Estimation of the Role of Predatory Epigeic Beetles (Coleoptera: Carabidae, Staphylinidae) in Regulation of Pest Population Density in Agroecosystems

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Abstract—Epigeic polyphagous predatory beetles can regulate the pest abundance. The range of population densities at which regulation is possible is specific to each predator-prey subsystem and can be determined experimentally. In the subsystem of ground and rove beetles (Carabidae and Staphylinidae) and the cabbage maggot *Delia brassicae* Bouché and in that of *Carabus hampei* Küst. and the Colorado potato beetle *Leptinotarsa decemlineata* Say, regulation occurs at low pest densities: in the former subsystem, at oviposition rates not exceeding 3 eggs per day per plant, and in the latter, at the pest density varying from 1 to 36 eggs per potato plant. Within these density ranges, both the absolute and relative number of pest individuals eliminated by the predatory beetles increase. The maximum fraction of the pests destroyed by these entomophages is observed at medium prey population densities, which corresponds to functional response of type III (Holling, 1965).

Predator-prey subsystems form a group of well-known regulatory mechanisms acting at the ecosystem level. They regulate population densities and reduce the risk of overpopulation (Odum, 1975).

Arable lands, with their loose soils, a high level of illumination, and abundant trophic resources, provide favorable conditions for life and reproduction of many epigeic ground and rove beetles (Coleoptera: Carabidae, Staphylinidae). Despite the vast literature devoted to the role of epigeic predators, their ability of regulating the density of pest populations in agroecosystems is still being questioned.

Regulation of population density is based on feedback between population density and parameters of natality, mortality, and migration (Viktorov, 1965, 1967). This feedback ensures "compensatory increase or decrease of a given population that neutralize the random fluctuations of its density" (Viktorov, 1967). Howard and Fiske (1911) were the first to subdivide all the mortality factors into density-dependent and density-independent ones. A density-dependent mortality factor increases not only the absolute but also the relative number of individuals eliminated as the population density grows. According to Solomon (1949), of all the density-dependent factors (such as natural enemies, diseases, limited amount of food, and

limited space), the effect of polyphagous predators should be the least dependent on the prey population density since such predators can use alternative sources of aliment. The dependence of the rate of prey consumption by a particular predator species on the prey density is referred to as functional response (Solomon, 1949). The most detailed theoretical analysis of the predator response to the prey population density was performed by Holling (1965), who distinguished three types of functional response, commonly known as Holling's types. Type I corresponds to a linear growth of the number of consumed prey individuals at low densities of the prey population, and is rarely observed in predatory animals. Type II is characterized by an asymptotic growth of the number of consumed prey individuals at increasing density of the prey population. Type III is described by a logistic curve. The differences between these types of functional response are of fundamental importance since they reflect the dynamics of the relative abundance of eliminated prey against the background of the growing population density of the prey. With functional response of type II, the fraction of prey individuals eliminated by predators decreases continuously. With functional response of type III, the fraction of eliminated individuals grows until the S-shaped logistic curve reaches the inflection point, and then gradually

decreases (Holling, 1965). Within a certain range of relative predator and prey densities, functional response of type III can regulate the density of phytophages. Its regulatory and stabilizing effect is determined by the fact that not only the absolute but also the relative number of eliminated prey individuals increases at relatively low prey densities (Solomon, 1949, 1964; Viktorov, 1967; Hassel et al., 1977; Khorkhordin and Losev, 1985; Fernandez-Arhez and Corley, 2003). Functional response of type III stabilizes the dynamics of interacting populations at low values of prey density (Begon et al., 1989).

Predators characterized by functional response of type III, including predatory beetles, deserve special attention as potential factors of regulation of phytophage density. This type of functional response is the necessary condition of the regulatory role of entomophages which do not have a distinct numerical response to the prey population density. It should be noted that in his analysis of functional response of predatory insects of the orders Orthoptera, Heteroptera, and Coleoptera to prey density, Holling (1965) used only the results of laboratory experiments with a single prey species. Many other studies of functional response of predatory invertebrates were also carried out in the laboratory, using only one species of prey (Nakamura, 1977). Under such conditions, the relation between the number of eliminated prey individuals and the prey population density corresponded to functional response of type II in most cases. In the laboratory experiments carried out at the All-Russia Institute of Plant Protection (Klishina, 1983), the number of cabbage fly eggs consumed by the rove beetle *Aleochara bilineata* Gyll. at different densities of the pest population also corresponded to functional response of type II. Holling (1965) himself believed that functional response of type II was typical of invertebrates, whereas the behavioral changes related to switching to the most common prey species (functional response of type III) were mostly characteristic of vertebrates. Later research showed, however, that even the same species of predator could display different types of functional response at different stages of development or under different conditions (in particular, when feeding on prey individuals of different size). For example, adults of the predatory bug *Nabis kinbergii* Reut. feeding on various pests of alfalfa under laboratory conditions displayed functional response of type II, whereas nymphs of the same species revealed response of type III (Siddique and Chapman, 1987). Many researchers

obtained data suggesting the presence of functional response of type III in various arthropods: sac spiders of the family Clubionidae (Mansour et al., 1980), lady beetles of the family Coccinellidae (Hassel et al., 1977), true bugs of the families Nabidae (Siddique and Chapman, 1987) and Miridae (Pazyuk, 2010), and also in parasitic hymenopterans infesting the larvae of various hosts (Burnett, 1958; Takahashi, 1968; Hassel et al., 1977).

It should also be taken into account that the type of functional response may depend on the population density of the predator. This conclusion was based on studying the functional response of caddisflies *Cyrnus flavidus* McLach. feeding on nymphs of the mayfly *Leptophlebia vespertina* L. When the predators were kept singly in Petri dishes, they revealed functional response of type II, whereas at a higher density (6 ind. per Petri dish) they revealed response of type III; this can be explained by a higher efficiency of hunting at high densities of the predator and prey (Ivanov, 2004).

The functional response of even the most common polyphagous predatory beetles of the families Carabidae and Staphylinidae is still insufficiently studied. There is almost no data on the quantitative aspects of interaction between a pest population and the complex of agroecosystem-inhabiting epigeic predators at different densities of the phytophage.

MATERIALS AND METHODS

We have studied the following two subsystems: "the complex of predatory ground and rove beetles (Carabidae and Staphylinidae)—the cabbage root fly *Delia brassicae* Bouché" and "the ground beetle *Carabus hampei* Küst.—the Colorado potato beetle *Leptinotarsa decemlineata* Say." The absolute and relative number of prey individuals eliminated by the predators was assessed in a series of experiments in plots with model plants at different values of the phytophage population density.

The effect of the ground beetle *C. hampei*, which is the dominant predator in many agroecosystems of the lowland Transcarpathia (Gusev and Koval, 1990; Koval, 1999), on survival rates of the Colorado potato beetle in a potato field (Velikaya Bakta, Transcarpathia Province, Ukraine, 1979–1980) was studied using the modified technique of Scherney (1960). The experiments were carried out in test plots with "Temp" potato cultivar varying in size from 1 to 10 m^2 and isolated with polyethylene film; the density of the

predatory beetle was 1–2 ind./m^2. A potato leaf with 1- or 2-day old egg batches of the Colorado potato beetle was glued with gum resin onto each model plant (from 25 to 100 eggs per plant). During this procedure and the subsequent examination of the test plots, all the potato beetles and their eggs that appeared in the plots were removed. The abundance of the Colorado potato beetle was surveyed with intervals of 3 to 7 days, until the beginning of pupation. This technique was described in greater detail in our earlier publications (Guseva and Koval, 2000; Koval, 2009).

The effect of the complex of epigeic predatory beetles on the survival rates of the cabbage root fly was studied in the fields of "Slava 1305" cabbage cultivar in the environs of Pushkin, Leningrad Province, in 1985–1986 (Guseva, 1988). During the experiments, the dominant predators in the agroecosystem were the ground beetles *Bembidion quadrimaculatum* L., *B. properans* Steph., *B. guttula* F. and the rove beetles *Anotylus rugosus* F. and *Aloconota gregaria* Er. The model cabbage plants were isolated from the predators using circular soil traps (Guseva and Koval, 2000). Each trap was made of polyethylene film fixed on a frame of three metal rings in such a way as to form a circular trough 5 cm deep and 2.5 cm wide, with an outer diameter of 20 cm. The trough was filled with 10% glycerol solution to 1/4 its volume and embedded with its rim level with the soil surface. This technique allowed us to compare the number of cabbage fly eggs left on soil near the stems of isolated and non-isolated plants. The number of the eggs consumed by the predators was determined as the difference between the quantities of eggs found near the isolated and non-isolated stems. We used from 17 to 32 circular traps, with control cabbage plants positioned between them. The surveys were carried out with intervals of 1 to 3 days during the entire field season. This technique was described in greater detail in our earlier publication (Guseva and Koval, 2000).

In order to study the seasonal dynamics of abundance of predatory ground and rove beetles in the model fields, examination of the surface soil layer (0 to 5 cm deep) from 10 sample plots measuring 33.3 × 30 cm was carried out every 10–14 days. Altogether, 180 samples were analyzed.

During data analysis, the results were grouped by intensity of oviposition of cabbage flies (less than 10 eggs per day per 10 plants; from 10 to 30 eggs; from 30 to 45 eggs; from 45 to 60; from 60 to 80;

more than 80), and the mean values of the pest density and mortality were calculated for each group. Then, we calculated the absolute number and the fraction (%) of eggs eliminated by one predator in an area of 1 m^2, proceeding from the assumption that given a certain prey density, the number of eliminated prey individuals should be proportional to the number of predators. The mean density of the predators varied from 38.3 to 72.7 ind./m^2.

The coefficients of the equations were determined from the empirical data using the least-squares method. The same method was applied to test the data obtained for their correspondence to functional response of type II or III. The maximum number of prey individuals which could be consumed by one predator was determined in laboratory experiments.

The concentration of a particular predator species near the cabbage plants heavily infested with cabbage root fly eggs was estimated by a special index, as a ratio of predator abundance within a 5 cm radius around the plant stem to their mean abundance per 1 m^2 during the same observation period.

RESULTS AND DISCUSSION

In spite of the different techniques used in our experiments with the Colorado potato beetle and the cabbage root fly, the results obtained were similar. The maximum relative number of pest individuals eliminated by predators was observed at medium prey densities, which corresponded to functional response of type III (Holling, 1965). The dependence between the number of prey individuals eliminated by predators and the prey population density, determined from the field data, was shown to be better described by a logistic curve than by an asymptotic growth curve. The fraction of prey individuals eliminated by predators could be calculated by the equation:

$$Y = (A/X)*(1+\text{EXP}(b-c*\text{LN}(X)))^{-1},$$

where Y is the fraction (percentage) of prey individuals eliminated during the observation period at a predator density of 1 ind./m^2. The duration of the observation period was 1 day in experiments with the cabbage fly eggs, and the entire period from the moment of oviposition to the end of larval development in experiments with the Colorado potato beetle. X is pest population density; in experiments with the cabbage flies this parameter corresponded to the mean

Table 1. The effect of ground and rove beetles on mortality of eggs of the cabbage root fly *Delia brassicae* Bouché at different densities of the pest in cabbage fields (Leningrad Province, 1985–1986)

Mean number of cabbage fly eggs laid on 1 plant in 1 day	Mean fraction of eggs eliminated in 1 day, %	Mean density of predators, ind./1 m^2	Fraction of cabbage fly eggs eliminated by 1 predator in 1 day in an area of 1 m^2, %	
			actual	calculated
0.5	10.3	38.3	0.27	0.15
1.3	30.2	65.7	0.46	0.49
3.7	36.6	50.1	0.73	0.76
5.5	49.9	70.3	0.71	0.63
7.0	26.2	72.7	0.36	0.52
9.4	14.7	52.5	0.28	0.41

number of eggs laid on 1 cabbage plant in 1 day, and in those with the Colorado potato beetle, to the mean number of eggs per 1 potato plant. *A* is the maximum number of prey individuals which can be consumed by a single predator in an area of 1 m^2 during the period of observation; *b* and *c* are coefficients calculated based on the results of field observations.

The following values were obtained for the "ground and rove beetles—the cabbage root fly" subsystem: $A = 4.0$, $b = 2.31$, $c = 2.42$. The corresponding values for the "*Carabus hampei—Leptinotarsa decemlineata*" subsystem were: $A = 20.0$, $b = 6.67$, $c = 1.83$.

The results of field experiments during which the number of cabbage fly eggs remaining on cabbage plants isolated and not isolated from epigeic predators was determined at different densities of the prey and the predator are shown in Table 1. The calculated values of the fraction of pest eggs eliminated by 1 predator in 1 day within an area of 1 m^2 are given in Fig. 1, and the correspondence between the calculated and actual values is shown in Table 1. The mean deviation of the calculated values from the actual ones was +7.6%; the best agreement between these values was observed at medium densities of the pest population.

At low densities of the pest population (with the cabbage fly oviposition rate not exceeding 3 eggs per 1 day per 1 plant), the percentage of eggs eliminated by predators increased abruptly with the prey density. However, after the prey population density exceeded a certain value, the situation changed drastically: the daily percentage of eggs eliminated by predatory ground and rove beetles started to decrease as the prey density grew (Fig. 1). This observation confirms the conclusion of Viktorov (1967) that polyphagous entomophages can regulate the abundance of phytophagous insects at low densities of the prey populations.

The same results were obtained in the "the ground beetle *Carabus hampei*—the Colorado potato beetle" subsystem. The data on survival of eggs and larvae of the Colorado potato beetle in test plots of potato at different initial densities of the pest are shown in Table 2. The calculated values are given in Fig. 2, and the correspondence between the calculated and actual values is shown in Table 2. The mean deviation of the calculated values from the actual ones was –2.2%.

When the pest density was lower than 36 eggs per 1 potato plant, the fraction of eliminated prey individuals increased with the prey density. However, at pest densities exceeding this value, the fraction of prey individuals consumed by the ground beetles decreased. Thus, the ground beetles exerted a regulatory influence on the abundance of the Colorado potato beetle within the pest density range of 1 to 36 eggs per 1 potato plant.
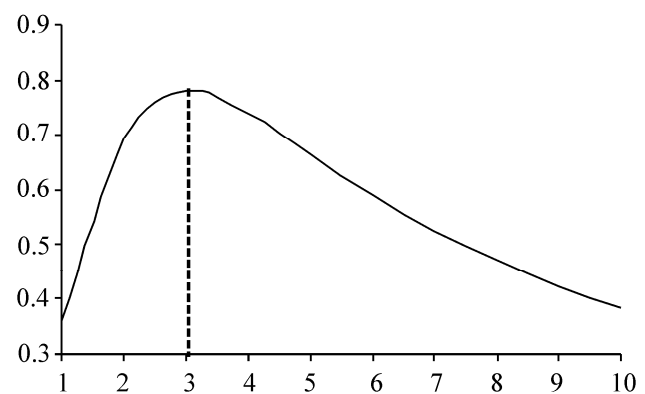

Fig. 1. The fraction of eggs of the cabbage root fly *Delia brassicae* Bouché eliminated by predatory beetles at different rates of oviposition. Abscissa: mean number of cabbage fly eggs laid in 1 day near 1 cabbage plant; ordinate: fraction (%) of the pest individuals eliminated in 1 day at a predator density of 1 ind./m^2. The dashed line drawn from the inflection point of the curve to the abscissa axis marks the density of the pest above which its abundance cannot be regulated by epigeic predatory beetles.

Table 2. The effect of the ground beetle *Carabus hampei* Küst. on mortality of the Colorado potato beetle at different densities of the pest in potato test plots (Transcarpathia, 1979–1980)

Number of pest eggs per 1 potato plant	Mean fraction of pests eliminated, %	Density of ground beetles, ind./1 m²	Fraction of eggs and larvae of the Colorado potato beetle eliminated by 1 ground beetle, %	
			actual	calculated
5	11.0	1.0	11.0	6.3
10	14.4	1.0	14.4	13.5
20	17.2	1.0	17.2	22.3
25	50.4	2.0	25.2	24.6
50	46.8	2.0	23.4	25.1
100	35.0	2.0	17.5	17.3

Analysis of the results of our observations and the data available in the literature has shown that the density-dependent increase in the pest mortality rate due to polyphagous predators can be determined by the following mechanisms.

1. Predator switching to a more abundant species of prey. As the population density of a particular pest increases, the fraction of individuals of polyphagous predators feeding on this prey also increases. Serological testing of the ground beetles *Pterostichus melanarius* Ill. for the presence of cabbage fly proteins showed that the fraction of ground beetles feeding on this particular pest increased with the pest population density (Guseva and Koval, 2010). A similar phe-
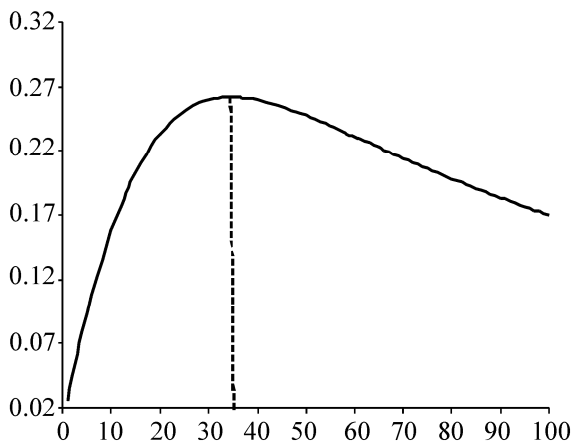
nomenon was observed in *P. melanarius* feeding on the codling moth *Cydia pomonella* L. (Hagley and Allen, 1990) and the Colorado potato beetle (Koval, 2007). Serological testing of a number of common species of ground and rove beetles for the presence of grain aphid proteins, combined with examination of the predators' gut contents, also confirmed that the fraction of individuals feeding on particular pests increased with the population densities of these pests (Sunderland et al., 1987).

2. An increase in the number of species of epigeic predators feeding on the abundant prey species. The ground beetles *Amara plebeja* Gyll., *A. aenea* De Geer, and *Notiophilus biguttatus* F. were found to feed on grain aphids at only high densities of the prey population (Sunderland and Vickerman, 1980). The number of ground beetle species feeding on the Colorado potato beetle was also found to increase depending on the time the pest had been present in the region as well as the pest population density (Koval, 2009).

3. Aggregation of polyphagous predators in areas with higher densities of the pest. This phenomenon, known also as aggregative responses of consumers (Begon et al., 1989), is related to the fact that some predators spend most of their time in the areas of the highest concentration of the prey. For example, rove beetles of the genus *Tachyporus* and larvae of various ground and rove beetles more often occur in test plots with a higher density of aphids (Monsrud and Toft, 1999). Various species of ground and rove beetles also tend to concentrate around the cabbage plants near which eggs of the cabbage root fly have been laid. The mean number of the cabbage fly eggs found within a 5 cm radius from cabbage stems was significantly

Fig. 2. The fraction of individuals of the Colorado potato beetle eliminated by 1 individual of *Carabus hampei* Küst. at different densities of the pest. Abscissa: mean number of eggs of the Colorado potato beetle per 1 potato plant; ordinate: fraction of the pest individuals eliminated by 1 ground beetle *C. hampei* in an area of 1 m² for the entire period of development of the eggs and larvae of the pest. The dashed line drawn from the inflection point of the curve to the abscissa axis marks the density of the pest above which its abundance cannot be regulated by *C. hampei*.

correlated with the index of predator aggregation near these plants. The coefficients of correlation were +0.60 and +0.41 for the ground beetles *Bembidion quadrimaculatum* and *B. guttula*, +0.48 and +0.35 for the rove beetles *Anotylus rugosus* and *Aloconota gregaria*, respectively (Guseva, 1988; Guseva and Koval, 2005).

4. An increase in the fraction of prey individuals damaged (but not immediately consumed) by the predators, in case of excess quantities of prey. The damaged individuals are usually nonviable. The quantitative aspects of this phenomenon were considered only during a study of the functional response of the *Lycosa* and *Pardosa* spiders feeding on adults of *Drosophila melanogaster* Mg. (Nakamura, 1977).

An increasing density of pest populations and the presence of different kinds of food may also affect the long-term dynamics of the predator abundance. In such cases, we are dealing with a numerical response to an increasing population density of certain prey species. For example, the fecundity of the ground beetle *Anchomenus dorsalis* Pont. was the lowest when the beetles consumed only earthworms, higher when they consumed aphids, and the highest on a mixed diet (Bilde and Toft, 1994).

Thus, the prey population density is the most important parameter determining the mode of interaction in the "epigeic predators—prey" subsystem. At low densities of the phytophage populations, the effect of the complex of epigeic polyphagous predators on pest survival rates increases with the pest population densities, ensuring regulation by the negative feedback principle (an increase in not only the absolute number but also the fraction of eliminated pests). It should be noted that the differences between agroecosystems and natural ecosystems "mostly concern the levels at which the population density of harmful and beneficial organisms is regulated" (Vilkova and Tansky, 1994). The density range within which regulation is possible is specific to each particular predator-prey subsystem and may be determined experimentally, as this was done herein by the example of the "ground and rove beetles—the cabbage root fly" and "*Carabus hampei*—*Leptinotarsa decemlineata*" subsystems.

When the population density of the phytophage exceeds a certain level, the regulatory role of polyphagous predators is reduced, whereas other mechanisms, such as specialized entomophages, epizootics, and intraspecific competition, become more significant

(Viktorov, 1967). In case of agroecosystems, pest control measures based on the economic damage thresholds (Tansky, 1997) may also be regarded as regulatory factors. However, preventive treatment of fields with insecticides at the pest densities not exceeding these thresholds should be excluded. When needed, it is more advisable to use selective-action insecticides with the smallest side effect on entomophages, such as biological preparations (bitoxybacillin, etc.) and chitin synthesis inhibitors (Koval, 1986, 1998), and also to grow pest-resistant cultivars which provide the means of long-term regulation of pest abundance (Shapiro et al., 1986). Such measures would create favorable conditions for the natural mechanisms of stabilization of phytophage populations.

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