Impact of ermine moth caterpillar developing time on the dynamics of its hemolymph structure and trophic relations in various biotopes

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The investigation of the hemolymph structure of the ermine moth (*Yponomeuta evonymella* L.) caterpillars developing in different time in various localities for 3 years in turn has proved its dynamics according to which the physiological state and relations with parasitoids and microorganisms of the ermine moth have changed. The physiological state of ermine moth caterpillars developing at any time in a coniferous and mixed forest was always better than in the aldery near a rivulet. The physiological state of ermine moth depends mostly on its caterpillar developing time: the earlier they develop, the stronger physiologically they are, because there is the greatest amount of cells performing a protective function of the organism in their hemolymph, and so the higher percentage of earlier developing moths in the population, the better the possibility for its increase. The earliest developing ermine moth caterpillars in separate years were even 1.4–1.9 times less damaged by the parasitoid *Diadegma armillata* Grav. and 1.3–2.8 times less perished by microorganisms than the latest developing caterpillars (the interval of developing time 16–22 days). The physiological state of the main ermine moth parasitoid *D. armillata* depends on its host physiological state. The weaker the host, the weaker the parasitoid develops in it, but it is less damaged by the superparasitoid *Mesochorus vittator* Zeet. and more frequently perish by microorganisms. So the physiological state of the insect-host is the main index of its relations with parasitoids and microorganisms and the abundance of host population depends on these relations. Thus the physiological state of insects is a basis of exact prognoses of insect abundance and vitality.

Key words: ermine moth *Yponomeuta evonymella* L., caterpillars, developing time, physiological state, hemolymph structure, parasitoids, microorganisms, trophic relations

INTRODUCTION

The development cycle of most insects is very extended, and so in one generation at the same time caterpillars of various instars and even pupae could be found. Such a development at different calendar time without any doubt acts on the insects' organism and could influence the abundance and vitality of their population, because thermal and food quality regimes influence the development synchrony between the insect-host and its parasitoids [1, 13, 15, 25]. Besides, the chemical composition of plant leaves changes with their age. For example, the concentration of tannin in leaves increases with age [20], and so the food quality of earlier developing caterpillars is different from that of later developing caterpillars [10, 18, 21], and food quality tells not only on insect's development but on its relations with parasitoids as well [9, 16, 17, 19, 26]. On low-nitrogen leaves caterpillars develop more slowly and devote more of their time to feeding than on high-nitrogen leaves, and such a prolonged development is one of the main reasons for a higher caterpillar mortality, because the "window of vulnerability" is extended for slow-developing insects [6]. Thus the "slow-growth-high-mortality" hypothesis is correct for many insects with a prolix developmental cycle, because slowly developing caterpillars for a longer period of time are of less instar and so are more often damaged by parasitoids [6, 13]. When caterpillars reach the third instar, they become much less vulnerable to parasitoids' attack through a more intensive mobility and an increased ability of their organisms to encapsulate parasitoid's eggs [4, 8, 12, 22].

The nutritional quality or allelochemistry of the host plant can influence the rate of caterpillar deve-

lopment [2, 9, 20, 21]. According to other authors [2], nicotine had consistent negative effects on tobacco hornworm and its parasitoid *Cotesia congregata* survivorship, adult mass and development time; rutin caused a significant prolongation of development, and hordenine was a feeding inhibitor and changed their development time and size. The amount of all these substances in plant leaves is changing with age.

The growth locality of plants also impacts the feeding quality of leaves: the concentration of nonstructural carbohydrates is lover in shaded plants [20]. It was determined that larval mortality increases and fecundity of females decreases due to a decreased nutritional quality of shaded foliage [21]. Thus, the insect caterpillars developing at different time and in various localities consume leaves with different feeding quality, and that undoubtedly can influence their physiological state.

The physiological state of insects has an influence on their relations with parasitoids and microorganisms: the weaker is insect-host, the more frequently it is parasitised and its mortality from microorganisms is high [3, 4, 23]. Investigation of the insect hemolymph structure enables to ascertain its physiological state, because the hemolymph is one of the main tissues in insect organisms that takes an active part in various vital processes and reacts to all biotic and abiotic factors. Even the slightest metabolic disorder in the organism of an insect reflects, first of all, on its hemolymph, and the percentage ratio of hemocytes in the hemolymph of an insect is not only the main index of the physiological state of an insect [28, 31], but also a very important taxonomic sign of every insect species [26]. The physiological state of insects is a basis of exact prognoses of insect abundance and vitality, and that is especially important in pests control [32]. Besides, the physiological state of insects allows not only to determine the pathogenicity of preparations used in pests control, but also is an important index of environmental pollution [11, 24, 30]. Thus, investigations of the hemolymph are of theoretical and practical significance.

The aim of this work was to analyze the dynamics of hemolymph structure of ermine moth caterpillars developing in various biotopes in different time and to determine what influence it has on the ermine moth trophic relations and on the physiological state of its main parasitoid.

MATERIALS AND METHODS

The studies of the hemolymph structure dynamics of ermine moth (*Yponomeuta evonymella* L.) and its main parasitoid (*Diadegma armillata* Grav.) and its influence on the relations of ermine moth with parasitoids and microorganisms were carried out in three biotopes. The experimental material was collected at different periods of bird-cherry (*Padus racemosa* Schneid.) vegetation in 3 successive years in the same locality. The caterpillars of the final instar and pupae of ermine moth were collected three times a season in the same place with 9–12-day interval in the following biotopes: I – coniferous forest (the preserve of Karoliniškės, Vilnius) where there were many bird-cherry trees in one place: II – locality in an aldery near a rivulet with many bird-cherry trees (the preserve of Karoliniškės, Vilnius); III – mixed forest, where many bird-cherry trees grew on the edge of the forest (Visoriai, a suburb of Vilnius).

The collected nests of ermine moth caterpillars were kept singly in 1.0 litre jars till the moths flew out and fed on the bird-cherry leaves. The cocoons of ichneumonidae *Diadegma armillata* Grav. formed in ermine moth cocoons were watched till the appearance of imago. All other ermine moth parasitoids were also observed till the imago phase. The dead caterpillars and pupae of the ermine moth and its parasitoid *D. armillata* were collected every day and analyzed applying the accepted microbiological methods.

The dynamics of the physiological state of ermine moth and its main parasitoid collected at different times in various localities was estimated according to their hemograms, *i.e*. from their hemolymphatic smears, which were prepared according to the accepted cytological methods. The hemolymph smears were fixed with methyl spirit, dyed by the Gizmsa-Romanowski method and microscoped with a MBI-1 microscope. Classification of hemocytes and their percentage ratio were studied applying the accepted entomological and cytological methods, and the obtained mathematical data were processed by methods of variational statistics [27, 29].

RESULTS AND DISCUSSION

The hemolymph structure of ermine moth *Yponomeuta evonymella* caterpillars collected in various biotopes at different time has proved that the physiological state of moth and its parasitoid *Diadegma armillata* is very dependent not only on the biotope, but on the caterpillar development time as well. The studies of the hemolymph of ermine moth for 3 years in turn in different periods of caterpillar developing showed the dynamics of the hemolymph structure according to which the physiological state of ermine moth and its relations with parasitoids and microorganisms were changing. Diverse changes of the hemolymph structure were established in

various biotopes. When the physiological state of the host changed, the physiological state of its main parasitoid changed too. The physiological state of the host and its parasitoid was ascertained from their hemolymph, which is its main index that reacts most rapidly to all changes in the organism and environment. The amount of cells performing the protective (macronucleocytes and phagocytes) and nutritional (micronucleocytes) functions of the organism and the amount of dead cells in hemolymph determine the physiological state of insects. The physiological state of *Y. evonymella* collected in coniferous and mixed forests was better in all three years of investigation, than of those collected in an aldery near a rivulet, where bird-cherry trees were growing in a shady place. Differences in the physiological state of caterpillars collected in these 3 localities were highly significant every year ($P > 0.01$ or $P > 0.001$). This can be exhaustively explained on the grounds of literature data maintaining that the growth locality of plants impacts on the nutritional quality of foliage [20, 21].

During the three years, the ermine moth population slightly weakened in all localities, which me-

Table 1. **Dynamics of the hemolymph structure of ermine moth *I. evonymella* in three years depending on its caterpillar developing time**

Locality	Year, data	Proleucocytes	Macronucleocytes	Micronucleocytes	Enocytoides	Phagocytes	Dead cells
I	1993						
	V 19	24.0 ± 0.70	28.3 ± 0.37	15.3 ± 0.56	2.1 ± 0.46	27.2 ± 0.46	3.1 ± 0.30
	VI 01	23.3 ± 0.70	26.5 ± 0.40	16.4 ± 0.54	2.4 ± 0.30	26.5 ± 0.48	4.9 ± 0.18
	VI 10	22.1 ± 0.90	25.1 ± 0.46	15.9 ± 0.46	1.8 ± 0.25	25.0 ± 0.49	10.1 ± 0.97
	1994						
	VI 03	23.3 ± 0.67	27.4 ± 0.31	14.8 ± 0.49	1.8 ± 0.33	26.5 ± 0.40	6.2 ± 0.44
	VI 15	22.9 ± 0.72	26.3 ± 0.56	15.4 ± 0.47	1.5 ± 0.37	25.6 ± 0.62	8.3 ± 0.69
	VI 25	21.9 ± 0.71	24.6 ± 0.65	15.4 ± 0.47	1.4 ± 0.27	24.8 ± 0.57	11.9 ± 0.67
	1995						
	VI 12	22.9 ± 0.82	26.3 ± 0.54	14.6 ± 0.50	1.7 ± 0.28	25.2 ± 0.39	9.3 ± 0.52
	VI 19	21.9 ± 0.89	25.4 ± 0.40	15.2 ± 0.57	1.6 ± 0.27	24.3 ± 0.49	11.6 ± 0.69
	VI 26	21.8 ± 0.93	24.8 ± 0.57	15.0 ± 0.61	1.4 ± 0.16	23.6 ± 0.50	13.4 ± 0.58
II	1993						
	V 19	23.4 ± 0.45	26.3 ± 0.17	15.0 ± 0.71	1.9 ± 0.31	25.8 ± 0.47	7.6 ± 0.47
	VI 01	21.4 ± 0.52	25.4 ± 0.27	14.9 ± 0.67	1.8 ± 0.29	24.7 ± 0.42	11.8 ± 0.36
	VI 10	20.1 ± 0.64	23.3 ± 2.36	14.5 ± 0.54	1.6 ± 0.22	22.7 ± 0.73	16.8 ± 1.64
	1994						
	VI 03	22.6 ± 0.49	25.5 ± 0.40	14.4 ± 0.72	1.5 ± 0.31	25.0 ± 0.47	11.0 ± 0.83
	VI 15	20.6 ± 0.52	23.7 ± 0.47	13.9 ± 0.69	1.2 ± 0.29	22.0 ± 0.54	18.6 ± 0.53
	VI 25	19.4 ± 0.45	21.9 ± 0.64	13.6 ± 0.62	0.9 ± 0.23	19.8 ± 0.63	24.4 ± 0.91
	1995						
	VI 12	22.1 ± 0.48	24.8 ± 0.44	14.2 ± 0.73	1.2 ± 0.23	24.5 ± 0.53	13.2 ± 1.09
	VI 19	20.7 ± 0.56	23.6 ± 1.21	13.8 ± 0.59	1.1 ± 0.28	21.7 ± 0.67	19.1 ± 0.59
	VI 26	19.6 ± 0.65	21.2 ± 0.51	13.3 ± 0.42	1.0 ± 0.21	18.7 ± 0.78	26.2 ± 0.79
III	1993						
	V 19	23.3 ± 0.70	27.6 ± 0.30	15.0 ± 0.47	2.3 ± 0.26	26.9 ± 0.31	4.9 ± 0.46
	VI 31	22.4 ± 0.60	26.2 ± 0.36	15.1 ± 0.41	2.2 ± 0.36	25.3 ± 0.42	8.8 ± 0.84
	VI 11	21.7 ± 0.63	25.2 ± 0.51	15.0 ± 0.44	2.0 ± 0.24	24.3 ± 0.54	11.8 ± 1.20
	1994						
	VI 06	21.8 ± 0.71	28.0 ± 0.26	15.9 ± 0.60	2.0 ± 0.29	27.5 ± 0.34	4.8 ± 0.47
	VI 14	21.6 ± 0.65	27.4 ± 0.37	16.6 ± 0.52	1.7 ± 0.26	26.8 ± 0.29	5.9 ± 0.35
	VI 26	20.6 ± 0.69	26.2 ± 0.51	16.3 ± 0.54	1.3 ± 0.15	25.5 ± 0.52	10.1 ± 0.46
	1995						
	VI 13	21.5 ± 0.62	27.0 ± 0.55	15.2 ± 0.51	1.7 ± 0.21	26.0 ± 1.21	8.6 ± 0.69
	VI 21	21.2 ± 0.65	26.3 ± 0.52	15.9 ± 0.43	1.6 ± 0.16	25.3 ± 0.58	9.7 ± 0.65
	VI 27	20.8 ± 0.53	26.1 ± 0.64	15.9 ± 0.38	1.4 ± 0.16	24.7 ± 0.70	11.1 ± 1.38

Note: I – coniferous forest, bird-cherry trees grow in a big area; II – aldery near rivulet with many bird-cherry trees; III – mixed forest.

ans that the amount of protective and trophic hemocytes in its hemolymph had decreased and the amount of dead cells increased (Table 1). During this period the amount of the hemocytes performing the protective function decreased in the hemolymph of the caterpillars collected in coniferous and mixed forests by 1.1–2.0% and the amount of dead cells increased by 1.5–2.9%. These amounts in the hemolymph of the caterpillars collected in the aldery near a rivulet changed by 1.2–3.4%, and 1.5–6.6%, respectively (Table 1). A comparison of the hemograms of the ermine moth caterpillars collected in various localities revealed that in the beginning of the investigation the physiological state was worst of caterpillars collected in the aldery biotope. Caterpillars in this biotope were physiologically weakest also three years later.

During the whole study period, when the physiological state of the ermine moth population was changing, the physiological state of its main parasitoid *Diadegma armillata* and the relations of the ermine moth with its parasitoids and microorganisms were changing too. The physiological state of the parasitoid was directly dependent on the physiological state of the host.

As we see in Tables 1 and 2, during 3 years the physiological state both of the host and parasitoid was the better the earlier the ermine moth caterpil-

Table 2. **Dynamics of the hemolymph structure of parasitoid *Diadegma armillata* Grav. depending on its host's developing time**

Locality	Year, data	Proleucocytes	Macronucleocytes	Micronucleocytes	Phagocytes	Dead cells
I	1993					
	V 19	20.9 ± 0.79	48.8 ± 1.28	24.5 ± 1.02	1.4 ± 0.27	4.4 ± 0.67
	VI 01	20.6 ± 0.80	47.3 ± 1.16	23.7 ± 0.97	0.9 ± 0.23	7.5 ± 0.50
	VI 10	20.3 ± 0.86	46.2 ± 1.18	22.9 ± 0.57	0.7 ± 0.26	9.9 ± 0.67
	1994					
	VI 03	20.3 ± 0.82	48.2 ± 1.16	24.0 ± 0.99	1.2 ± 0.29	6.3 ± 0.67
	VI 15	19.7 ± 0.73	47.4 ± 0.40	23.5 ± 0.97	0.8 ± 0.25	8.6 ± 0.47
	VI 25	19.3 ± 0.71	46.5 ± 1.07	22.9 ± 0.85	0.5 ± 0.22	10.8 ± 0.51
	1995					
	VI 12	20.0 ± 0.80	46.2 ± 1.08	23.4 ± 0.90	1.1 ± 0.26	9.3 ± 0.73
	VI 19	19.8 ± 0.70	45.4 ± 1.01	22.7 ± 1.27	1.0 ± 0.26	11.1 ± 0.61
	VI 26	19.6 ± 0.70	44.5 ± 0.83	22.0 ± 0.73	0.8 ± 0.20	13.1 ± 0.55
II	1993					
	V 19	19.7 ± 0.83	47.4 ± 1.20	23.3 ± 0.94	1.2 ± 0.25	8.4 ± 0.73
	VI 01	18.9 ± 0.78	45.9 ± 1.16	22.5 ± 0.85	0.8 ± 0.20	11.9 ± 0.57
	VI 10	17.7 ± 0.71	43.6 ± 0.92	21.0 ± 0.83	0.2 ± 0.13	17.5 ± 0.65
	1994					
	VI 03	19.4 ± 0.73	46.6 ± 1.15	23.0 ± 0.94	0.9 ± 0.23	10.1 ± 0.72
	VI 15	18.6 ± 0.64	44.6 ± 1.04	22.1 ± 0.98	0.6 ± 0.22	14.1 ± 0.71
	VI 25	16.9 ± 0.69	41.2 ± 0.64	20.8 ± 0.92	0.3 ± 0.15	20.8 ± 1.02
	1995					
	VI 12	19.0 ± 0.74	45.4 ± 0.97	22.5 ± 1.09	0.8 ± 0.25	12.3 ± 0.70
	VI 19	18.4 ± 0.75	43.1 ± 0.86	21.7 ± 0.89	0.6 ± 0.22	16.2 ± 0.63
	VI 26	17.3 ± 0.68	40.3 ± 0.52	19.9 ± 0.59	0.3 ± 0.15	22.2 ± 0.77
III	1993					
	V 20	20.5 ± 0.56	49.1 ± 0.47	24.2 ± 1.05	1.5 ± 0.25	4.7 ± 0.47
	VI 31	20.1 ± 0.59	47.9 ± 1.29	23.8 ± 0.88	1.0 ± 0.30	7.2 ± 0.53
	VI 11	20.0 ± 0.63	46.6 ± 1.30	23.4 ± 0.96	0.9 ± 0.28	9.1 ± 0.81
	1994					
	VI 06	20.3 ± 0.52	48.8 ± 0.95	23.8 ± 0.97	1.3 ± 0.26	5.8 ± 0.53
	VI 14	20.2 ± 0.47	48.6 ± 0.94	23.1 ± 0.89	1.0 ± 0.21	7.1 ± 0.46
	VI 26	19.7 ± 0.49	47.5 ± 0.85	22.9 ± 0.91	0.8 ± 0.20	9.1 ± 0.52
	1995					
	VI 13	19.7 ± 0.52	47.9 ± 0.97	23.2 ± 1.06	1.0 ± 0.30	8.2 ± 0.49
	VI 21	19.7 ± 0.65	47.1 ± 0.94	22.8 ± 0.88	1.0 ± 0.30	9.4 ± 0.50
	VI 27	19.2 ± 0.57	46.7 ± 0.78	22.5 ± 0.78	0.8 ± 0.20	10.8 ± 0.57

Note: Marking of localities is the same as in Table 1.

lars were developing. In the first year in the hemolymph of the earliest developing *Y. evonymella* caterpillars collected in various localities the hemocytes performing the protective function of the organism made up 52.1–55.5%, the trophic cells 15.0–15.3%, and the dead cells 3.1–7.6%, and in the hemolymph of the parasitoid *D. armillata* which was developing in moth caterpillars the numbers were 48.6–50.6% and 23.3–24.5%, respectively.

Caterpillars of *Y. evonymella* that reached the last instar 12 days later and parasitoids developing in them at this time were physiologically weaker, as the percentage ratio of separate groups of hemocytes in their hemolymph was changed: in the hemolymph of hosts collected in various localities the amount of hemocytes performing the protective function was decreased by 2.0–3.0%, in parasitoids' hemolymph by 1.7–2.0%, and the amount of dead cells in host hemolymph increased by 1.8–4.2%, in parasitoids' hemolymph by 1.3–3.5%, (Tables 1, 2).

The physiological state of *Y. evonymella* whose caterpillars reached the last instar still ten days later, was still weaker, and the physiological state of parasitoids developing in such hosts was weaker, too. The amount of hemocytes performing the protective function in the hemolymph of ermine moth caterpillars collected in various biotopes at this time was by 5.0–6.1% less than in the hemolymph of the earliest developing caterpillars and by 2.0–4.1% less than in the hemolymph of the caterpillars that reached such a level of development 10 days before, and the amount of dead cells was larger even 2.2–3.2 and 1.3–2.1 times, respectively (Table 1). The amount of hemocytes performing the protective function of

Table 3. **Dynamics of the physiological state of ermine moth *Yponomeuta evonymella* depending on its caterpillar developing time**

Developing time	Protective cells	t	P	Dead cells	t	P
		Coniferous forest				
1993						
I*	55.5 ± 0.42			3.1 ± 0.30		
II	53.0 ± 0.44	2.65	<0.05	4.9 ± 0.18	3.05	<0.01
III	50.1 ± 0.48	3.11	<0.01	10.1 ± 0.97	4.77	<0.001
Between I and III developing time		5.74	<0.001		6.86	<0.001
1994						
I	53.9 ± 0.36			6.2 ± 0.44		
II	51.9 ± 0.59	1.92	>0.05	8.3 ± 0.69	2.50	<0.05
III	49.4 ± 0.61	2.04	=0.05	11.9 ± 0.67	3.67	<0.01
Between I and III developing time		3.38	<0.01		7.12	<0.001
1995						
I	51.5 ± 0.47			9.3 ± 0.52		
II	49.7 ± 0.45	2.27	<0.05	11.6 ± 0.69	2.67	<0.05
III	48.4 ± 0.53	1.42	>0.05	13.4 ± 0.58	2.02	=0.05
Between I and III developing time		3.22	<0.01		5.25	<0.001
		Aldery near rivulet				
1993						
I	52.1 ± 0.32			7.6 ± 0.47		
II	50.1 ± 0.73	2.27	<0.05	11.8 ± 0.36	7.11	<0.001
III	46.0 ± 1.54	3.05	<0.01	16.8 ± 1.64	2.97	<0.01
Between I and III developing time		4.29	<0.001		5.25	<0.001
1994						
I	50.5 ± 0.43			11.0 ± 0.83		
II	45.7 ± 0.51	4.36	<0.001	18.6 ± 0.53	7.37	<0.001
III	41.7 ± 0.64	3.42	<0.01	24.4 ± 0.91	5.04	<0.001
Between I and III developing time		8.00	<0.001		10.46	<0.001
1995						
I	49.3 ± 0.49			13.2 ± 1.09		
II	45.3 ± 0.94	3.66	<0.01	19.1 ± 0.59	4.18	<0.001
III	39.9 ± 0.69	3.75	<0.01	26.2 ± 0.79	4.49	<0.001
Between I and III developing time		7.83	<0.001		9.92	<0.001

Note: I – the earliest; II – later; III – latest developing caterpillars

the organisms in the hemolymph of the parasitoids *D. armillata* from the latest developing ermine moths was by 3.1–4.8% less compared with these from the earliest developing moths and by 1.3–2.9% less than in the hemolymph of parasitoids from caterpillars developed 10 days before, and the amount of dead cells was larger even 1.9–2.2 and 1.3–1.5% times, respectively (Table 2).

During the next two years in all localities the tendency of changing the hemolymph structure of caterpillars developing at different time was that same: the later the caterpillars developed, the less amount of all types of hemocytes, especially hemocytes performing the protective function of the organism, and the greater amount of dead hemocytes were found in its hemolymph (Table 1). Analogous changes in the hemolymph structure we also observed in the hemolymph of the parasitoid *D. armillata* from ermine moths developing at different time (Table 2). The weaker according to its hemolymph structure was a host, the weaker parasitoid developed in it.

Table 3 shows changes in the physiological state of ermine moth during the period of 3 years depending on its caterpillar development time. As the difference of physiological state of ermine moth in coniferous and mixed forests was negligible during the whole study period ($P > 0.05$), in Table 3 we present data only from coniferous forests. These results show that the dynamics of the physiological state of insects is observable during the development of even one generation of *Y. evonymella* depending on its caterpillar's development time. The earliest developing caterpillars were of the best physiological state in all localities. The later *Y. evonymella* developed, the less amount of hemocytes performing the protective function of the organism and the greater amount of dead hemocytes was found in its hemolymph, showing that moths were physiologically weaker.

Every year the physiological state was best in the earliest developing caterpillars, as the largest amount of protective cells and the least amount of dead cells were found in their hemolymph: in separate years in the hemolymph of caterpillars collected in coniferous forest the amount of hemocytes performing the protective function of the organism made up 51.5–55.5% and dead cells 3.1–9.3%, and in the hemolymph of caterpillars collected in the aldery near a rivulet 49.3–52.1% and 7.6–13.2%, respectively (Table 3). The amount of protective cells in the hemolymph of caterpillars that reached the last instar 10–12 days later in coniferous forest made up 49.7–53.0% and dead cells 4.9–11.6% and in the aldery – 45.3–50.1% and 11.8–19.1%, respectively, the difference in these cells being statistically reliable ($P < 0.05$) and very reliable ($P < 0.01$) (Table 3).

The least amount of protective cells was found in the hemolymph of caterpillars that reached the last instar 8–10 days later: in coniferous forest it made up 48.4–50.1% and in the aldery only 39.9–46.0%. The amount of dead cells in the hemolymph of caterpillars developing at this time was the largest and made 10.1–13.4% and 16.8–26.2%, respectively. Differences in the amount of protective cells in the hemolymph of the earliest and the latest developing caterpillars from various localities were highly significant every year ($P < 0.05$ or $P < 0.01$), and differences in the amount of dead cells were very highly significant ($P < 0.01$ or $P < 0.001$) (Table 3). There is no doubt that caterpillars developing at different time consume leaves of different feeding quality [2, 20, 21]. So, the biochemical changes in plants during their development have an undoubted influence on the physiological state of ermine moth.

Having studied the dynamics of the hemolymph structure of ermine moth developing in different time, we tried to explain to a certain extent its influence on the relations of the insect with its parasitoids and microorganisms. We ascertained that changes of the physiological state of *Y. evonymella* developing in different time were the main reason for its different vitality. Referring to data on the physiological state of *Y. evonymella* developing in different time (Table 3), we established that the later it developed, the weaker it was, and the more often it was damaged by parasitoid *D. armillata* and chalcides and more intensively killed by microorganisms. As we can see in Table 4, during the whole study period in various biotopes even 52.4–86.2% of the earliest developing *Y. evonymella* caterpillars successfully completed their development, while in the latest developing caterpillars only 29.6–74.5% completed it.

As stated above, the earliest developing ermine moth caterpillars during the whole period of study in all localities had the best physiological state (Tables 1 and 3) and so they were even 1.4–1.9 times less damaged by parasitoid *D. armillata* and 1.3–2.8 times less destroyed by microorganisms than the latest developing caterpillars which had the worst physiological state. In separate years in various localities, depending on ermine moth caterpillar developing time, this difference in its damage by *D. armillata* and death from microorganisms was still more expressive (Table 4). This can be based on the published data which show that the stronger the physiological state of an insect, the larger the amount of hemocytes performing the protective function of the organism in the hemolymph. Thus, the eggs laid by

the parasitoid in the host organism are more intensively encapsulated, and the phagocytosis of pathogenic bacteria penetrating into the host organism from the environment is more intensive [5, 7].

The damage of ermine moth caterpillars by chalcides depended on host developing time and locality, and that means that damage of caterpillars by chalcides depended on their physiological state too. The earlier ermine moth caterpillars developed, the less they were damaged by chalcides, however, their amount in one damaged caterpillar was larger than in later developing hosts (Tables 4 and 5). In separate years in various localities there were by 13.9–31.9 individuals of chalcides more in one damaged

Table 4. **Dynamics of trophic relations of *Yponomeuta evonymella* and its parasitoid *Diadegma armillata* depending on moth caterpillar developing time**

Locality	Date	*Yponomeuta evonymella*				*Diadegma armillata*		
		Developed, %	Damage, %			Developed, %	Damage, %	
			D. armillata	Chalcides	Microorganisms		*Mesochorus vittator*	Microorganisms
					1993			
I	V 19	77.5	16.6	3.6	2.3	74.1	22.2	3.7
	VI 01	61.8	25.3	8.0	4.9	77.4	14.3	8.3
	VI 10	60.5	28.0	5.4	6.1	67.6	10.8	21.6
II	V 19	67.0	22.8	6.6	3.6	70.8	22.9	6.3
	VI 01	41.2	32.1	18.1	8.6	74.1	11.1	14.8
	VI 10	38.7	37.6	13.4	10.3	61.4	8.6	24.3
III	V 20	86.2	9.4	1.8	2.5	75.5	20.4	4.1
	V 31	77.3	14.9	4.4	3.4	71.1	18.5	7.4
	VI 11	74.5	18.4	2.8	4.3	61.9	14.3	23.8
					1994			
I	VI 03	70.2	21.3	3.9	4.6	73.3	20.0	6.7
	VI 15	57.3	31.5	5.2	6.0	77.3	13.6	9.1
	VI 25	55.1	34.7	3.1	7.1	65.4	7.7	26.9
II	VI 03	59.2	27.2	6.3	7.3	66.7	16.7	16.6
	VI 15	39.5	37.4	9.8	13.3	70.0	10.0	20.0
	VI 25	33.3	40.2	11.2	15.3	56.7	6.7	36.6
III	VI 06	83.8	10.7	3.0	2.5	66.6	26.7	6.7
	VI 14	75.7	16.5	4.1	3.7	71.9	18.7	9.4
	VI 24	72.8	19.7	2.7	4.8	66.7	14.8	18.5
					1995			
I	VI 12	65.1	26.8	4.6	3.5	63.3	16.7	20.0
	VI 19	54.8	35.7	6.5	3.0	46.7	20.0	33.3
	VI 26	51.7	37.2	6.1	5.0	40.0	13.3	46.7
II	VI 12	52.4	30.7	8.8	8.1	56.7	13.3	30.0
	VI 19	34.2	41.2	13.6	11.0	36.7	13.3	50.0
	VI 26	29.6	43.7	15.4	11.3	30.0	10.0	60.0
III	VI 13	81.5	11.9	4.2	2.4	56.7	26.7	16.6
	VI 21	74.9	18.1	4.9	3.1	52.0	24.0	24.0
	VI 27	70.9	23.4	2.5	3.2	56.7	23.3	20.0

Note: Marking of localities is the same as in Table 1.

earliest developing caterpillar than in one damaged latest developing caterpillar.

Thus the physiological state of an insect-host is the main index in its relations with parasitoids and microorganisms, and on the basis of the data on the hemolymph structure of insects we can forecast their abundance and vitality for the next generation.

Table 5. **Dynamics of chalcides in one damaged ermine moth caterpillar depending on host developing time**

Locality	Date	Average amount of chalcides in one damaged caterpillar	Min and max amount of chalcides in one damaged caterpillar
		1993	
I	V 19	113.2 ± 7.23	80–151
	VI 01	98.6 ± 7.74	61–137
	VI 10	81.3 ± 13.43	41–120
II	V 19	101.3 ± 8.99	58–128
	VI 01	89.4 ± 6.44	51–123
	VI 10	78.2 ± 11.63	36–117
III	V 20	122.4 ± 9.24	79–161
	V 31	110.1 ± 7.30	73–145
	VI 11	91.8 ± 10.70	69–127
		1994	
I	VI 03	95.6 ± 9.67	60–149
	VI 15	86.2 ± 8.74	55–128
	VI 25	78.1 ± 6.30	51–124
II	VI 03	90.5 ± 7.75	52–130
	VI 15	80.2 ± 8.37	47–120
	VI 25	73.8 ± 8.81	41–118
III	VI 06	101.7 ± 8.45	67–155
	VI 14	92.6 ± 8.80	61–138
	VI 24	83.4 ± 8.87	56–128
		1995	
I	VI 12	87.3 ± 6.47	47–125
	VI 19	76.6 ± 6.10	39–101
	VI 26	68.5 ± 5.87	37–99
II	VI 12	84.1 ± 7.16	36–120
	VI 19	74.3 ± 7.53	38–117
	VI 26	65.1 ± 5.77	32–91
III	VI 13	96.2 ± 5.13	67–128
	VI 21	87.8 ± 5.22	56–118
	VI 27	82.3 ± 5.40	49–112

Note: Marking of localities is the same as in Table 1.

As later developing *Y. evonymella* caterpillars were physiologically weaker (Tables 1 and 3), the parasitoid *D. armillata* developing in them was also physiologically weaker (Table 2), but the weaker the parasitoid was, the less it was damaged by the secondary parasitoid *Mesochorus vittator* Zett. and more frequently destroyed by microorganisms. In separate years in various localities, depending on parasitoid's *D. armillata* developing time (interval 16–22 days), its damage by the secondary parasitoid decreased 1.4–2.6 times and killing by microorganisms increased even 2.0–5.8 times (Table 4). The obtained results show that the weaker was the population of a host, the more frequently a shorter chain of trophic relations was observed in it. Thus, the physiological state of the insect-host is the main index of its relations with parasitoids and microorganisms on which the abundance of the population depends. The locality in which ermine moths develop undoubtedly differently influences its physiological state, and that is why in different localities the physiological state of moths is different and the increase or decrease of the population depends on it.

Research of the dynamics of the hemolymph structure of ermine moth caterpillars developing in different time in various biotopes revealed that a very important role in the functioning of the population falls to the first member of the food chain – the plant on which the physiological state of an insect depends.

All these findings show that many biotic and abiotic factors determine the better physiological state of earlier developing moths, and so the higher the percentage of earlier developing moths in the population, the better possibility for its increase. So, the physiological state of the insect not only determines the structure of its trophic relations, but also allows us to estimate the state of its population. Thus, on the basis of data on the dynamics of the hemolymph structure of the insect we are able to forecast its abundance and vitality for the next generation, what is very important in the forecast of pests abundance.

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IEVINĖS VORATINKLINĖS KANDIES VIKŠRŲ VYSTYMOSI LAIKO POVEIKIS JŲ HEMOLIMFOS STRUKTŪROS IR TROFINIŲ RYŠIŲ DINAMIKAI ĮVAIRIUOSE BIOTOPUOSE

S a n t r a u k a

Trejus metus paeiliui atlikti ievinės voratinklinės kandies vikšrų, besivystančių skirtingu laiku ir skirtinguose biotopuose, hemolimfos struktūros tyrimai parodė, kaip kito ievinės kandies fiziologinė būklė, jos santykiai su parazitais ir mikroorganizmais. Ievinės kandies vikšrų, besivystančių bet kuriuo metu spygliuočių arba mišriame miške, fiziologinė būklė visada buvo geresnė negu juodalksnyne prie upelio. Ievinės kandies fiziologinė būklė labiausiai

priklausė nuo jos vikšrų vystymosi laiko: kuo anksčiau vystosi vikšrai, tuo fiziologiškai jie stipresni, nes jų hemolimfoje yra daugiausia ląstelių, atliekančių apsauginę organizmo funkciją. Taigi kuo daugiau anksčiausiai besivystančių vikšrų yra populiacijoje, tuo didesnė galimybė jai didėti.

Kai kuriais metais anksčiausiai besivystantys ievinės kandies vikšrai buvo net 1,4–1,9 karto mažiau pažeisti parazito *Diadegma armillata* ir 1,3–2,8 karto mažiau žuvo nuo mikroorganizmų negu vėliausiai besivystantys vikšrai (vystymosi intervalas 16–22 dienos). Ievinės voratinklinės kandies parazito *D. armillata* fiziologinė būklė priklauso nuo šeimininko fiziologinės būklės. Silpnesniame šeimininke vystosi silpnesnis parazitas, kuris rečiau pažeidžiamas antrinio parazito *Mesochorus vittator*, bet dažniau žūsta nuo mikroorganizmų. Gauti rezultatai rodo, kad pagrindinis vabzdžio-šeimininko santykių su parazitais ir mikroorganizmais rodiklis yra jo fiziologinė būklė ir nuo jos priklauso šeimininko populiacijos gausumas, todėl vabzdžių kenkėjų hemolimfos tyrimai yra tikslių jų gausumo prognozių pagrindas.

Raktažodžiai: ievinė voratinklinė kandis *Yponomeuta evonymella* L., vikšrai, vystymosi laikas, fiziologinė būklė, hemolimfos struktūra, parazitai, trofiniai ryšiai