticosa*, *C. arborescens*. These species are also often found in artificial forest plantations (except for *P. suffruticosa*).

The minimum consumption of leaves (median – 0.21–0.38 mg/specimen per day or 0.42–0.76% of body weight per day) was recorded for *R. idaeus*,

Table 2. Change in body weight (mg/specimen per day) of imagines of *O. sabulosum* when fed on dried leaves of various trees, shrubs and lianas in laboratory conditions ($n = 8$, average live body weight of one specimen – 49.77 ± 7.57 mg)

Family	Plant species	Median	$x \pm SD$	Min – Max	Tukey's test
Salicaceae	*Populus nigra* L.	–0.23	–0.23 ± 0.46	–1.0 – +0.4	a
Fabaceae	*Robinia pseudoacacia* L.	–0.40	–0.38 ± 0.26	–0.9 – +0.2	b
Moraceae	*Morus nigra* L.	–0.48	–0.48 ± 0.27	–0.9 – +0.0	b
Paeoniaceae	*Paeonia suffruticosa* Andrews.	–0.80	–0.54 ± 0.70	–1.1 – +1.2	c
Moraceae	*Morus alba* L.	–0.55	–0.55 ± 0.30	–0.8 – +0.2	c
Tiliaceae	*Tilia cordata* Mill.	–0.65	–0.56 ± 0.58	–1.4 – +0.7	c
Aceraceae	*Acer platanoides* L.	–0.58	–0.58 ± 0.32	–1.2 – –0.2	c
Aceraceae	*Acer negundo* L.	–0.65	–0.60 ± 0.24	–1.0 – –0.2	c
Rosaceae	*Persica vulgaris* Mill.	–0.63	–0.63 ± 0.31	–1.2 – –0.3	c
Rosaceae	*Malus domestica* Borkh.	–0.67	–0.67 ± 0.47	–1.4 – +0.4	c
Hydrangeaceae	*Philadelphus coronarius* L.	–0.77	–0.77 ± 0.41	–1.5 – –0.2	c
Salicaceae	*Salix alba* L.	–0.78	–0.78 ± 0.09	–1.0 – –0.7	c
Cornaceae	*Cornus mas* L.	–0.80	–0.78 ± 0.17	–1.0 – –0.6	c
Grossulariaceae	*Ribes nigrum* L.	–0.80	–0.79 ± 0.23	–1.2 – –0.4	c
Fagaceae	*Quercus robur* L.	–0.80	–0.80 ± 0.21	–1.2 – –0.6	c
Vitaceae	*Parthenocissus quinquefolia* (L.) Planch.	–0.80	–0.81 ± 0.31	–1.3 – –0.4	c
Elaeagnaceae	*Elaeagnus angustifolia* L.	–0.84	–0.82 ± 0.21	–1.1 – –0.6	c
Rosaceae	*Armeniaca vulgaris* Lam.	–0.80	–0.82 ± 0.25	–1.2 – –0.4	c
Rhamnaceae	*Rhamnus cathartica* L.	–0.70	–0.82 ± 0.39	–1.8 – –0.5	c
Salicaceae	*Populus alba* L.	–0.80	–0.84 ± 0.35	–1.5 – –0.4	c
Ulmaceae	*Ulmus laevis* Pall.	–0.87	–0.87 ± 0.51	–1.6 – –0.2	c
Rosaceae	*Crataegus monogyna* Jacq.	–0.80	–0.88 ± 0.43	–1.9 – –0.4	c
Vitaceae	*Vitis vinifera* L.	–0.88	–0.88 ± 1.21	–3.2 – +1.5	c
Fabaceae	*Caragana arborescens* Lam.	–0.80	–0.89 ± 0.52	–2.2 – –0.3	c
Rosaceae	*Prunus spinosa* L.	–0.95	–0.91 ± 0.23	–1.2 – –0.4	c
Rosaceae	*Padus avium* Mill.	–0.95	–0.92 ± 0.22	–1.2 – –0.6	c
Ulmaceae	*Ulmus minor* Mill.	–0.95	–0.94 ± 0.36	–1.6 – –0.3	c
Rosaceae	*Rubus idaeus* L.	–0.96	–0.96 ± 0.37	–1.6 – –0.4	c
Sambucaceae	*Sambucus nigra* L.	–0.98	–0.98 ± 0.24	–1.4 – –0.7	c
Without food resources		–1.00	–1.02 ± 0.27	–1.6 – –0.4	c
Rosaceae	*Cerasus vulgaris* Mill.	–1.00	–1.11 ± 0.44	–2.0 – –0.6	c
Juglandaceae	*Juglans regia* L.	–1.20	–1.17 ± 0.34	–1.8 – –0.6	c
Viburnaceae	*Viburnum opulus* L.	–1.26	–1.26 ± 0.50	–2.0 – –0.4	d
Rosaceae	*Prunus cerasifera* Ehrh.	–0.95	–1.49 ± 1.37	–5.1 – –0.7	e

Note: different letters in the last column indicate statistically significant differences among means (Tukey's test, $P < 0.05$).

A. platanoides, *U. minor*, *V. vinifera*, *A. vulgaris*, *E. angustifolia*, *J. regia*, *R. nigrum*, *T. cordata*, *M. domestica*, *M. alba*. This group includes *J. regia*, a toxic plant for most insect species, and *E. angustifolia*, which is the commonest shrub/tree species on steppe slopes.

Consumption of tree and shrub species such as *C. monogyna*, *Ph. coronarius*, *R. pseudoacacia*, *P. nigra*, *P. alba*, *A. negundo*, *S. alba* (median – 0.08–0.17 mg/specimen per day or 0.16–0.34% of body weight per day) did not significantly differ from the control (practically not eaten in the most of the containers).

Ranging of the list of tree and shrub species by the median for most food items of *O. sabulosum* corresponds to their division into groups according to average values. Only for *P. quinquefolia* and *V. vinifera* were essential differences between the median and average values of food consumption recorded. This is connected with sharp increase in leaf consumption (to 5.14 and 6.50 mg/specimen per day) in some of the experimental containers. A

Table 3. Intensity of formation of faeces (mg/specimen per day) by imagines of *O. sabulosum* when fed on dried leaves of various trees, shrubs and lianas in laboratory conditions ($n = 8$ for each plant species and control)

Family	Plant species	Median	$x \pm SD$	Min – Max	Tukey's test
	Without food resources	0.00	0.00 ± 0.00	$0.00 - 0.00$	a
Salicaceae	*Populus alba* L.	0.00	0.00 ± 0.00	$0.00 - 0.00$	a
Vitaceae	*Vitis vinifera* L.	0.00	0.00 ± 0.00	$0.00 - 0.00$	a
Moraceae	*Morus alba* L.	0.00	0.00 ± 0.00	$0.00 - 0.00$	a
Elaeagnaceae	*Elaeagnus angustifolia* L.	0.00	0.00 ± 0.00	$0.00 - 0.00$	a
Vitaceae	*Parthenocissus quinquefolia* (L.) Planch.	0.00	0.03 ± 0.07	$0.00 - 0.20$	a
Ulmaceae	*Ulmus laevis* Pall.	0.00	0.04 ± 0.05	$0.00 - 0.15$	b
Salicaceae	*Populus nigra* L.	0.06	0.06 ± 0.06	$0.00 - 0.15$	c
Fabaceae	*Caragana arborescens* Lam.	0.00	0.08 ± 0.20	$0.00 - 0.60$	d
Rhamnaceae	*Rhamnus cathartica* L.	0.10	0.13 ± 0.14	$0.00 - 0.45$	d
Rosaceae	*Rubus idaeus* L.	0.15	0.17 ± 0.16	$0.00 - 0.45$	e
Fabaceae	*Robinia pseudoacacia* L.	0.10	0.19 ± 0.29	$0.00 - 0.90$	e
Sambucaceae	*Sambucus nigra* L.	0.14	0.24 ± 0.27	$0.00 - 0.80$	e
Salicaceae	*Salix alba* L.	0.20	0.26 ± 0.39	$0.00 - 1.20$	f
Rosaceae	*Malus domestica* Borkh.	0.20	0.33 ± 0.30	$0.05 - 0.95$	f
Aceraceae	*Acer platanoides* L.	0.35	0.35 ± 0.27	$0.00 - 0.80$	f
Rosaceae	*Persica vulgaris* Mill.	0.20	0.39 ± 0.44	$0.00 - 1.15$	g
Paeoniaceae	*Paeonia suffruticosa* Andrews.	0.20	0.42 ± 0.46	$0.00 - 1.10$	g
Cornaceae	*Cornus mas* L.	0.40	0.43 ± 0.14	$0.20 - 0.60$	g
Juglandaceae	*Juglans regia* L.	0.43	0.43 ± 0.17	$0.20 - 0.70$	g
Aceraceae	*Acer negundo* L.	0.45	0.45 ± 0.19	$0.25 - 0.75$	g
Rosaceae	*Armeniaca vulgaris* Lam.	0.40	0.46 ± 0.27	$0.10 - 1.00$	g
Rosaceae	*Padus avium* Mill.	0.65	0.56 ± 0.34	$0.00 - 0.95$	g
Viburnaceae	*Viburnum opulus* L.	0.56	0.56 ± 0.44	$0.15 - 1.60$	h
Rosaceae	*Cerasus vulgaris* Mill.	0.60	0.58 ± 0.34	$0.15 - 1.10$	i
Rosaceae	*Prunus spinosa* L.	0.60	0.58 ± 0.44	$0.00 - 1.25$	i
Ulmaceae	*Ulmus minor* Mill.	0.62	0.62 ± 0.39	$0.20 - 1.10$	i
Hydrangeaceae	*Philadelphus coronarius* L.	0.60	0.63 ± 0.20	$0.45 - 1.05$	i
Fagaceae	*Quercus robur* L	0.64	0.64 ± 0.60	$0.10 - 1.85$	i
Rosaceae	*Crataegus monogyna* Jacq.	0.60	0.75 ± 0.54	$0.20 - 2.00$	j
Grossulariaceae	*Ribes nigrum* L.	0.70	0.77 ± 0.44	$0.20 - 1.45$	k
Tiliaceae	*Tilia cordata* Mill.	0.85	0.84 ± 0.24	$0.40 - 1.20$	l
Rosaceae	*Prunus cerasifera* Ehrh.	0.95	0.92 ± 0.43	$0.00 - 1.40$	m
Moraceae	*Morus nigra* L.	0.65	1.06 ± 0.99	$0.20 - 3.05$	n

Note: different letters in the last column indicate statistically significant differences among means (Tukey's test, $P < 0.05$).

similar "outlying" of maximum values was recorded also for *U. laevis* (up to 5.51 mg/specimen per day). It is worth noting the significant gap in consumption of litter of *M. nigra* and *M. alba* (median – 0.75 and 0.21 mg/specimen per day).

Cases were observed for practically all food plant species (except *M. nigra*, *U. laevis* and some other species) where the beetles in the containers holding four specimens did not consume any food during the 5 days of the experiment (see Min in the last column of Table 1). The beetles' food consumption did not depend on their weight before the start of the experiment (Fig. 2).

Changes in *O. sabulosum* body weight with various diets

According to results of one-way analysis of variance, the body weight of *O. sabulosum* (Table 2) fell insignificantly compared with the control (median –1.02 mg/day) when beetles are kept on a diet of *P. alba*, *R. nigrum*, *P. suffruticosa*, *C. mas*, *C. arborescens*, *Q. robur*, *C. monogyna*, *P.*

Table 4. Evaluation of metabolic value for imagines of *O. sabulosum* of dried leaves of various trees, shrubs and lianas in laboratory conditions

Family	Plant species	Food consumption*	Change in body weight*	Formation of faeces*	Metabolic value, $x \pm SD$
Moraceae	*Morus nigra* L.	1.00	1.50	1.06	1.19 ± 0.27
Ulmaceae	*Ulmus laevis* Pall.	2.18	–0.39	0.96	0.92 ± 1.29
Tiliaceae	*Tilia cordata* Mill.	–0.62	0.68	1.76	0.61 ± 1.19
Rosaceae	*Armeniaca vulgaris* Lam.	1.69	–0.05	0.19	0.61 ± 0.94
Rosaceae	*Prunus cerasifera* Ehrh.	0.34	–0.77	2.11	0.56 ± 1.45
Fagaceae	*Quercus robur* L.	0.60	–0.05	1.03	0.53 ± 0.54
Cornaceae	*Cornus mas* L.	0.93	–0.05	0.19	0.36 ± 0.51
Aceraceae	*Acer platanoides* L.	–0.32	1.02	0.02	0.24 ± 0.70
Salicaceae	*Populus nigra* L.	–1.08	2.71	–1.00	0.21 ± 2.16
Rosaceae	*Prunus spinosa* L.	0.50	–0.77	0.89	0.21 ± 0.87
Grossulariaceae	*Ribes nigrum* L.	–0.58	–0.05	1.24	0.20 ± 0.94
Vitaceae	*Parthenocissus quinquefolia* (L.) Planch.	1.79	–0.05	–1.21	0.18 ± 1.51
Rosaceae	*Padus avium* Mill.	0.08	–0.77	1.06	0.12 ± 0.92
Fabaceae	*Robinia pseudoacacia* L.	–0.98	1.89	–0.86	0.02 ± 1.62
Hydrangeaceae	*Philadelphus coronarius* L.	–0.91	0.10	0.89	0.02 ± 0.90
Rosaceae	*Cerasus vulgaris* Mill.	0.14	–1.01	0.89	0.01 ± 0.96
Vitaceae	*Vitis vinifera* L.	–0.39	–0.43	0.75	–0.02 ± 0.67
Rosaceae	*Crataegus monogyna* Jacq.	–0.91	–0.05	0.89	–0.02 ± 0.90
Rhamnaceae	*Rhamnus cathartica* L.	0.34	0.44	–0.86	–0.03 ± 0.72
Aceraceae	*Acer negundo* L.	–1.18	0.68	0.37	–0.04 ± 0.99
Rosaceae	*Persica vulgaris* Mill.	–0.45	0.77	–0.51	–0.06 ± 0.72
Paeoniaceae	*Paeonia suffruticosa* Andrews.	–0.02	–0.05	–0.51	–0.19 ± 0.27
Rosaceae	*Malus domestica* Borkh.	–0.65	0.58	–0.51	–0.19 ± 0.67
Viburnaceae	*Viburnum opulus* L.	2.68	–2.27	–1.21	–0.27 ± 2.61
Moraceae	*Morus alba* L.	–0.78	1.16	–1.21	–0.28 ± 1.26
Sambucaceae	*Sambucus nigra* L.	0.64	–0.92	–0.72	–0.33 ± 0.84
Fabaceae	*Caragana arborescens* Lam.	–0.06	–0.05	–1.21	–0.44 ± 0.67
Salicaceae	*Salix alba* L.	–1.21	0.05	–0.51	–0.56 ± 0.63
Rosaceae	*Rubus idaeus* L.	–0.22	–0.82	–0.68	–0.57 ± 0.31
Elaeagnaceae	*Elaeagnus angustifolia* L.	–0.52	–0.24	–1.21	–0.65 ± 0.50
Juglandaceae	*Juglans regia* L.	–0.55	–1.98	0.30	–0.75 ± 1.15
Ulmaceae	*Ulmus minor* Mill.	–0.39	–0.77	–1.21	–0.79 ± 0.41
Salicaceae	*Populus alba* L.	–1.11	–0.05	–1.21	–0.79 ± 0.64
	$x \pm SD$	0.00 ± 1.00	0.00 ± 1.00	0.00 ± 1.00	0.00 ± 0.48

Note: * – Rated value of the $x \pm SD$, from the relevant columns of Tables 1–3.

quinquefolia, *A. vulgaris*, *E. angustifolia*, *V. vinifera*, *P. avium*, *P. spinosa*, *U. minor*, *P. cerasifera*, *R. idaeus*, *S. nigra* and *C. vulgaris* (from –0.80 to –1.00 mg/day or 1.61–2.01%/day).

Increase in the body weight of *O. sabulosum* in comparison to beetles kept with no access to food is promoted by their feeding on the dried leaves of *A. vulgaris*, *T. cordata*, *A. negundo*, *M. domestica*, *R. cathartica*, *Ph. coronarius* and *S. alba* (median of body weight change varies in the range from –0.63 to –0.78 mg/day or 1.27–1.57%/day).

The loss of weight of the beetles subject to the experiment was in inverse ration to their intial weight,

the greater a beetle's initial weight, the less weight it lost (Fig. 2). There was absolutely no dependence of change of weight on food consumption in the course of the experiment.

Intensity of faecal formation of *O. sabulosum* with various diets

The amount of faeces can be connected, on the one hand, with enhancement of the intestinal motility and release of undigested food consumed before the 5-day experiment (as a result of laxative action of compounds contained in leaves or activ-
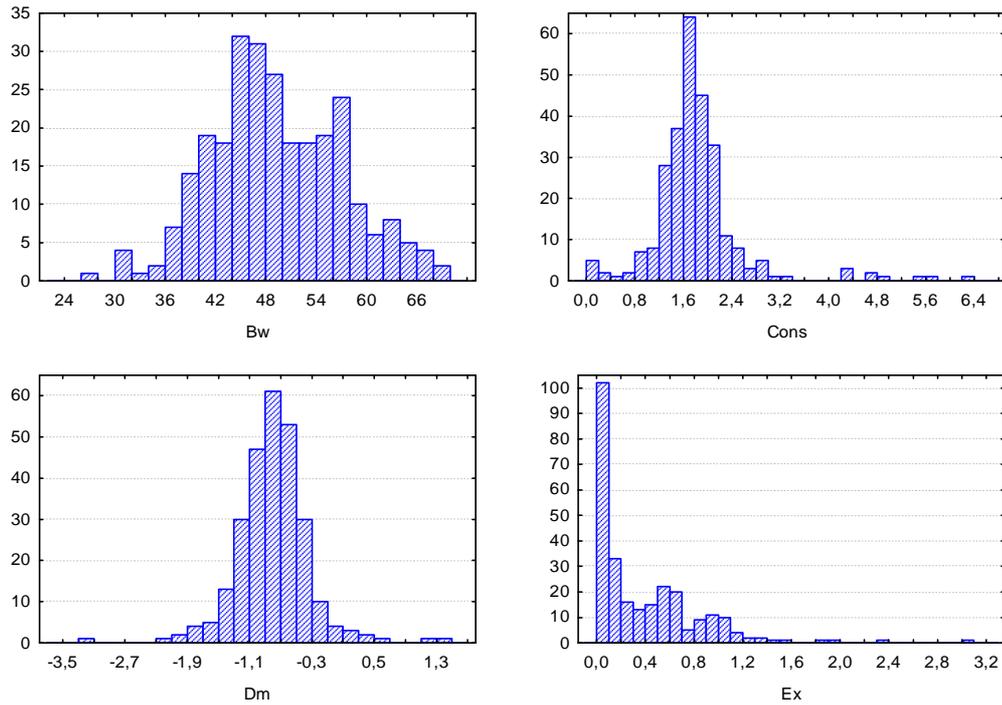
Fig. 1. Characteristics of distribution of body weight (Bw, mg live weight), food consumption (Cons, mg dry weight), change in body weight (Dm, mg live weight in 24 hours) and formation of faeces (Ex, mg dry weight): ordinate – number of observations
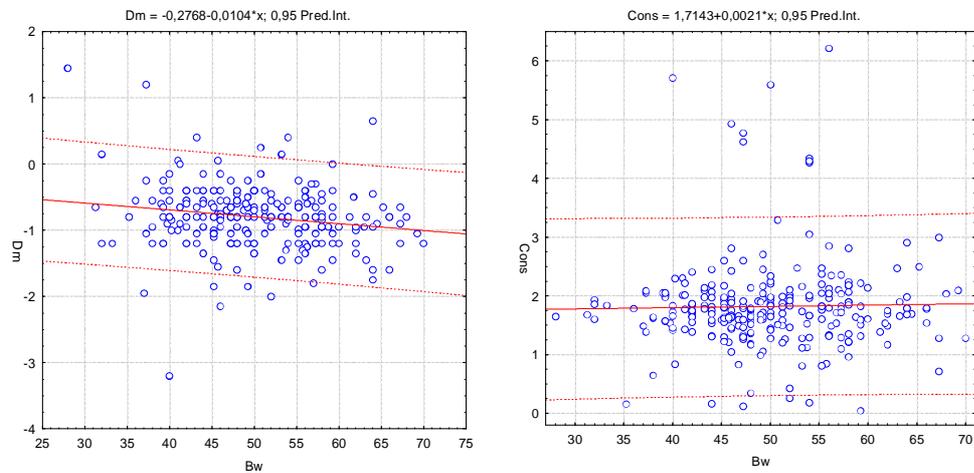

Fig. 2. Dependence of change in body weight (Dm, mg live weight in 24 hours) and food consumption (Cons, mg dry weight) on body weight of beetles in the experiment (Bw, mg live weight)
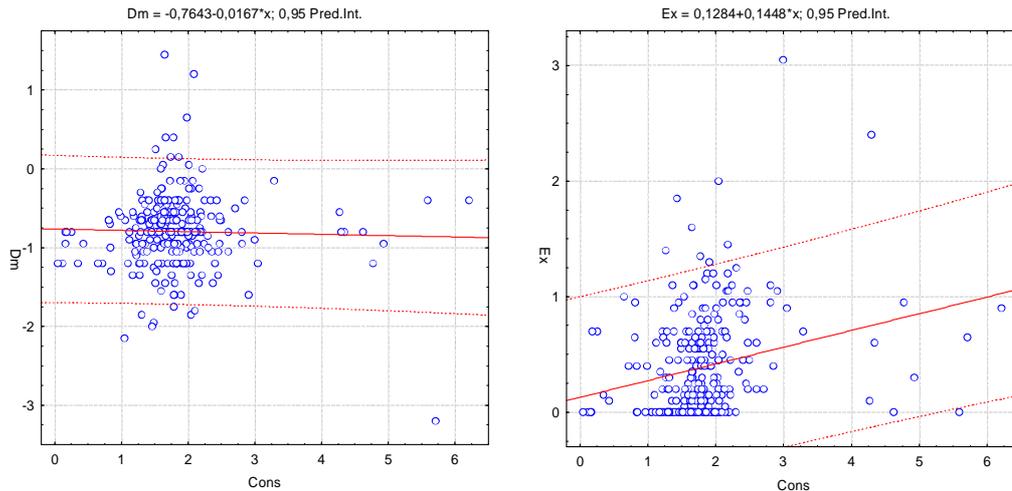
Fig. 3. Dependence of change in in body weight (Dm, mg live weight in 24 hours) and formation of faeces (Ex, mg dry weight) on food consumption (Cons, mg dry weight)

ity of leaf microorganisms), and on the other hand – with consumption and digestion of food in the course of the experiment itself.

When beetles were fed on *U. minor*, *P. quinquefolia*, *C. arborescens*, *V. opulus*, *E. angustifolia*, *P. alba* and *M. alba*, the median of the mass of excreted faeces was equal to 0 mg. For variants of experiments with *S. alba*, *A. vulgaris*, *P. suffruticosa*, *M. domestica*, *R. idaeus*, *S. nigra*, *R. cathartica*, *R. pseudoacacia*, *P. nigra* the amount of faeces was minimal (0.06–0.20 mg/day). For *C. vulgaris*, *C. monogyna*, *Ph. coronarius*, *P. spinosa*, *V. vinifera*, *A. negundo*, *J. regia*, *A. vulgaris*, *C. mas*, *A. platanoides* excretory activity of *O. sabulosum* stayed at the medium level of (0.35–0.60 mg/day). Maximum values of intensity of faecal formation were observed with *P. cerasifera*, *T. cordata*, *R. nigrum*, *P. avium*, *M. nigra*, *Q. robur* and *U. laevis* (0.62–0.95 mg/day).

Therefore, excretory activity of *O. sabulosum* when fed on leaves of various trees, shrubs and liana plants varied by a wide range: from 0 mg/day in each of the 8 experimental containers with beetles for *M. alba*, *P. alba*, *E. angustifolia*, *P. quinquefolia*, to 0.95 mg for *P. cerasifera*. In certain containers very significant variations in excretion of faeces by the beetles were observed: for *M.*

nigra – to 3.05 mg/day, for *C. monogyna* – to 2.00, for *Q. robur* – to 1.85, for *V. vinifera* – to 1.60, for *R. nigrum* – to 1.45, *P. cerasifera* – to 1.40 mg/day. The formation of excrement did not significantly change in relation to the rate of food consumption (Fig. 3).

Metabolic values of the studied plant species for *O. sabulosum*

The leaves with the maximum metabolic value for *O. sabulosum* (Table 4) were those of *M. nigra* (1.19), *U. laevis* (0.92), *A. vulgaris* (0.61), *T. cordata* (0.61), *P. cerasifera* (0.56) and *Q. robur* (0.52). A lesser metabolic value for this beetle species was observed with *C. mas* (0.36), *A. platanoides* (0.24), *P. nigra* (0.21), *P. spinosa* (0.21), *R. nigrum* (0.20). The metabolic value of *V. vinifera* (–0.02), *C. monogyna* (–0.02), *R. cathartica* (–0.03), *A. negundo* (–0.04) and *A. vulgaris* (–0.06) was characterized by medium intensity. *M. domestica* (–0.19), *P. suffruticosa* (–0.19), *V. opulus* (–0.27), *M. alba* (–0.28), *S. nigra* (–0.33), *C. arborescens* (–0.44), *S. alba* (–0.56), *R. idaeus* (–0.57), *E. angustifolia* (–0.66), *J. regia* (–0.75), *P. alba* (–0.79) and *U. minor* (–0.79) have practically no metabolic value for *O. sabulosum*. Maximum differences of studied characteristics (values of standard errors in the last column of Table 4) were recorded for *V. opulus* (2.61), *P. nigra* (2.16), *R.*

pseudoacacia (1.62), *P. quinquefolia* (1.51), *P. cerasifera* (1.45), *U. laevis* (1.29) and *M. alba* (1.26). Discrepancies between food consumption, increase in body weight and amount of faeces formed (enhanced or, on the contrary, delayed defecation) are displayed to a greater or lesser extent for half the plant species studied.

DISCUSSION

For any insect specimen, the absolute quantity of food consumed is less significant than the changing of the insect's body weight in response to consumption of any particular food item. In our experiments on all diets *O. sabulosum* beetles showed a decrease in their body weight. This is most likely due to the complete exclusion of access to water (Naidu & Hattingh 1986). However, this restriction was necessary in order to avoid the death of laboratory insects under the influence of parasites and diseases, which often spread among the *O. sabulosum* in laboratory culture due to contact of the imagines with water droplets on the cage walls applied with a spray nozzle (imitation of morning dew), or with water contained in specially equipped water troughs (1–2 ml containers, of up to 4 mm deep).

The excess of each of the studied food items in our experiments allows us to say that the quantity of a food item has less impact on laboratory insects' body weight (in natural conditions the food is available in larger quantities that that required for beetles) than its quality. With no access to any food, *O. sabulosum* beetles' body weight decreased by 1.02 ± 0.27 mg/day (2.05%/day). The keeping of beetles in a container with *J. regia* and *V. opulus* led to more significant loss of body weight (–1.20 and –1.26 mg/day or 2.41 and 2.53%/day, respectively). Probably, leaves of these plant species contain substances causing intoxication of the beetles' organisms.

To the maximum extent, preservation of the original body weight is facilitated by feeding on leaves of *P. nigra*, *R. pseudoacacia*, *M. nigra*, *M. alba* and *A. platanoides* (median of body weight change is –

0.23 – –0.58 mg/day or 0.46–1.17%/day). Litter of these tree species in the composition of leaf and plant litter of forest plantations (except *P. nigra*) may promote preservation of the population of the pest species under study during drought-affected summer periods. In some containers when beetles were fed on dry leaves of the plants under study (see Max in the last column of Table 2) they gained body weight up to 1.5 mg, when kept on *V. vinifera*, 1.2 mg – on *P. suffruticosa*, 0.4 mg – on *P. nigra* and *M. domestica*, 0.2 – *R. pseudoacacia* and *M. alba*, even without any access to moisture.

Delay in defecation of *O. sabulosum* occurred when it was fed on leaves of *P. quinquefolia*, *V. opulus*, *R. pseudoacacia*, *P. nigra*, *M. alba.* This being the case, (1) the first two species featured rather high rates of consumption by beetles, while the three latter plants, on the contrary, showed low rates; (2) feeding on *V. opulus* caused a marked decrease in beetles' body weight, while *R. pseudoacacia* and *P. nigra* increased the weight of beetles' bodies considerably.

The production of excrement significantly differed from the normal distribution, possibly because of the physiological peculiarities of the digestive process in this species in periods of insufficient moisture in their food and consequent delay in defaecation. The statistically significant differences from the normal distribution in food consumption connected with the high positive asymetrical distribution could be explained by the total lack of consumption by beetles in certain containers. The absence of statistically significant asymetries in the distribution of initial body weight and changing body weight during the course of the experiment indicate that the conditions set up in the experiment corresponded to the normal survival conditions for this species.

Enhanced formation of faeces is recorded both at very high rates of food consumption (*U. laevis*), and at low levels thereof (*T. cordata* and *R. nigrum*). At both extremes of food consumption there could be average changes in body weight, as well as those higher or lower than the mean value for the given series of experiments.

It is difficult to make an *a priori* determination of the optimal metabolic value for any *O. sabulosum* individual. For an imago to be maintained at constant weight the metabolic value would have to be zero or close to zero. A positive metabolic value for a beetle at the imago or larval stage of development would correspond to the domination of anabolic processes. For example, at the larval stage of development the main biological objective is to gain weight as quickly as possible. A negative metabolic value corresponds to the domination of catabolic processes at the egg and pupal stages in the insect's life cycle. In this case at the pupal and egg stages the weight decreases, food is not consumed, and àn acceleration in the oxidisation of organic material takes place. The *O. sabulosum* imagines collected for the experiment were mostly two years old, i.e. their weight was constant, and thus for most trophic objects the metabolic value should be close to zero for their optimal survival.

For assessment of the metabolic value we used average normalized characteristics of the 33 plant species used in the experiment for three parameters: food consumption, ñhange in body weight, formation of faeces. Variation in the three parameters for different plant species, for example *V. opulus* (2.68, –2.27 and –1.21) or *T. cordata* (–0.62, 0.68 and 1.76), does not permit the reliable division of the overall data into different groups using the Tukey difference test.

It is difficult to predict which of the plant species studied by us could play the most important role in maintaining the population of this pest in various parts of its range and different ecosystems (Parmenter & Macmahon 1984, Carpaneto & Fattorini 2001). Currently, there is a significant gap between the level of knowledge of the metabolic values of various trophic items for those species ordinarily used in laboratory experiments and those which do not flourish under laboratory conditions, such as *O. sabulosum* (Dolin 1975, Chernej 2005). Darkling beetles *O. sabulosum*, like many other species of the family, are sensitive to changes in humidity, air temperature, and soil characteristics (Medvedev 1968, Kabanov 1977). Our previous experiments demonstrated that *O. sabulosum* lost

their body weight in different ways in the course of relatively long-term feeding on various types of leaf litter (Nazimov & Brygadyrenko 2013). The series of experiments discussed in this paper showed significant differences in consumption of dried leaves of various trees, shrubs and liana plants. We consider the method of rating of various characteristics of the laboratory insects proposed in this paper to be reasonably efficient, and suggest the use of this method for evaluating the potential trophic niches (Chernyshev 1996) of other invertebrates.

We have observed that consumption of the green parts of plants (even in dry form), which contain the complete range of low and high molecular food compounds, allows us to identify within certain limits the degrees of this beetle species' preference for green leaves of different species. According to our observations, *O. sabulosum* is capable of climbing stems in search of food to a considerable height – up to 1 meter. This enables them to feed on the leaves of young trees and shrubs. It is mentioned in the literature (Dolin 1975) that this species of darkling beetles prefers to utilise decaying parts of plants as a source of moisture, though our previous research does not allow us to be confident on this point insofar as it has yielded contrary results. The authors of this report appreciate that trees and shrubs provide less metabolic value for *O. sabulosum* than grasses do. However, as this weaker aspect is not negligible and is seriously under-researched, our investigation is intended to construct a more adequate system of the trophic relations of *O. sabulosum* with tree and shrub species.

For species with a wide range of food items, feeding on some of them leads to accumulation of body weight (increases anabolism), while feeding on others, on the contrary, contributes to its reduction (stimulates catabolism). With a correctly chosen program of experiments and elimination of extraneous environmental effects, it is possible to determine the peculiar features of both potential and implemented trophic niches for individual ecosystems and the invertebrate species which inhabit them.

REFERENCES

Allsopp P.G. 1980. The biology of false wireworms and their adults (soil-inhabiting Tenebrionidae) (Coleoptera): A review. Bulletin of Entomological Research 70: 343-379.

Carpaneto G.M., Fattorini S. 2001. Spatial and seasonal organization of a darkling beetle (Coleoptera, Tenebrionidae) community inhabiting a Mediterranean coastal dune system. Italian Journal of Zoology 68: 207-214.

Chen X., Thompson M.B., Dickman C.R. 2004. Energy density and its seasonal variation in desert beetles. Journal of Arid Environments 56: 559-567.

Chernej L.S. 2005. Zhuki-chernotelki (Coleoptera, Tenebrionidae) (Darkling beetles (Coleoptera, Tenebrionidae)). Naukova Dumka, Kiev (In Russian; abstract in English).

Chernyshev V.B. 1996. Ekologija nasekomykh (Insect Ecology). Moscow University Press, Moskow (In Russian; abstract in English).

Crawford C.S. 1988. Nutrition and habitat selection in desert detritivores. Journal of Arid Environments 14: 111-121.

David J.-F. 1998. How to calculate leaf litter consumption by saprophagous macrofauna? European Journal of Soil Biology 34: 111-115.

De Los Santos A., Montes C., Ramírez L. 1988. Life histories of some darkling beetles (Coleoptera: Tenebrionidae) in two mediterranean ecosystems in the lower Guadalquivir (southwest, Spain). Environmental Entomology 17: 799-814.

Dolin V.G. 1975. Chernotelki – Tenebrionidae [The family of Darkling beetles – Tenebrionidae] In: Vasil'ev, V.P. (Ed.). Vrediteli Sel'skohozjajstvennyh Kul'tur i Lesnyh Nasazhdenij (Pests of Agricultural Crops and Forest Plantations). Urozhaj, Kiev. Vol. 2, pp. 9–21 (In Russian).

Fattorini S. 2011. Insect extinction by urbanization: A long term study in Rome. Biological Conservation 144: 370-375.

Gehrken U., Sømme L. 1994. Tolerance of desiccation in beetles from the High Atlas Mountains. Comparative Biochemistry and Physiology 109A: 913-922.

Jia L., Guo-Dong R., You-Zhi Y. 2013. Descriptions of eleven Opatrini pupae (Coleoptera, Tenebrionidae) from China. ZooKeys 291: 83-105.

Kabanov V.A. 1977. Biologija peschanogo medljaka (*Opatrum sabulosum* L.) v lesostepnoj i stepnoj zonah Evropejskoj chasti SSSR (Biology of *Opatrum sabulosum* L. in the forest-steppe and steppe zones of the European part of the USSR). Nauchnye Doklady Vysshej Shkoly. Biologicheskie Nauki (Scientific Reports of High School. Biological Sciences) 9: 47–53 (in Russian; abstract in English).

Kabanov V.A. 1981. O troficheskih svjazjah polevyh vidov zhukov chernotelok (Tenebrionidae) (On the trophic relations of field species of darkling beetles (Tenebrionidae)). Vestnik Zoologii 4: 82–85 (In Russian; abstract in English).

Kabanov V.A., Sedin I.F. 1981. Biologija polevyh vidov chernotelok Evropejskoj chasti SSSR (Field species Biology of darkling beetles in the European part of the USSR). Fauna i Jekologija Bespozvonochnyh Lesostepnoj Zony. Nauchnye Trudy Kurskogo Pedagogicheskogo Instituta (Invertebrate Fauna and Ecology of the Forest-Steppe Zone. Scientific Papers of the Kursk Pedagogical Institute) 210: 86-93 (In Russian; abstract in English).

Knor I.B. 1975. Life cycles of darkling beetles (Coleoptera, Tenebrionidae) of Tuva. Soviet Journal Ecology 6: 458-461.

Leo P., Soldati F., Soldati L. 2011. A new species of the genus *Opatrum* Fabricius from southeastern Corsica (Insecta: Coleoptera:

Tenebrionidae). Annales Zoologici 61: 277–280.

Medvedev S.I. 1968. Zhuki-chernotelki (Tenebrionidae) (Darkling beetles (Tenebrionidae)). Nauka, Moskow – Leningrad (In Russian; abstract in English).

Miller R.W., Redfern R.E. 1988. Feed additives for control of lesser mealworm (Coleoptera: Tenebrionidae) in poultry broiler houses. Journal of Economic Entomology 81: 1137-1139.

Minoranskij V.A. 1978. Nekotorye osobennosti biologii i povedenija peschanogo medljaka *Opatrum sabulosum* L. (Coleoptera, Tenerionidae) na Severnom Kavkaze (Some features of the biology and behavior of *Opatrum sabulosum* L. (Coleoptera, Tenerionidae) in the North Caucasus). Entomological Review 57: 37-47 (In Russian; abstract in English).

Naidu S.G., Hattingh J. 1986. Water balance and osmoregulation in *Stips stali*, a nocturnal tenebrionid beetle from the Namib Desert. Journal of Insect Physiology 32: 891-896.

Nazimov S.S., Brygadyrenko V.V. 2013. Does saprophagy play a significant role in nutrition of *Opatrum sabulosum* (Coleoptera, Tenebrionidae)? Visnyk of Dnipropetrovsk University. Biology, Ecology 21: 43-50 (In Russian; abstract in English).

Parmenter R.R., Macmahon J.A. 1984. Factors influencing the distribution and abundance of ground-dwelling beetles (Coleoptera) in a shrub-steppe ecosystem: The role of shrub architecture. Pedobiologia 26: 21-34.

Parmenter R.R., Parmenter C.A., Cheney C.D. 1989a. Factors influencing microhabitat partitioning among coexisting species of arid-land darkling beetles (Tenebrionidae): Behavioral response to vegetation architecture. Southwestern Naturalist 34: 319-329.

Parmenter R.R., Parmenter C.A., Cheney C.D. 1989b. Factors influencing microhabitat partitioning among coexisting species of arid-land

darkling beetles (Tenebrionidae): Temperature and water conservation. Journal of Arid Environments 17: 57-67.

Rejnhardt A.N. 1936. Zhuki-chernotelki triby Opatrini Palearkticheskoj oblasti (Darkling beetles of the tribe Opatrini of Palearctic region). Izdatel'stvo AN SSSR Moskow, Leningrad (In Russian; abstract in English).

Rogers L.E., Woodley N.E., Sheldon J.K., Beedlow P.A. 1988. Diets of darkling beetles (Coleoptera: Tenebrionidae) within a shrub-steppe ecosystem. Annals of the Entomological Society of America 81: 782-791.

Semida F.M., Abdel-Dayem M.S., Zalat S.M., Gilbert F.S. 2001. Habitat heterogeneity and altitudinal gradients in relation to beetle diversity in South Sinai, Egypt. Egyptian Journal of Biology 3: 137-146.

Whicker A.D., Tracy C.R. 1987. Tenebrionid beetles in the shortgrass prairie: Daily and seasonal patterns of activity and temperature. Ecological Entomology 12: 97-108.

Wise D.H. 1981. A removal experiment with darkling beetles: Lack of evidence for interespecific competition. Ecology 62: 727-738.