TRAVAUX DU MUSÉUM NATIONAL D'HISTOIRE NATURELLE «GRIGORE ANTIPA»
THE JOURNAL OF "GRIGORE ANTIPA" NATIONAL MUSEUM OF NATURAL HISTORY

Travaux du Muséum National d'Histoire Naturelle "Grigore Antipa" 63 (2): 175–187 (2020)
doi: 10.3897/travaux.63.e54116

RESEARCH ARTICLE

Seasonal dynamics of dominant species of soil predators (Coleoptera: Carabidae, Staphylinidae) in agrolandscapes and their potential gluttony

Fazlitdin Halimov[1]

1 *Department of Biology, Samarkand State University, Uzbekistan*

Corresponding author: Fazlitdin Halimov (xalimov1968@list.ru)

Received 10 May 2020 | Accepted 10 November 2020 | Published 31 December 2020

Citation: Halimov F (2020) Seasonal dynamics of dominant species of soil predators (Coleoptera: Carabidae, Staphylinidae) in agrolandscapes and their potential gluttony. Travaux du Muséum National d'Histoire Naturelle "Grigore Antipa" 63(2): 175–187. https://doi.org/10.3897/travaux.63.e54116

Abstract

We studied the seasonal change in the number of dominant species of predatory beetles on vegetable crops and determined their potential gluttony. A total of 1,472 beetles were collected, belonging to 22 species of ground beetles (Carabidae) and 27 species of rove beetles (Staphylinidae). The dominant species are: *Harpalus rufipes* (De Geer, 1774) (17.6% dominance), *Amara fulva* (De Geer) (13.28%), *Bembidion properans* (Stephens, 1828) (10.39%), *Trechus quadristriatus* (Schrank, 1781) (6.20%), *Calathus melanocephalus* (Linnaeus, 1758) (5.39%), *Poecilus cupreus* Linnaeus, 1758 (5.3%), *Bembidion femoratum* Sturm, 1825 (5.10%), *Aleochara bilineata,* (Gyllenhaal, 1810) (17.6%), *Aloconota gregagia* (Erichson, 1839) (10.21%), *Amischa analis* (Gravenhorst, 1802) (6.01%), *Amischa bifoveotata* (Mannerheim, 1830) (5.41%). During the season, there is a change in dominant species. At the beginning of the season, smaller species dominate, while larger species dominate in the second half of the plant vegetation. The maximum number of predators are observed in June and August. The periods of the maximum abundance of ground beetles and rove beetles do not coincide in time, which is the evolutionary adaptation of two groups of predators that coexist. In laboratory experiments, when pest eggs were offered as food, *Aleochara bilineata* and *Bembidion femoratum* were the most voracious. Larger predator species showed high voracity when larvae of flies were offered as food.

Keywords

Agrolandscape, gluttony, ground beetles, predator, rove beetles, seasonal dynamics

Introduction

One way to increase the effectiveness of biological regulation of pest numbers in agrolandscapes is to preserve and enhance the functional activity of natural entomophagous predators and parasites (Landis et al. 2000). Universal predators with a wide food spectrum can act as an essential component of biological regulation (Symondson et al. 2002; Stiling and Cornelissen 2005).

In agrolandscapes, the most numerous predators are beetles from the families Carabidae and Staphylinidae, which play a very significant role in reducing the number of pests (Edwards et al. 1979; Sunderland and Vickerman 1980; Kromp 1999; Brewer and Elliott 2003; Koval and Guseva 2008).

An essential feature of predatory insects is that, depending on the number of prey, they can move from one species of prey to another and thereby play an important role in regulating the number of several pests (Riechert 1992; Losey and Denno 1998; Cardinale et al. 2003; Snyder et al. 2006). The ability to accumulate and increase the feeding activity of ground beetles in places and regions of mass reproduction of pests shows their importance as entomophagous predators (Winder et al. 2005; Bell et al. 2010).

However, the existence of alternative food sources is also a factor in reducing the effectiveness of predators in regulating specific types of pests. Thus, a high population of aphids in the fields, an alternative food source, reduces predators' effectiveness in killing eggs of harmful flies (Prasad and Snyder 2004).

Factors that negatively affect the effectiveness of predators can also include the consumption of predators by other predators, the characteristics and timing of their development (Rosenheim et al. 1995; Snyder and Ives 2003; Koss and Snyder 2005), the body size of beetles, gluttony, seasonal eating patterns and colonization ability (Lovei and Sunderland 1996; Honek et al. 2006). These circumstances make it difficult to predict the effectiveness of the natural predator population in reducing the number of harmful insects (Symondson et al. 2002; Snyder and Ives 2003).

A study of the trophic links of ground beetles showed that 43% of them are trophically related to pests from the Lepidoptera order, 20% to the pests of the Diptera order, 12% to the Coleoptera order, and 12% to the Hymenoptera order (Sunderland 2002).

Many studies indicate that the effectiveness of ground beetles as exterminators of harmful insects in agrocenoses largely depends on the size of their bodies (Rouabah et al. 2014; Rusch et al. 2015). The size of the body of the predator serves as the determining factor affecting the number of killed victims (Russell et al. 2017).

Other researchers argued that trophic relationships and the functional response of predators largely depend on the ratio of the size of the bodies of predator and prey (Brose 2010; Vucic Pestic et al. 2010; Kalinkat et al. 2011). For ground beetles, as the predator-prey size ratio increases, an increase in the intensity of attack and a decrease in feeding time are observed (Ball et al. 2015). Moreover, even some authors (Finch 1996; Woodward and Hildrew 2002; Honek et al. 2007; Russell et al. 2017) argue that the size of the bodies of ground beetles and other polyphagous predators can predict their eating behavior and voracity. Besides, information about the size of beetles can be effectively used as indicators of many of their features, including the characteristics of seasonal use of their habitat (Russell 2013).

Some laboratory studies have been carried out to study the voracity of certain species of predatory ground beetles, mainly large and medium-sized species, using butterfly larvae or pupa of flies as food, and somewhat contradictory results have been obtained (Voronin et al. 1988; Russell et al. 2017).

However, larger species of ground beetles are few in agrocenoses in comparison with smaller species. Human regulatory activities, in particular, soil cultivation and the use of pesticides have a greater effect on larger species compared to smaller species. Larger ground beetle species are usually associated with natural or semi-natural biocenoses (Blake et al. 1994; Ribera et al. 2001; Kotze and O'hara 2003; Rusch et al. 2013; Winqvist et al. 2014).

Although, in the literature, information about ground beetles is pervasive, specific data on their effectiveness in reducing a particular pest is not sufficient. And the role of rove beetles , which are also a large group in agrolandscapes, is not well understood (Guseva 2017).

The purpose of our research was to study the seasonal dynamics of the dominant species of ground beetles and rove beetles in agrocenoses, as well as to determine their potential gluttony in laboratory studies.

Materials and methods

The studies were carried out on farms in the Samarkand and Taylak districts of the Samarkand region of Uzbekistan in the period 2015–2017. These farms are specialized in vegetable crops. Four agrocenoses of cabbage (varieties Slava 1305 and Toshkent 10), two agrocenoses of potatoes (varieties Sante, Pikasso) and 2 agrocenoses of tomato (varieties Volgograd 5/95 and Vostok-36) were selected. The area of each agrocenosis is not less than 0.5 hectares. In each study area, 10 traps were placed.

To study the relative abundance of dominant species of predatory beetles, soil traps of the Barber-Heydemann type were used (Barber 1931; Heydemann 1955). Glass jars (Karpova and Matalin 1992) with a capacity of 0.5 l and a hole diameter of 72 mm were used as traps (buried in the soil so that the rims were at the level of the soil), they were placed in a line that consisted of 10 jars at a distance of 5 m from each other. Some of the traps were without a retainer, and some contained a fixing liquid. As a fixative, a 4% formalin solution was used, which filled soil traps in 1/3—1/2 of the volume. Traps were sampled once every 7–10 days. The sampled beetles were identified up to the species level, counted and placed in cotton mattresses.

Beetles necessary for laboratory experiments were caught manually or with the help of an exhaustor.

A total of 1,472 beetles were collected.

A series of experiments was carried out to determine the potential gluttony of carnivorous beetles in the laboratory. As a food, predators were offered eggs and larvae of cabbage flies (*Delia brassicae*). In the first series of experiments, beetles were kept in Petri dishes on moistened filter paper. In the experiments, three options were included: in the first version, the predator: prey ratio was 1:20, in the second - 1:50, in the third - 1:100.

The second series of experiments was carried out in special high glassware on the soil layer (the thickness of the soil layer was 2 cm.). This made it possible to more accurately determine the voracity of the studied species. In each dish, two beetles, a female, and a male, were placed. The options were slightly changed: 1st option - 2 beetles : 20 eggs; 2nd option - 2 beetles : 50 eggs; 3rd option - 2 beetles : 100 eggs and an additional 4th option - 2 beetles : 20 larvae. The eaten number of eggs and larvae were counted every day. Uneaten eggs were thrown away and fresh eggs were placed.

Results and Discussion

Seasonal dynamics of dominating kinds of predator beetles

22 species of ground beetles belonging to 14 genera were identified. The dominant species of ground beetles in vegetable agrocenoses are *Harpalus rufipes* (17.6% dominance), *Amara fulva* (13.28%), *Bembidion properans* (10.39%), *Trechus quadristriatus* (6.20%), *Calathus melanocephalus* (5.39%), *Poecilus cupreus* (5.3%), *Bembidion femoratum* (5.10%), *Clivina fossor* L. (4.63%).

From the family Staphylinidae, 27 species belonging to 14 genera were identified. Among the rove beetles, the dominant species are: *Aleochara bilineata* (17.6% dominance), *Aloconota gregagia* (10.21%), *Amischa analis* (6.01%), *Amischa bifoveotata* (5.41%).

The study shows that the diversity of predatory beetles in agrocenoses is not very high. Firstly, the reason for this is the dry and hot climate of the plains of Central Asia and, secondly, the depletion of vegetation caused by the cultivation of a certain culture in agrocenoses. The species of predatory beetles existing in agrocenoses are trophically associated with pests of agricultural crops, which are usually numerous, and therefore the number of predatory beetles of existing species here is relatively high. The quantity of predators differs greatly depending on the season and has two peak periods (Fig. 1).

The first peak of ground beetles is observed in mid-June. During this period, an increase in the number of ground beetles occurs due to the spring species (*Bembidion properans, B. quadrimaculatum, Clivina fossor*, etc.). In the month of

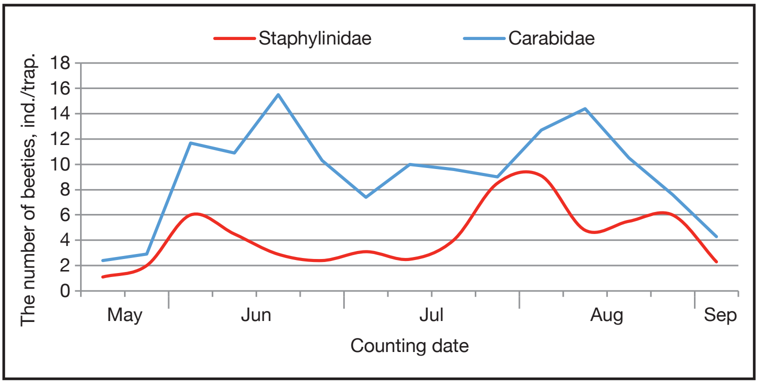

Figure 1. The dynamics of the number of carnivorous beetles (a complex of species) in vegetable fields.

July, a slight decrease in the number of beetles can be observed. The reason for this trend can probably be the dry and hot weather, which, apparently, directly or indirectly (through a decrease in the number of pests that serve as a food for predatory beetles) affects the number of beetles. The second peak in the number of ground beetles is observed in mid-August, due to the high number of summer-autumn species. The same situation was observed for rove beetles. However, their abundance in the surveyed areas was slightly lower in comparison with ground beetles, and also the spring peak of abundance occurs a little earlier, in early June. It should be noted that during the second peak of the number of ground beetles there is a slight decrease in the number of rove beetles. In a nutshell, the peak number of ground beetles and rove beetles does not coincide in time.

The most abundant species among ground beetles is *Harpalus rufipes*. In Uzbekistan, the first individuals of this species appear at the end of March, but they migrate to vegetable crops in early May. Although the *H. rufipes* was present in agrocenoses throughout the growing season, their maximum numbers are observed in late July and early August (Fig. 2). The results coincide with the data treated in the cotton fields of the Tashkent region (Adashkevich and Rashidov 1990). According to Kolesnikov (1984), *H. rufipes* dominates in all agrocenoses of the forest-steppe zone of Ukraine and is especially numerous in July–August.

It should be noted that the structure of the carabidofauna of vegetable fields undergoes significant changes not only in years, but also during one growing season. The terms of the appearance of ground beetles on the field can be divided into spring and autumn species. Spring species from our collections include *Bembidion properans, B. quadrimaculatum, Clivina fossor,* etc. In the first period of plant vegetation, dominant species are species of the genus *Bembidion* (*B. properans, B. quadrimaculatum, B. femoratum*) and *Calathus melanocephalus*. During this period, *B. properans* is most abundant. The maximum abundance of this beetle species is observed in mid-June and amounts to 9 specimens/trap. However, in July their

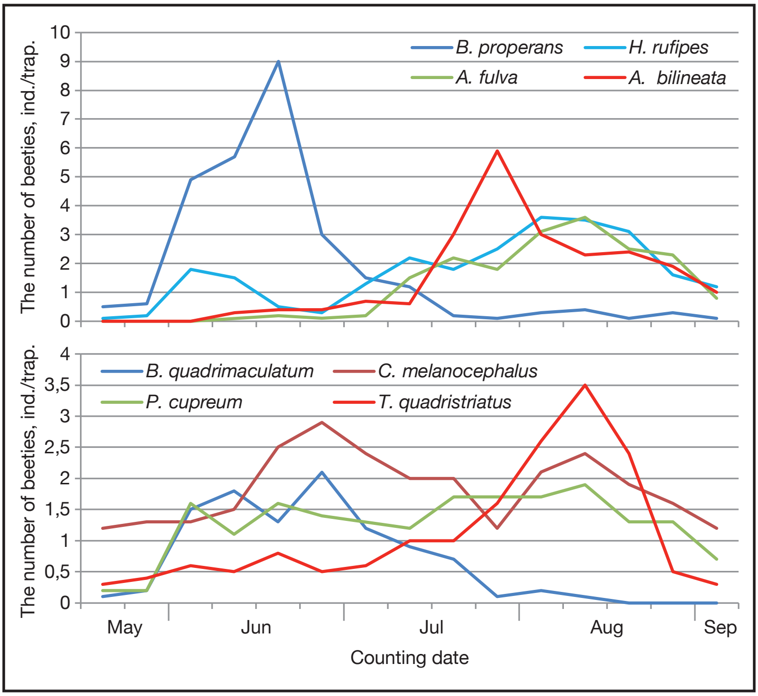

Figure 2. The dynamics of the number of dominant species of carnivorous beetles in vegetable fields.

number decreases to a minimum, but beetles are present in the fields until the end of the plant vegetation. The same trend is observed in the numbers of *Bembidion quadrimaculatum*.

Representatives of the genus *Bembidion* are active in daylight hours, especially on warm sunny days. They are polyphagous predators and play a significant role in reducing the number of eggs and larvae of insect pests.

The greatest abundance of *Calatus melanocephalus* was observed at the end of June, but usually, it retains its relatively high abundance until the end of the season.

Since July, significant changes in the structure of the ground beetles fauna take place in agrobiocenoses. During this growing season in the fields, summer-autumn ground beetle species predominate in numbers: *Harpalus rufipes, Amara fulva, Trechus quadristriatus*, etc.

H. rufipes and *A. fulva* are found in small quantities on vegetable fields in the spring, but a sharp increase in their numbers is observed in early July. Despite the fact that there is a slight decrease in the number of these species in mid-July, their maximum number is noted in early August. The hairy ground beetle (*H. rufipes*) and species of the genus *Amara* are active at night, and in the afternoon they are in the soil.

The decrease in the number of smaller and medium-sized species in late summer and early autumn can be explained by the dominance of larger ground beetles during this period, since large species can readily eat small species (Russell et al. 2017, Prasad and Snyder 2006). This can also explain the mismatch in time of the period of the maximum number of ground beetles and rove beetles. In addition, such rearrangements in the structure of the fauna of carnivorous beetles may be related to their phenological features, since the phenological development of different species differs significantly (Russell 2013). It is also noted that on grain crops and legumes, spring-summer species with daytime activity (*B. properans*, *P. cupreus*) are the most numerous, and on beets, corn, sunflower, summer-autumn species with nighttime activity are more abundant - *Harpalus rufipes*, *Pterostichus melanarius* and others (Kolesnikov 1984).

The most abundant species of Staphylinidae *Aleohara bilineata* in the initial periods of plant vegetation is scarce, but since July there has been an increase in the number of these beetles and, at the end of July, their maximum number has been observed. The low density of *Aleohara* at the beginning of the season is associated with its developmental features. The larva of *A. bilineata* is a parasite of pupae of flies and its appearance in the fields is confined to the appearance of the host pupal stage.

Potential gluttony

The trophic connections of carnivorous beetles on vegetable fields are extensive. Smaller species of ground beetles prefer to eat eggs and larvae of I–II phases of harmful insects (cabbage flies, scoops), and larger ones - older larvae of pests. However, the latter, due to a hidden lifestyle (some are located on the apical part of plants), are usually inaccessible to predatory ground beetles, while they more easily detect egg clutches lying more openly.

Small species of ground beetles, primarily Bembidiini and rove beetles, are most active in the search and extermination of egg-laying pests. Their role is especially high in the extermination of eggs and larvae of younger ages of pests in the first period of plant vegetation, when specialized entomophagous ones are absent on the fields of vegetable crops. Bembidion species: *B. properans, B. quadimaculatum, B. femoratum* and some rove beetles: *Aleachara bilineata, Aloconota gregaria* that expresses feature of predation strongly and willingly feed on eggs and larvae of pests. Although some authors (Ball et al. 2015; Michael et al. 2017) believe that larger species of predators are most effective in exterminating larvae and pupae of pests, it seems to us that small species, destroying pest eggs, make a more significant contribution to biological control, since the destruction of pests in earlier periods of their development is more important from an economic point of view.

Ground beetles, prevailing in numbers during the second period of plant vegetation (*Harpalus rufipes* and species of the genus *Amara*) have a mixed type of nutrition. There are different opinions on the value of ground beetles with a mixed type of nutrition in the literature. While some authors attribute them as harmful species (Kryzhanovsky 1974), others consider them useful (Razumov 1983). In the field, we did not observe damage to plants by these beetles. And in the laboratory, these beetles willingly ate the larvae of the cabbage flies.

A very difficult task is to consider the effectiveness of predators in the field. To clarify the role of predators in the extermination of eggs and larvae of pests in laboratory conditions, a series of experiments were conducted. In the first series of experiments, beetles were kept in Petri dishes on moistened filter paper. *Aleochara bilineata* was the most voracious . With the number of 20 eggs of the pest, the beetles completely destroyed them per day. And with the number of 50 and 100 eggs of the pest, the beetles consumed, on average, 45.66 and 82 eggs per day, respectively (Fig. 3).

Among ground beetles, larger species, *Harpalus rufipes, Bembidion femoratum, Cilivina fossor*, turned out to be the most voracious. The least amount of gluttony was noted in *Bembidion quadrimaculatum*. Four-pointed bembidion beetles killed an average of 7.33 eggs per day with 20 eggs, and with a density of 50 and 100 eggs, 14 and 27.66 eggs, respectively. However, it should be noted that under natural conditions, large species are less willing to eat eggs, in comparison with small species, preferring larger victims.

As the results of the experiment showed, out of the six species of tested predators, only one - *Bembidion properans* - showed a decrease in predator gluttony as the prey population density increased.

In the second series of experiments, in order to bring the conditions closer to the field, the beetles were contained in special glassware with a soil layer. During the experiments, we monitored room temperature and soil moisture. The results obtained were much different from the first series of experiments and the voracity of predators was much lower (Table 1). However, *Aleochara bilineata* was also the most

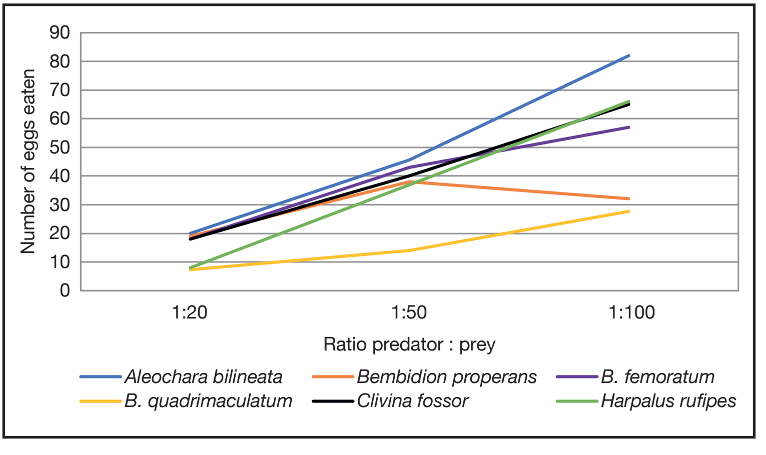

Figure 3. Voracity of predators depending on the density of the prey.

Table 1. Voracity of predators depending on the density of prey in the laboratory.

Predator species	The number of eggs destroyed by one beetle, pcs. Ratio predator : prey		
	2 : 50	**2 : 100**	**2 : 200**
Aleochara bilineata	25.0	49.5	55.7
Bembidion femoratum	24.9	43.0	48.4
Aloconota gregaria	22.2	23.4	30.1
Bembidion properans	21.0	24.5	25.2
Bembidion quadrimaculatum	14.8	18.1	20.66

voracious here. Observations of the behavior of *Aleochara* during feeding showed that with a small number of eggs, beetles bite an egg in the middle, suck out its contents, and then break the egg into pieces. If there are large number of eggs, beetles bite an egg and attack other eggs, without completely eating the first ones. Quite a high gluttony was also observed at *Aloconota gregaria*. Among the bembidion beetles the most voracious was the *Bembidion femoratum*.

When larvae of flies were offered as food to predators, higher voracity was observed in the large species. Each day *Amara fulva* destroyed up to 5.7 larvae of older ages on average per individual, showing the highest gluttony. The number of larvae destroyed by *Harpalus rufipes* averaged 5.4 larvae per beetle. The number of larvae eaten by *Bembidion femoratum* and *B. quadrimaculatum* were 3.5 and 2.7 larvae per beetle, respectively. Least gluttony was observed in *B. properans*, eating only 2.3 larvae per day.

In our experiments, *Trechus quadristriatus* did not feed on eggs of cabbage flies, and *Aloconota gregaria*, having shown rather high voracity in experiments with eggs, refused to feed on the larvae of flies. Apparently, these species under natural conditions have other preferred victims. As it is known, different types of predators are adapted to feeding on different types of prey (Digweed 1993; Penney 1969; Warner et al. 2008).

As the study showed, predators dominating in agrocenoses significantly differ in voracity. Small species are more likely to feed on pest eggs, while larger species prefer insect larvae as food. Although the results of laboratory studies cannot accurately reflect the activities of predators in the field, research shows their importance in reducing the number of pests. Therefore, in the development of a biological control strategy, it is necessary to take into account both functional features and seasonal changes in the structure of the predator fauna.

References

Adashkevich BP, Rashidov MI (1990) Hlopkovaya sovka i ee entomofagi na tomatah v Uzbekistane [Cotton scoop and its entomophages on tomatoes in Uzbekistan]. V: Biologicheskij metod borby s vreditelyami ovoshchnyh kultur [Biological method of pest control of vegetable crops]: Agropromizdat, Maskva, pp. 133–143. [in Russian]

Ball SL, Woodcock BA, Potts SG, Heard MS (2015) Size matters: body size determines functional responses of ground beetle interactions. Basic and Applied Ecology 16(7): 621–628.

Barber HS (1931) Traps for cave-inhabiting insects. Journal of the Elisha Mitchell Scientific Society 46(2): 259–266.

Bell JR, King RA, Bohan DA, Symondson WO (2010) Spatial cooccurrence networks predict the feeding histories of polyphagous arthropod predators at field scales. Ecography 33 (1): 64–72.

Blake S, Foster GN, Eyre MD, Luff ML (1994) Effects of habitat type and grassland management practices on the body size distribution of carabid beetles. Pedobiologia 38: 502–512.

Brewer MJ, Elliott NC (2003) Biological control of cereal aphids in North America and Mediating effects of host plant and habitat manipulations. Annual Review of Entomology 49: 219–242.

Brose U (2010) Body mass constraints on foraging behaviour determine population and food web dynamics. Functional ecology 24(1): 28–34.

Cardinale BJ, Harvey CT, Gross K, Ives AR (2003) Biodiversity and biocontrol: emergent impacts of a multi-enemy assemblage on pest suppression and crop yield in an agroecosystem. Ecology Letters 6(9): 857–865.

Digweed SC (1993) Selection of terrestrial gastropod prey by Cychrine and Pterostichine ground beetles (Coleoptera: Carabidae). Canadian Entomologist 125(3): 463–472.

Edwards CA, Sunderland KD, George KS (1979) Studies of polyphagous predators of cereal aphids. Journal of Applied Ecology 16(3): 811–823.

Finch S (1996) Effect of beetle size on predation of cabbage root fly eggs by ground beetles. Entomologia Experimental et Applicata 8(2): 199–206.

Guseva OG (2017) Rove beetles (Coleoptera, Staphylinidae) in agricultural landscape of Leningrad Region. Plant Protection News 4(94): 39–42.

Heydemann B (1955) Carabiden der Kulturfelder als ekologische Indikatoren. [Carabids of the cultivated fields as ecological indicators]. Berber die 7 Wander Sammlung Deutscher Entomologen, pp. 172–185. [in German]

Honek A, Saska P, Martinkova Z (2006) Seasonal variation in seed predation by adult carabid beetles. Entomologia Experimentalis et Applicata 118(2): 157–162.

Honek A, Martinkova Z, Saska P, Pekar S (2007) Size and taxonomic constraints determine the seed preferences of Carabidae (Coleoptera). Basic and Applied Ecology 8(4): 343–353.

Kalinkat G, Rall BC, Vucic-Pestic O, Brose U (2011) The allometry of prey preferences. PLoS ONE 6(10): e25937.

Karpova VE, Matalin AV (1992) Effektivnost otlova jujelits (Coleoptera, Carabidae) lovushkami Barbera raznogo tipa [Efficiency of catching ground beetles (Coleoptera, Carabidae) with different types of Barber traps]. Biological Sciences 5, pp. 84–88. [in Russian]

Kolesnikov LO (1984) Rasprostranenie i dinamika chislennosti hishchnyh zhuzhelic (Coleoptera, Carabidae) na posevah ozimoj pshenicy pri bezotval'noj obrabotke pochvy v Levoberezhnoj lesostepi USSR [Distribution and dynamics of the number of carnivorous ground beetles (Coleoptera, Carabidae) on winter wheat crops with non-moldboard tillage in the Left-Bank forest-steppe of the Ukrainian SSR]. Abstract of Dissertation for the degree of candidate of Biological Sciences, Poltava, p. 168 [in Russian]

Koss AM, Snyder WE (2005) Alternative prey disrupt biocontrol by a guild of generalist predators. Biological Control 32(2): 243–251.

Kotze DJ, O'hara RB (2003) Species decline - but why? Explanations of carabid beetle (Coleoptera, Carabidae) declines in Europe. Oecologia 135(1): 138–148.

Koval AG, Guseva OG (2008) Structure of ground beetle complexes (Coleoptera, Carabidae) potato agrocenosis under various soil conditions in the North-Western Russia. Entomological Review 87(2): 303–312.

Kryzhanovskij OL (1974) Sem. Carabidae – Zhuzhelicy [Ground Beetles]. Nasekomye i kleshchi - vrediteli sel'skohozyajstvennyh kul'tur [Insects and ticks - pests of crops], Leningrad, Nauka, pp. 8–14. [in Russian]

Kromp B (1999) Carabid beetles in sustainable agriculture: a review on pest control efficacy, cultivation impacts, and enhancements. Agriculture, Ecosystems & Environment 74: 187–228.

Landis DA, Wratten SD, Gurr GM (2000) Habitat management to conserve natural enemies of arthropod pests in agriculture. Annual Review of Entomology 45(1): 175–201.

Losey JE, Denno, RF (1998) Positive predator-predator interactions: enhanced predation rates and synergistic suppression of aphid populations. Ecology 79(6): 2143–2152.

Lovei GL, Sunderland KD (1996) Ecology and behavior of ground beetles (Coleoptera: Carabidae). Annual Review of Entomology 41: 231–256.

Penney MM (1969) Diapause and reproduction in *Nebria brevicollis* (F.) (Coleoptera: Carabidae). Journal of Animal Ecology 38(1): 219–233.

Prasad RP, Snyder WE (2004) Predator interference limits fly egg biological control by a guild of ground active beetles. Biological Control 31: 428–437.

Prasad RP, Snyder WE (2006) Polyphagy complicates conservation control that targets generalist predators. Journal of Applied Ecology 43: 343–352.

Razumov VP (1983) Biologicheskoe obosnovanie kriteriev effektivnosti prirodnyh entomofagov vreditelej kapusty v Volgo-Vyatskom regione Nechernozemnoj zony RSFSR [Biological substantiation of the criteria for the effectiveness of natural entomophages of cabbage pests in the Volga-Vyatka region of the Non-Black Earth Zone of the RSFSR]. Biocenoticheskoe obosnovanie kriteriev effektivnosti prirodnyh entomofagov [Biocenotic substantiation of criteria for the effectiveness of natural entomophages]. VIZR, Leningrad, pp. 55–61. [in Russian]

Ribera I, Doledec S, Downie IS, Foster GN (2001) Effect of land disturbance and stress on species traits of ground beetle assemblages. Ecology 82: 1112–1129.

Riechert SE (1992) Spiders as representative 'Sit-and-wait' predators. In: Crawley MJ (Ed.) Natural Enemies: The Population Biology of Predators, Parasites and Diseases, Blackwell Scientific, pp. 313–328.

Rosenheim JA, Kaya HK, Ehler LE, Marois JJ, Jaffee BA (1995) Intraguild predation among biological-control agents: theory and evidence. Biological Control 5: 303–335.

Rouabah A, Lasserre-Joulin F, Amiaud B, Plantureux S (2014) Emergent effects of ground beetles size diversity on the strength of prey suppression. Ecological Entomology 39(1): 47–57.

Rusch A, Bommarco R, Chiverton P, Oberg PS, Wallin H, Wiktelius S, Ekbom B (2013) Response of ground beetle (Coleoptera, Carabidae) communities to changes in agricultural policies in Sweden over two decades. Agriculture, Ecosystems & Environment 176: 63–69.

Rusch A, Birkhofer K, Bommarco R, Smith HG, Ekbom B (2015) Predator body sizes and habitat preferences predict predation rates in an agroecosystem. Basic and Applied Ecology 16(3): 250–259.

Russell MC (2013) Seasonal activity and feeding patterns of Ground beetles (Carabidae: Coleoptera) in a western Oregon agricultural landscape. In: Habitat Management for Beneficial Insects on Willamette Valley Vegetable and Berry Farms (PhD dissertation). Oregon State University, pp. 90–133.

Russell MC, Lambrinos J, Records E, Ellen FG (2017) Seasonal shifts in ground beetle (Coleoptera: Carabidae) species and functional composition maintain prey consumption in Western Oregon agricultural landscapes. Biological Control 106: 54–63.

Snyder WE, Ives AR (2003) Interactions between specialist and generalist natural enemies: parasitoids, predators, and pea aphid biocontrol. Ecology 84(1): 91–107.

Snyder WE, Snyder GB, Finke DL, Straub CS (2006) Predator biodiversity strengthens herbivore suppression. Ecology Letters 9(7): 789–796.

Stiling P, Cornelissen T (2005) What makes a successful biocontrol agent? A metaanalysis of biological control agent performance. Biological Control 34(3): 236–246.

Sunderland KD, Vickerman P (1980) Aphid feeding by some polyphagous predators in relation to aphid density in cereal fields. Journal of Applied Ecology 17: 389–396.

Sunderland KD (2002) Invertebrate pest control by carabids. The agroecology of carabid beetles. Intercept, Andover, pp. 165–214.

Symondson WOC, Sunderland KD, Greenstone MH (2002) Can generalist predators be effective biocontrol agents? Annual Review of Entomology 47(1): 561–594.

Voronin KE, Shapiro VA, Pukinskaya GA (1988) Biologicheskaya zashchita zernovyh kul'tur ot vreditelej [Biological protection of grain crops from pests]. Agropromizdat, Moskva, p. 197 [in Russian]

Vucic Pestic O, Rall BC, Kalinkat G, Brose U (2010) Allometric functional response model: body masses constrain interaction strengths. Journal of Animal Ecology 79(1): 249–256.

Warner DJ, Allen-Williams LJ, Warrington S, Ferguson AW, Williams IH (2008) Implications for conservation biocontrol of spatio temporal relationships between carabid beetles and coleopterous pests in winter oilseed rape. Agricultural and Forest Entomology 10: 375–387.

Winder L, Alexander CJ, Holland JM, Symondson WO, Perry J, Woolley C (2005) Predator activity and spatial pattern: the response of carabids to their aphid prey. Journal of Animal Ecology 74: 443–454.

Winqvist C, Bengtsson J, Ockinger E, Aavik T, Berendse F, Clement LW, Fischer C, Flohre A, Geiger F, Liira J, Thies C, Tscharntke T, Weisser WW, Bommarco R (2014) Species' traits influence ground beetle responses to farm and landscape level agricultural intensification in Europe. Journal of Insect Conservation 18(5): 837–846.

Woodward G, Hildrew AG (2002) Body size determinants of niche overlap and intraguild predation within a complex food web. Journal of Animal Ecology 71(6): 1063–1074.