Influence of individual variation in the trophic spectra of *Pterostichus melanarius* (Coleoptera, Carabidae) on the adaptation possibilities of its population

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Abstract

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Data on the selection of food items by *Pterostichus melanarius* (Illiger, 1798) obtained under laboratory conditions are discussed. An average of 40 prey species was offered to each individual during each separate experiment. Individual *P. melanarius* in forest ecosystems in the steppe zone of Ukraine eat zoophages of the I, II, and III orders, phytosaprophages and phytophages. Most ground beetle individuals prefer phytophages (up to 85%) in laboratory experiments, but certain individuals eat mostly zoophages of the II order, which make up more than 90% in their ration. The trophic preferences of *P. melanarius* can be classified into 5 clusters. In each of the clusters, there are representatives of 3 or 4 orders that belong to different trophic groups. One third of *P. melanarius* individuals feed on the representatives of the Lumbricomorpha order, one quarter on prey items from the Coleoptera and Isopoda orders. In 30% of the individuals studied it is difficult to single out a dominant taxonomic group in the feeding spectrum. During our laboratory experiments half the *P. melanarius* individuals selected prey items with a body mass of less than their own weight, others selected prey items that exceeded their own size. No distinct dependence exists between the individual variation in the trophic spectra of *P. melanarius* and their morphometric characteristics. Thus, *P. melanarius* is able to influence differentially various trophic, size-and-weight and taxonomic groups of invertebrate animals, producing a significant effect on the structure of invertebrate animal communities of the leaf litter.

Key words

Carabidae, feeding spectrum, *Pterostichus melanarius*, trophic preference

Introduction

The trophic pressure of a population on its forage base is defined not only by the number of its individuals, but also by the variety of its trophic preferences, the potential breadth of the trophic niche, its ontogenetic changeability, the influence exerted upon it by anthropogenic factors, the seasonal changeability of the number of prey items, etc. Some authors have studied variations in the trophic spectra of vertebrate species. Trophic variation in invertebrates has been studied to a much lesser degree. There are no data even on the breadth of the feeding spectra for the majority of ground beetle species (Thiele, 1977).

The question of the influence of the variety of individual trophic preferences on the resilience of a population as a whole has yet to be analyzed in the modern scientific literature. The increase in the changeabilty of the forage base (seasonal, spatial, multi-year, anthropogenic, etc.) has caused the disappearance of many species of litter zoophages. This process, first and foremost, concerns the family of ground beetles, among which polyphages are the most widespread.

In the conditions of urban agglomerations, the trophic base becomes extremely atrophied, and the size-and-weight structure of the leaf litter fauna becomes simplified. Therefore, adaptation possibilities for most ground beetle species disappear, which leads to the decrease in the number of species of the latter in the litter complexes of city ecosystems; in a typical urban ecosystem only 3–5 species remain, among which one of the most widespread and, at the same time, most ecologically adaptable species in the majority of European city ecosystems is the dominant – *Pterostichus melanarius* (Illiger, 1798). Many studies have been devoted to the ecological peculiarities of the genus *Pterostichus*: feeding ecology (Pollet and Desender, 1985, 1987; Mauremootoa et al., 1995), egg production (Mols, 1987), effects of landscape and ecosystem structure on diversity of beetles (Burel, 1992), dispersal activity (Frampton et al., 1995).

The incidence and activity of *P. melanarius* in arable land have been analyzed by Fadl et al. (1996), Thomas et al. (1998), Fournier and Loreau (2002), Irmler (2003). This species of beetle plays an important role in forest ecosystems (Magura, 2002). The territorial distribution of *P. melanarius* individuals is connected with the numbers of their potential prey (Guillemain et al., 1997). Behavioral and physiological aspects (Plotkin, 1981; Symondson, 1997; Symondson et al., 1999a, 1999b; Lindqvist and Block, 2001; Paill et al., 2002; Raworth et al., 2004; Thomas et al., 2008) and trophic connections (Skuhravý, 1959; Currie and Digweed, 1996; Currie et al., 1996; Johansen, 1997; Lang et al., 1999; Snyder and Wise, 1999; Collins et al., 2002; Prasad and Snyder, 2004) of *P. melanarius* and other species within this genus have been studied fairly thoroughly.

This species of ground beetle is situated at the top of a trophic pyramid. According to the results of our previous research, its individuals are able to eat not only phytophages and saprophages that are constantly or temporarily present in the litter horizon, but also zoophages of different orders (Brygadyrenko and Korolev, 2006; Korolev, 2010; Korolev and Brygadyrenko, 2012a, 2012b). A complex trophic system is formed, which is capable of self-regulating and is, at the same time, extremely changeable in response to the influence of factors of natural and anthropogenic origin. In our opinion, it is this changeability in the functional role of the *P. melanarius* population that allows the species to survive in the extremely unfavorable conditions under which the majority of other ground beetle species disappear.

The mechanisms and methods of avoiding extreme intra species competition in *P. melanarius* rather than the width of the trophic niche demand thorough study. There are certainly insufficient examples of similar research on polyphages with a rather wide feeding spectrum.

The analysis of morphological variation within populations (which has partially been studied in our previous papers) and its connections with the possibility of the existence of individual trophic preferences for this species of polyphage requires special attention. Specific features of the internal and external structure of Carabidae representatives have been widely used for defining trophic connections of ground beetles (Davies, 1953; Skuhravý, 1959; Zhavoronkova, 1969; Forbes, 1983).

In the work by Simchuk and Ivashov (2012) fermentational polymorphism was studied. This secures maximum adaptation of *Tortrix viridana* L. (Lepidoptera, Tortricidae) individuals to a forage plant of a certain genotype with a certain ratio of phenols in the cell juice. Similar studies for phytophages are few, and, as for polyphages, are not known to us at all. Recently molecular-genetic analysis of the gut content of predator invertebrates has been popular (Kitaev et al., 2011). An enzyme-linked immunosorbent assay was applied by Hagler and Naranjo (1997) in predator gut content research. Bacher et al. (1999) have described the development of a monoclonal antibody (MAb) to the hemolymph of fifth-instar larvae of *Cassida rubiginosa* Muell. (Coleoptera, Chrysomelidae) and concluded that MAb can be used as a tool to identify predator-prey interactions and identify the trophic complex of *C. rubiginosa* Muell.

The assessment of trophic specialization by *P. melanarius* individuals is important for making connections between specific features of one and another species of a polyphage population feeding and their adaptation characteristics.

The aim of this paper is to evaluate the degree of influence of variations in the trophic spectra of individual *P. melanarius* on the adaptation abilities of its population.

Material and methods

The study of trophic spectra individual changeability of *P. melanarius*

The series of experiments on the study of the potential of polyphages to eat various species of invertebrates is described in our previous papers (Brygadyrenko and Korolev, 2006; Korolev, 2010; Korolev and Pokchylenko, 2009; Korolev and Brygadyrenko, 2012a, 2012b), but a potential trophic niche has not always been realized for every *P. melanarius* individual. Like vertebrate-panthophages, *P. melanarius* individuals combine different species of trophic objects in a daily ration in a certain way. The literature is completely lacking in data on research techniques for assessing individual trophic spectra of invertebrate-polyphages. For this reason we have had no option but to develop and suggest our own techniques.

The considerable migration capability of this species prevents us assessing the variety of its trophic spectrum under conditions close to reality (an imago migrates for 10–50 m during 24 hours). It is impossible for us to make an experimental plot of this size, that is why insectariums with the size of 30 × 20 cm were used. They were filled with screen soil of 4–5 cm thick from the imago collection sites, and the natural composition of the litter was imitated. The total number of invertebrates offered to all *P. melanarius* individuals was 190 species, which corresponded to the number and types of litter macrofauna species present in *P. melanarius*'s natural habitat in the region under study.

The invertebrates were collected in the Samarskyi pine forest (Novomoskovsk distr., Dnipropetrovsk region). The study of individual trophic preferences of *P. melanarius* was carried out at the Prysamarskyi International Biological Station named after A.L. Belgard. Of course, this species is common in the urban environment of Dnipropetrovsk. However, due to the likelihood of human disturbance to the collection process, we avoided collection in the city and took our specimens from a relatively natural ecosystem.

A total of 16 specimens of *P. melanarius* imago were taken, 3 male (No 6, 15, 16) and 13 females, the experiments being conducted between approximately 12 and 28 July 2010, just before the reproductive season for this species. Each specimen was placed on its own in a separate insectarium and offered live invertebrate prey items over a period of 24 hours. All 16 specimens underwent experiment simultaneously. A total of 10 to 15 of these experiments were conducted for each individual without interruption. Before each experiment each specimen had been fully fed with larvae of *Calliphora vicina* R.-D. Each *P. melanarius* individual was offered on average 40 species of invertebrates during 24 hours, a single specimen of each potential prey item being provided. On average around 35 samples of those 40 species were eaten. The maximum number of invertebrate species offered to any single *P. melanarius* individual in the course of all the 24 hour experiments was 75 (out of the 190 species offered to the 16 *P. melanarius* specimens as a whole). The species composition of prey was determined according to the real species composition of the litter macrofauna in the modeled population of *P. melanarius*. Consumption of a prey specimen was determined by the presence, absence or partially devoured remains of each potential trophic item through carefully examining the contents in the insectarium at the end of every experiment.

A "points" system of assessment was introduced in order to compare the trophic spectra of *P. melanarius* individuals. 100% consumption of a prey item by an individual *P. melanarius* was assessed at 2 points. 1 point was given for the partial consumption by a *P. melanarius* specimen of a prey item (1–99% consumption of the specimen). Minus 1 (–1) point was given when a *P. melanarius* specimen completely ignored a prey item offered. When a potential prey species was absent in an experiment the score of zero was given. The sum total of points obtained in the course of 10–15 experiments was calculated. Individual feeding spectra of 16 *P. melanarius* individuals were analyzed and 6,840 offerings of potential prey species (sub-experiments) were made in the process of the research.

The data obtained was compared with the use of the cluster analysis methods (Statistica 8.0). The summary table enables us to assess the trophic preferences of *P. melanarius* individuals and illustrates divergences of the feeding spectra of separate individuals of the species under research.

The study of the morphometric characteristics of *P. melanarius* individuals

In order to find out the connections between the morphometric characteristics and the specific features of variations in the trophic spectra of *P. melanarius* individuals, measurements were obtained of the morphological parameters of the imagoes whose feeding spectra were studied in laboratory conditions. The size of the beetles was determined with the help a binocular micrometer eyepiece MBS-10. Fourteen (14) measurements were used which characterize linear dimensions of the body sizes of the individuals under research.

The length of the body regions and their components (head, labrum, clypeus, pronotum, elytra) was determined according to the average line of the body.The length of the head was measured from the front edge of the clypeus to the back edge of the head (excluding the mandibles and labrum). Measuring the width of the head and elytra was performed at the widest point. The pronotum was measured at three points (top, bottom, and the widest point). The length of the body was determined from the labrum to the top of elytra, and the height – according to the average line of the metathorax.

Results

The *P. melanarius* individuals studied show a wide divergence in trophic preferences (Fig. 1). The prey items of *P. melanarius* form 5 clusters, each of which comprises the representatives of different groups of soil-and-litter macrofauna. An interesting specific feature of forage feeding by *P. melanarius* is the frequent combination of quite large prey items (*Aporrectodea caliginosa* (Savigni, 1826), *Rossiulus kessleri* (Lohmander, 1927), *Trochosa terricola* Thorell, 1856, *Porcellio scaber* (Latreille, 1804)) with small prey items

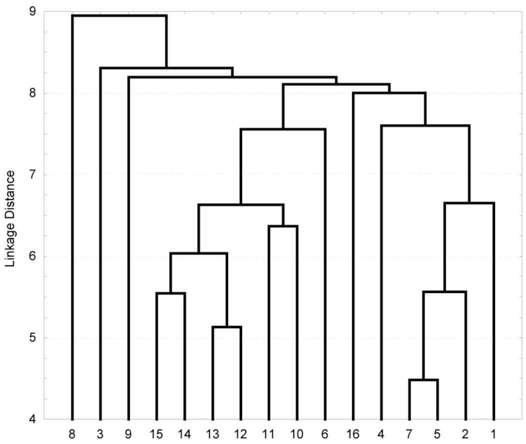

Fig. 1. Grouping of *P. melanarius* individuals according to trophic preferences.

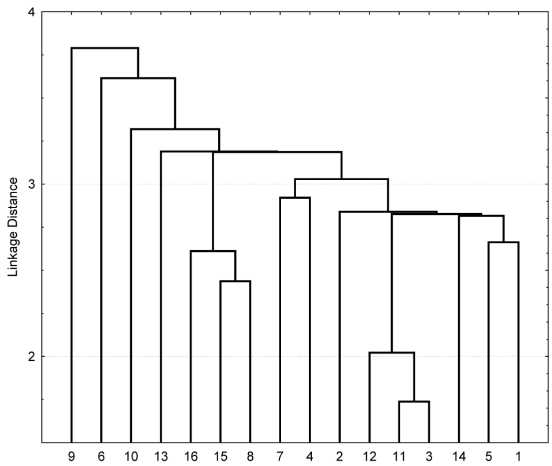

Fig. 3. Groupings of *P. melanarius* individuals based on morphological characteristics.

(*Drusilla canaliculata* (Fabricius, 1787), *Coccinella septempunctata* Linnaeus, 1758, *Bembidion properans* (Stephens, 1829)). It is possible for the representatives of taxons which have rather hard exteriors to be in the same cluster as weakly chitinous objects (Fig. 2). The prey consumption of *P. melanarius* has an almost random character, which is also confirmed by the indiscriminate consumption by the individuals studied of species which belong to different biogeohorizons (inhabitants of litter, soil and herbage).

It has proved impossible to identify any definite clusters of correlation between the trophic specialization of *P. melanarius* individuals and their specific morphological features (Fig. 3). Interestingly, it is impossible to observe even minimum similarity between groups of individuals sharing trophic preferences and the complexes of individuals singled out according to morphological features (see Figs 1 and 3).

For instance, in one cluster of ground beetles, specimen No 1 selected mostly average-sized zoophages,

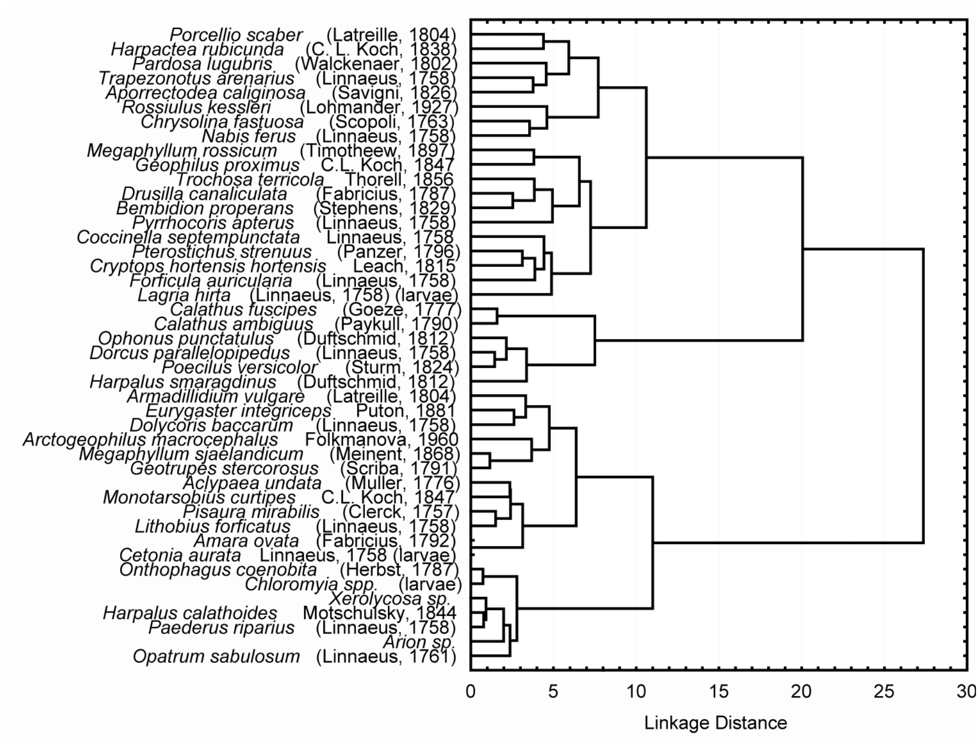

Fig. 2. Cluster analysis of consumption of invertebrate species by *P. melanarius* individuals.

among which the beetles of the Carabidae family, inhabitants of open steppe areas covered with xerophytic vegetation, dominate. At the same time, it is possible to see in the ration of specimen No 14 chiefly large-sized individuals of the Julidae family, which are widespread in a variety of ecosystems. The latter play a primary role in breaking down vegetable organic substances. In another cluster of *P. melanarius*, specimen No 8 consumed large soil-dwelling herbivorous Scarabaeidae larvae, while specimen No 16 preferred small panthophages of the Formicidae family, which are widespread in forest habitats.

The feeding spectra of *P. melanarius* individuals which are similar in morphotype have certain differences. Among invertebrates that were eaten by specimen No 4, phytosaprophages of the Porcellionidae family greatly predominated. They play an active role in breaking down litter and dead wood (Soma and Saito, 1983; Walton, 1987), while *P. melanarius* individual No 7 is characterized by active predation of endogenous Lumbricidae species. Julidae representatives formed an insignificant part of the ration of the both specimens of ground beetles.

In the ration of different *P. melanarius* individuals (average body mass – 214.5 mg) combined by morphological characteristics in one cluster, it is possible to find invertebrates whose weight and size vary widely (Fig. 4). Some *P. melanarius* individuals ate small or average-sized victims (8–511.9 mg), others preferred prey weighing more than 512 mg. Small objects weighing 2–7.9 mg made up an insignificant part (up to 4%) of the ration of specimens No 1–15, while specimen No 16 ate such objects in 34% of cases.

The analysis of the taxonomic structure of invertebrates eaten by *P. melanarius* shows that most of the 16 specimens studied preferred representatives of the Coleoptera, Julida, Isopoda and Lumbricomorpha orders (Fig. 5), to which dominant elements of litter and soil fauna belong. It was observed that some of the *P. melanarius* specimens actively consumed soil pupae of various Lepidoptera species as well as pupae of abundant Formicidae species. This is one of the most abundant groups of the soil-and-litter complex, and its representatives have a very important functional meaning for ecosystems because they take an active part in various environmental processes. A significant percentage of consumption (more than 20%) in the rations of *P. melanarius* specimens No 1, 3 and 5 was made up by fast-moving litter Aranei species (see Fig. 5).

Analysis of the potential prey of *P. melanarius* according to trophic specialization indicates that phytophages, phytosaprophages and zoophages dominate in the rations of individuals of this species (Fig. 6).

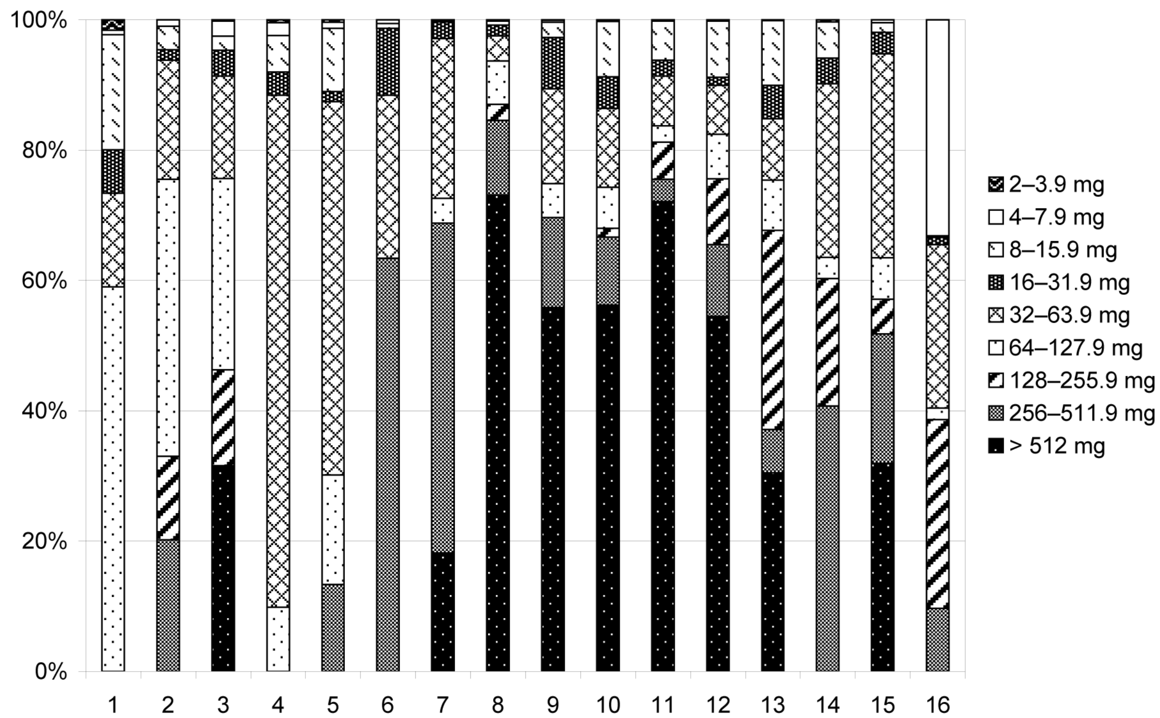

Fig. 4. Size-and-weight structure of the rations eaten by *P. melanarius* individuals under conditions of free choice of trophic objects.

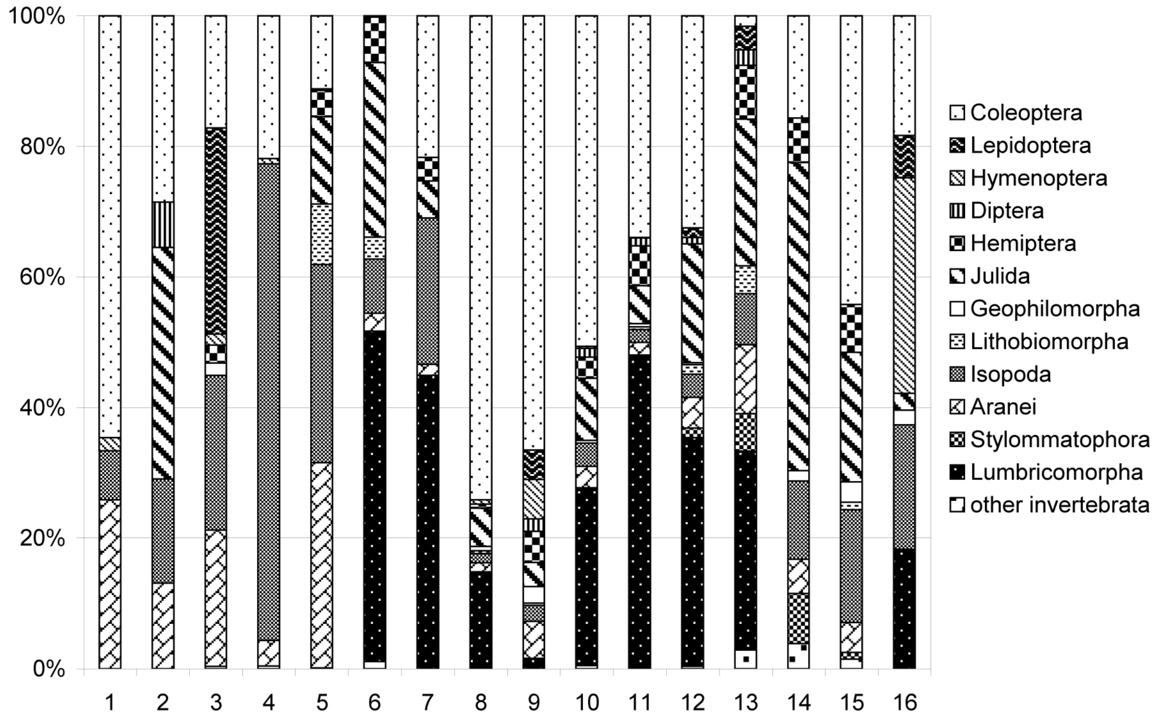

Fig. 5. Taxonomic structure of the rations eaten by *P. melanarius* individuals under conditions of free choice of trophic objects.

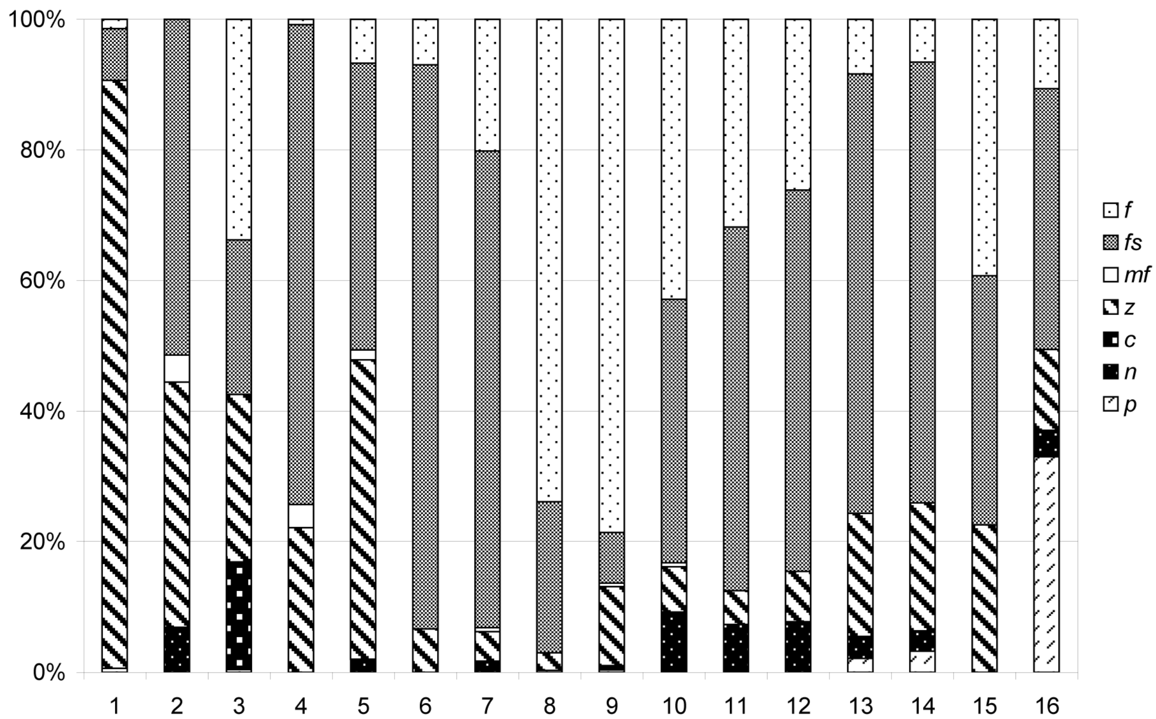

Fig. 6. Taxonomic structure of the rations eaten by *P. melanarius* individuals under conditions of free choice of trophic objects: *f*, phytophages; *fs*, phytosaprophages; *mf*, mixophytophages; *z*, zoophages; *c*, coprophages; *n*, necrophages; *p*, panthophages.

This reveals a strong possibility that the *P. melanarius* population has a strong influence on the formation of the trophic connections of invertebrates at the bottom of the trophic pyramid. The significant percentage of coprophages in the ration of specimen No 3 *P. melanarius* is connected with the occasions of consumption by this individual of fresh *Geotrupes stercorosus* (Scriba, 1791) (Geotrupidae family) corpses. Necrophages in the diet of *P. melanarius* individuals are represented mainly by larvae and puparia of the Calliphoridae and Sarcophagidae families (Diptera) as well as by the Silphidae and Dermestidae families (Coleoptera).

Among invertebrates that make up the base of the feeding spectra of *P. melanarius*, the majority consist of forest forms and habitat generalists (Fig. 7) which are widespread in a variety of biotopes. This testifies to the ecological plasticity and high adaptation possibilities of the population of the ground beetle species under study, which is an integral element of the litter invertebrate communities of most forest ecosystems in Ukraine's steppe zone.

Discussion

Trophic connections of *P. melanarius* have been studied at the level of discrete populations (in a particular field, wood, wetland, etc.). Skuhravý (1959) researched the protein content in the stomachs of this species and found that this beetle has great potential for destruction of agricultural pests. Researchers in the past 20 years (Currie and Digweed, 1996; Currie et al., 1996; Johansen, 1997; Lang et al., 1999; Snyder and Wise, 1999; Collins et al., 2002; Prasad and Snyder, 2004) have developed more modern methods of field investigation, involving such technology as radio-isotope and radio-telemetry. However, field research on the diet of *P. melanarius* has been held back by the limited variety of prey objects at any particular study site (typically about 10–30 species at any site in Ukraine). By studying the trophic spectrum of *P. melanarius* in laboratory conditions we are able to evaluate a much fuller range of potential trophic items.

Our study indicates that in the case of *P. melanarius* there are no groups of individuals clearly differentiated from each other as to trophic specialization. It is astonishing how different individual trophic spectra of *P. melanarius* are with regard to the size groups of their food objects and their taxonomic, trophic, ecosystemic affiliation. However, only 140 species out of 190 studied species of invertebrates were consumed, which is, nevertheless, considerably more than for the other species of ground beetles whose feeding spectra we have studied in laboratory conditions (Brygadyrenko and Korolev, 2006). On the one hand, this is connected with the greater size of *P. melanarius* compared to *P. oblongopunctatus* (Fabricius, 1787), *Harpalus rufipes*

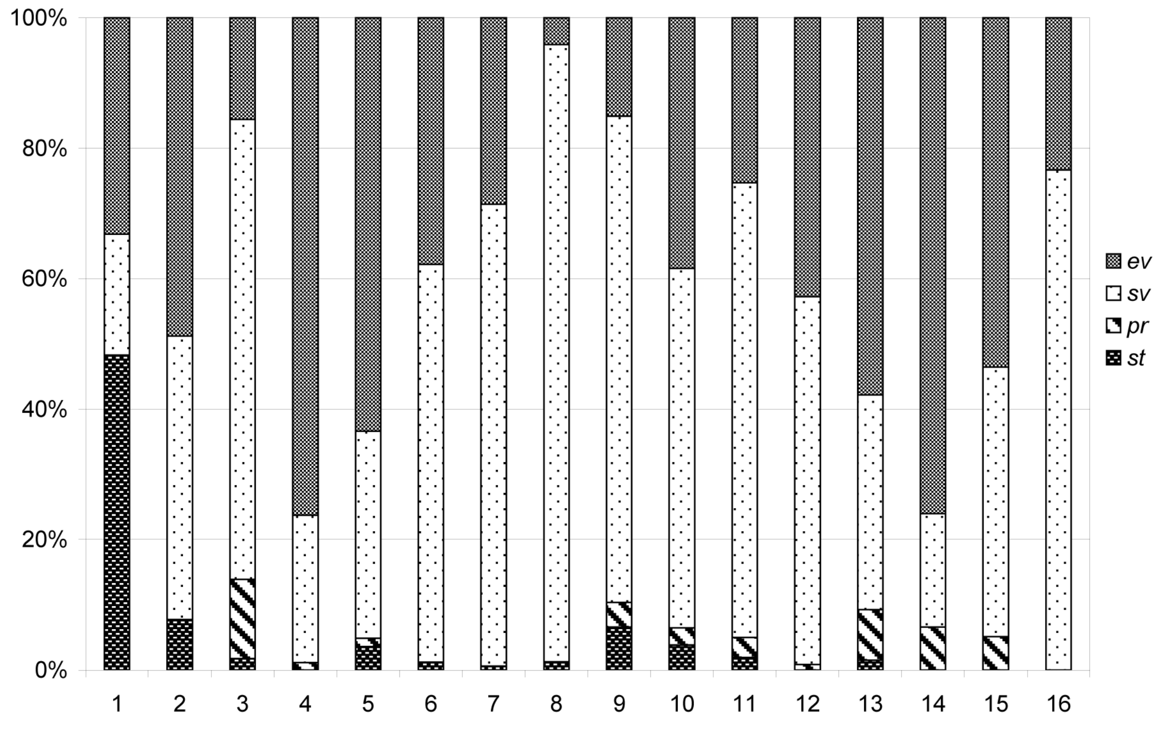

Fig. 7. Ecosystemic structure of the rations eaten by *P. melanarius* individuals under conditions of free choice of trophic objects: *ev*, habitat generalists; *sv*, forest species; *pr*, meadow species; *st*, steppe species.

(De Geer, 1774), *Poecilus versicolor* (Sturm, 1824), *Calathus melanocephalus* (Linnaeus 1758), on the other hand – with the hardness of shells, mobility and the fact that this species belongs to the greatest size-and-weight class in the litter and soil fauna.

Before starting the present research we did not expect to obtain such different trophic spectra for different individuals. The data obtained in the course of experiments provide evidence of the extremely wide trophic preferences of *P. melanarius* compared to other species of ground beetles.

As a result of the ration correlation analysis at the level of orders among 16 *P. melanarius* specimens, only 42 correlation coefficients were found reliable ($P < 0.05$) while 214 correlation coefficients were found to be unreliable. That is, similarity of feeding spectra was registered only in 16.4% of cases. The extremely high percentage of divergence in feeding spectra permits us to state that the variable ration at the individual level is one of the mechanisms by which populations of *P. melanarius* adapt to the conditions of an anthropogenically transformed environment.

Thus, an individual-based approach to tropho-ecological research on ground beetles needs to be extended in order to find the reasons for the extinction of rare species and survival of hardy taxa under the influence of factors of natural and anthropogenic origin (Korolev and Brygadyrenko, 2012a). The ecosystems in which the species with variable individual feeding spectra dominate can probably be considered to be more anthropogenically transformed than the communities in which species with a stable ration dominate.

Conclusions

The *P. melanarius* population that inhabits the forest of Ukraine's steppe zone is situated at trophic level IV in the ecosystem. *P. melanarius* individuals eat zoophages of orders I, II, and III, phyto-saprophages and phytophages as well as panthophages, necrophages and coprophages. Most of the individuals studied preferred phytophages (up to 85%) in laboratory experiments, some individuals consumed predominantly zoophages of order II (zoophages made up over 90% of their ration).

Analysis of the trophic preferences within the *P. melanarius* population reveals 5 clusters, each of which contains representatives of 3 or 4 orders that belong to different trophic groups. A clear association was not found between variation in the trophic spectra of *P. melanarius* individuals and their morphometric characteristics.

In laboratory experiments, half of *P. melanarius* individuals fed on victims with a body mass of less than their own weight while others fed on prey items larger than their own size.

The range of food shows a great variety in taxonomic preferences. One third of the *P. melanarius* specimens studied fed on representatives of the Lumbricomorpha order, one quarter fed on Coleoptera and Isopoda species. It is difficult to single out the dominant taxonomic group in the feeding spectrum in 30% of cases.

Thus, *P. melanarius* is capable of having a differential impact on different trophic, size-and-weight and taxonomic groups of invertebrates. In this manner it influences the structure of soil and litter macrofauna communities.

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