ISSN 0013-8738, Entomological Review, 2019, Vol. 99, No. 4, pp. 494–503. © Pleiades Publishing, Inc., 2019.
Russian Text © The Author(s), 2019, published in Zoologicheskii Zhurnal, 2019, Vol. 98, No. 5, pp. 525–534.

Parasitoids (Hymenoptera, Eulophidae, Braconidae) as a Mortality Factor for the Aspen Leafminer *Phyllonorycter apparella* (Lepidoptera, Gracillariidae) in Its Outbreak Site in Udmurtia

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Received June 17, 2018
Revised July 17, 2018
Accepted August 8, 2018

Abstract—The assemblage of hymenopteran parasitoids associated with the leafminer *Phyllonorycter apparella* (Lepidoptera: Gracillariidae) developing on the aspen *Populus tremula* L. was studied near Izhevsk in Udmurtia in 2014–2016. Eighteen species (Hymenoptera: Eulophidae and Braconidae) were reared from *Ph. apparella*, four of them (*Pnigalio mediterraneus*, *Sympiesis dolichogaster*, *Chrysocharis phryne*, and *Neochrysocharis formosus*) representing the first records as parasitoids of this pest. Monitoring a steady outbreak site of *Ph. apparella* revealed an annual increase in the number of species in the parasitoid complex: 6 species in 2014, 9 in 2015, and 16 in 2016. Accordingly, the rate of infestation of the leafminer larvae and pupae increased from 7.4 ± 1.4% in 2014 to 19.6 ± 1.6% in 2016. The dominant parasitoid species changed annually. In 2014 there was only one dominant species, *P. circumscriptus* (92.4%); in 2015, two dominants: *M. frontalis* + *C. trifasciatus* (65.6%); in 2016, three species: *C. trifasciatus* + *C. pictus* + *M. frontalis* (59.5%). The percentage of each species declined in subsequent years. The ratio of ecto- to endoparasitoid species was similar in the three years of research: 1 : 1 in 2014, 1 : 1.25 in 2015, and 1.29 : 1 in 2016. The shares of endoparasitoids in 2014, 2015, and 2016 were 95.1, 50.3, and 56.9%, respectively. The role of endoparasitoids in controlling the leafminer was slightly greater than that of ectoparasitoids.

DOI: 10.1134/S0013873819040080

The aspen leafminer *Phyllonorycter apparella* (Herrich-Schäffer, 1855) (Lepidoptera, Gracillariidae) is a Holarctic species occurring in Europe (excluding the south), the Caucasus (Kuznetsov, 1981), Turkey (Tozlu et al., 2002), and Kazakhstan (*Harmful Animals*…, 1949; Shlykov, 1952). In Russia, the species is known in the European part, the Urals, Siberia, and the Amur region (Kuznetsov, 1981). Now it is also widely distributed in the US and Canada (Davis and Deschka, 2001).

Phyllonorycter apparella is a broadly oligophagous species which develops on six species of aspen and poplar in Eurasia (Table 1). Its main host plant is the common aspen *Populus tremula* L., whose distribution area in Eurasia has a total area of 24 320 000 km^2.

The Palaearctic distribution of *Ph. apparella* (Fig. 1) may be conditionally divided into the Central European and the East European-Asian parts.

The leafminer is extremely rare in the Central European part of its distribution area. Not a single specimen of *Ph. apparella* has been found for the last hundred years in Germany (Nuss and Stübner, 2000) or in the

Table 1. Host plants of the aspen leafminer *Ph. apparella* in Eurasia

Country	Host plant species	Reference
Germany	*Populus tremula*	Herrich-Schäffer, 1855
	P. nigra L.	Schütze, 1902
Austria	*P. alba* L., *P. nigra*	Knitschke, 1927
Slovakia	*P. alba*	Kollár, 2007
	P. nigra, *P. simonii* Carr.	Kollár and Hrubik, 2009
Hungary	*Populus* spp., *Salix* spp.	Fazekas and Schreurs, 2014
Poland	*P. tremula*	Vidal and Buszko, 1990
Belarus	*P. tremula*	Sinchuk et al., 2017
Ukraine	*P. tremula*	Lisovii et al., 2017
Russia	*P. tremula*	Tomilina, 1973
	P. alba	Dovnar-Zapolsky and Tomilova, 1978
	P. nigra	Kuznetsov, 1981
	P. pyramidalis Salisb.	Kutenkova, 1989
	Populus spp.	Mishchenko and Zolotuhin, 2003
	Salix alba L.	Olshvang et al., 2004
	Salix spp.	Belskaya and Vorobeichik, 2013; Bayanov et al., 2015; Anikin et al., 2016; Akulov et al., 2018
Turkey	*P. tremula*	Tozlu et al., 2002
Kazakhstan	*P. tremula*	*Harmful Animals*..., 1949; Shlykov, 1952

Czech Republic (Laštůvka and Liška, 2011). Due to the absence of reliable records, the species was excluded from the list of the Slovakian fauna (Tokár et al., 2010). It is also absent in the modern list of Lepidoptera of Austria (Huemer and Tarmann, 1993) and is very rarely recorded in Hungary (Fazekas and Schreurs, 2014). The absence of noticeable numbers of *Ph. apparella* in Central Europe is confirmed by the fact that this leafminer was not even mentioned as a potential host in the major reviews of parasitoid insects (Fulmek, 1962; Bouček and Askew, 1968).

The second part of *Ph. apparella* distribution area, mostly covering the former Soviet republics and the adjacent territories, is characterized by regular outbreaks. In particular, this phenomenon has been recorded in Finland, in Leningrad and Novgorod provinces of Russia (Selikhovkin et al., 2016a, 2016b), in Ulyanovsk Province (Yefremova and Mishchenko, 2009), the Republic of Tatarstan (Selikhovkin et al., 2014), the Republic of Udmurtia, Perm Territory (our data), Novosibirsk Province (Kryvolutskaya, 1962; Selikhovkin, 1989), Kemerovo Province, Krasnoyarsk Territory (Kryvolutskaya, 1962), and also in Kazakhstan (*Harmful Animals*…, 1949; Shlykov, 1952) and Turkey (Tozlu et al., 2002) (Fig. 1). Eruptive densities of the leafminer (exceeding 1 mine per leaf; see Auerbach et al., 1995) are commonly observed in tree stands containing aspen, regardless of the anthropogenic impact level, and are often persistent. The leafminer density on *P. tremula* may reach 10 (Kryvolutskaya, 1962; Selikhovkin et al., 2016; Sinchuk et al., 2017) and even 20 mines per leaf (Yefremova et al., 2011), with the highest recorded density of 26 mines per leaf (Tozlu et al., 2002). The second part of *Ph. apparella* distribution may have been formed relatively recently, as the result of eastward expansion over the distribution of the host plant. One of the first records of this leafminer in the Asian part of the USSR was related to considerable damage to aspen caused by *Ph. apparella* larvae in Almaty Nature Reserve, the environs of the city of Almaty (*Harmful Animals*..., 1949), and the mountains of Trans-Ili Alatau (Shlykov, 1952). The species had not been found in an earlier special study of mining moths associated with poplars in Central Asia (Gerasimov, 1932).

The species structure of parasitoids attacking *Ph. apparella* in West Europe is poorly studied. *Pholetesor*

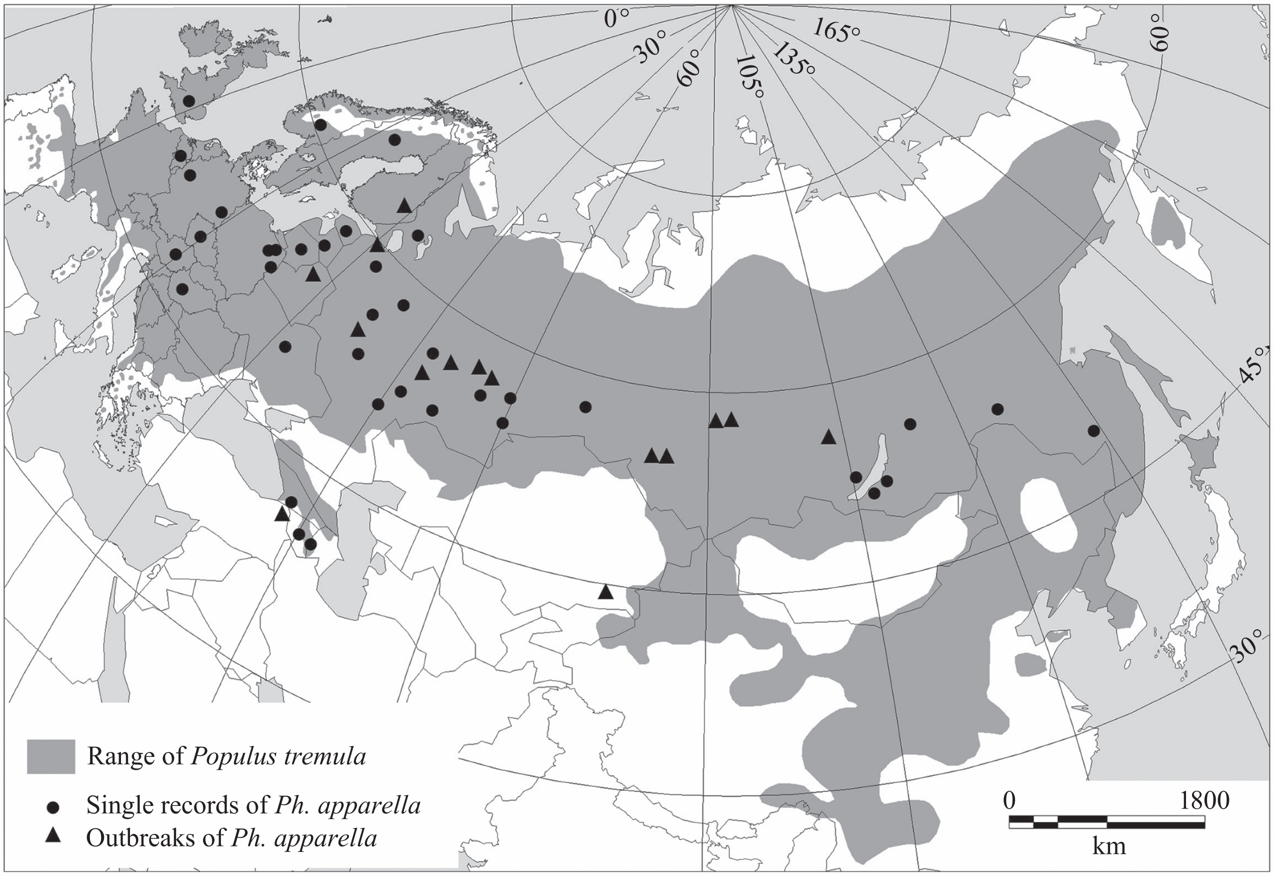

Fig. 1. Distribution of the aspen leafminer *Phyllonorycter apparella* in Eurasia.

nanus (Reinhard, 1880) of the family Braconidae was recorded in Germany (Herting, 1975), and four species of Eulophidae were found in Poland: *Sympiesis sericeicornis* (Nees, 1834), *Cirrospilus elegantissimus* Westwood, 1832, *Chrysocharis nephereus* (Walker, 1839), and *Achrysocharoides splendens* (Delucchi, 1954) (Vidal and Buszko, 1990).

The complex of parasitoids associated with *Ph. apparella* in Russia is non-uniformly studied. Four species of the family Eulophidae were recorded in Moscow Province: *Pnigalio agraules* (Walker, 1839), *Sympiesis sericeicornis*, *Cirrospilus pictus* Nees, 1834, and *Chrysocharis albipes* (Ashmead, 1904) (Gokhman et al., 2014); 22 species of this family were recorded in Ulyanovsk Province: *Pnigalio agraules*, *P. pectinicornis* (Linnaeus, 1758), *P. soemius* (Walker, 1839), *Sympiesis acalle* (Walker, 1848), *S. gordius* (Walker, 1839), *S. sericeicornis*, *Diaulinopsis arenaria* (Erdös, 1951), *Cirrospilus diallus* Walker, 1838, *C. elegantissimus*, *C. lyncus* Walker, 1838, *C. viticola* (Rondani, 1877), *C. vittatus* Walker, 1838, *Hyssopus geniculatus* (Hartig, 1838), *H. nigritulus* (Zetterstedt, 1838), *Chrysocharis amanus* (Walker, 1839), *Ch. eurynota* Graham, 1963, *Ch. laomedon* Walker, 1839, *Ch. nautius* (Walker, 1846), *Ch. pentheus* (Walker, 1839), *Ch. submutica* Graham, 1963, *Ch. viridis* (Nees, 1834), and *Minotetrastichus frontalis* Nees, 1834 (Yefremova et al., 2009; Yefremova and Mishchenko, 2009; Yefremova et al., 2011). The dominant members of this complex were *M. frontalis*, *P. agraules*, and *P. soemius*.

Only two species were revealed in West Siberia: *Closterocerus trifasciatus* Westwood, 1833 (Eulophidae) (Kryvolutskaya, 1962) and *Pholetesor circumscriptus* (Nees, 1834) (Braconidae) (Kryvolutskaya, 1962; Kolomiets, 1965; Tobias, 1971).

Studying the functioning of *Ph. apparella* outbreaks is of considerable interest from both theoretical and practical viewpoints. The objectives of this research were to characterize the species structure of parasitoids

Fig. 2. Mines of the aspen leafminer *Phyllonorycter apparella* on aspen leaves in the sample plot. Photo by I.V. Ermolaev, 2014.

attacking *Ph. apparella* in a persistent outbreak site of this leafminer on aspen near Izhevsk and to estimate the effect of ecto- and endoparasitoids on host mortality.

MATERIALS AND METHODS

The distribution map of *Populus tremula* in Eurasia was compiled based on the map "*Populus tremula* in Asian Russia" (Koropachinsky and Vstovskaya, 2002), the "Distribution map of *Populus tremula*" (*Populus tremula*..., 2017), and the "Distribution map of *Populus tremula* in Europe" (Distribution Maps, 2009). The records of *Ph. apparella* were plotted on this map according to the available literature (Fig. 1). This work was carried out using MapInfo Professional 12.5 geographic information system at the Geoinformation laboratory of Udmurt State University.

Pupal mortality of *Ph. apparella* was studied in 2014–2016 in a persistent outbreak site of this leafminer in the city of Izhevsk; the exact time of origin of this focus is unknown. According to Industrial Standard 56-69-83, a sample plot 0.5 ha in area was marked out in a young stand of the common aspen *Populus tremula* L. (56°88′N, 53°17′E), with trees 12.7 ± 0.3 m tall and 12.9 ± 0.7 cm in diameter ($n = 100$). The tree height was measured with a Haglöf EC II electronic clinometer, and the trunk diameter 1.3 m above the ground, with a caliper. Research was carried out on 40 model aspen trees. Every year, 70–80 leaves were collected from the lower crown layer of each model tree during the period of pupation of *Ph. apparella*. The mines were cut out with scissors and placed in Petri dishes. Emergence of adult leafminers and parasitoids was recorded daily under the conditions of the field laboratory.

Altogether, in 3 years of research 11 209 mines were cut out from the collected leaves, over 5800 ind. of *Ph. apparella* and 1322 ind. of parasitoids were reared. Identification of *Ph. apparella* was confirmed by S.V. Baryshnikova (Zoological Institute, Russian Academy of Sciences, St. Petersburg). All the hymenopteran parasitoids were identified by Z.A. Yefremova.

The density of the leafminer in model trees, the survival rate of its pupae, and the rate of infestation with parasitoids were calculated as described in our earlier paper (Ermolaev et al., 2018).

Table 2. Survival and mortality of pupae of the aspen leafminer *Ph. apparella* and correlation between these parameters and the density of host tree infestation with the leafminer in the sample plot in 2014–2016

Year	Infestation density, mines per leaf	Survival, %	Mortality, %	
			due to parasitoids	due to unknown factors
2014	4.3 ± 0.4	66.9 ± 3.2, $r = 0.46$*	7.4 ± 1.4, $r = -0.48$*	25.7 ± 2.2, $r = -0.37$*
2015	7.4 ± 0.4	63.2 ± 1.7, $r = 0.18$	8.7 ± 0.9, $r = -0.09$	28.1 ± 1.7, $r = -0.13$
2016	7.8 ± 0.4	25.2 ± 1.4, $r = 0.16$	19.6 ± 1.6, $r = 0.30$	55.2 ± 2.1, $r = -0.33$*

In all the cases, 40 model aspen trees were examined. * The correlation is significant at $P < 0.05$.

The mean value and its error were calculated in all the cases. Data were statistically processed by the standard methods (Ivanter and Korosov, 2011).

RESULTS AND DISCUSSION

Eruptive densities of *Ph. apparella* were recorded by us in 2007–2017 in Uvinsky, Mozhginsky, Alnashsky, Zavyalovsky, Votkinsky, and some other districts of the Republic of Udmurtia. Infestation of aspen was often complete, irrespective of the level of anthropogenic impact.

Phyllonorycter apparella in Udmurtia has one generation per season. The overwintered adults emerge in May and stay on the bark and branches until the unfolding of aspen leaves. Then mating occurs, and at the beginning of June females lay eggs singly on the leaf underside. Embryonic development takes about 10 days. The larvae pass through five instars in a month and form oval mines well visible from the upper side of the leaves (Fig. 2). Pupation takes place inside the mine; pupal development lasts 7–10 days. Before the emergence of the adult, the pupa ruptures the epidermis on the leaf underside so that 2/3 of its body sticks out of the mine. In 2014–2016, emergence was recorded during the middle third of July (Fig. 3), with 91.8, 68.6, and 98.3% of all the adults emerging between July 15 and July 20 in 2014, 2015, and 2016, respectively. Before overwintering, the moths hide in the bark crevices of the host trees and other nearby trees.

The density of *Ph. apparella* on aspen within the sample plot was 4.3 ± 0.4, 7.4 ± 0.4, and 7.8 ± 0.4 mines per leaf in 2014, 2015, and 2016, respectively (Table 2).

The leafminer survival rates in 2014 and 2015 were similar: 66.9 ± 3.2 and 63.2 ± 1.7%, respectively. This parameter was positively and significantly correlated with the density of host tree infestation only in 2014. The survival rates of the leafminer in 2016 decreased abruptly to 25.2 ± 1.4%.

Mortality of *Ph. apparella* was mostly caused by unknown factors. The percentage of mortality due to these factors increased from 25.7 ± 2.2% in 2014 to 55.2 ± 2.1% in 2016. At the same time, in both seasons mortality due to unknown factors was significantly lower in aspen trees with higher density of the leafminer.

The rate of *Ph. apparella* infestation with parasitoids increased from 7.4 ± 1.4% in 2014 to 19.6 ± 1.6% in 2016. This parameter was positively and significantly correlated with the density of host tree infestation only in 2014. The parasitoids emerged over a period of 3 weeks and more (Fig. 4): from July 9 to July 30, 2014 with a peak on July 13; from July 4 to July 30, 2015 with a peak on July 21; from July 8 to July 30, 2016 with a peak on July 15.

As the result of our study, 17 species of Eulophidae and 1 species of Braconidae were revealed in the complex of parasitoids associated with *Ph. apparella* near Izhevsk (Table 3).

Comparing the structure of the parasitoid complexes of *Ph. apparella* in the Republic of Udmurtia and Ulyanovsk Province (Yefremova et al., 2009, 2011; Yefremova and Mishchenko, 2009) demonstrated a considerable difference between them, with a Jaccard similarity index value of only 0.33. Such difference may be related both to the different living conditions (typical nemoral and forest-steppe ones, respectively) and to differences in the material sampling (1 and 5 collection localities, respectively).

In the course of this research transformation of the parasitoid complex of *Ph. apparella* both in the number

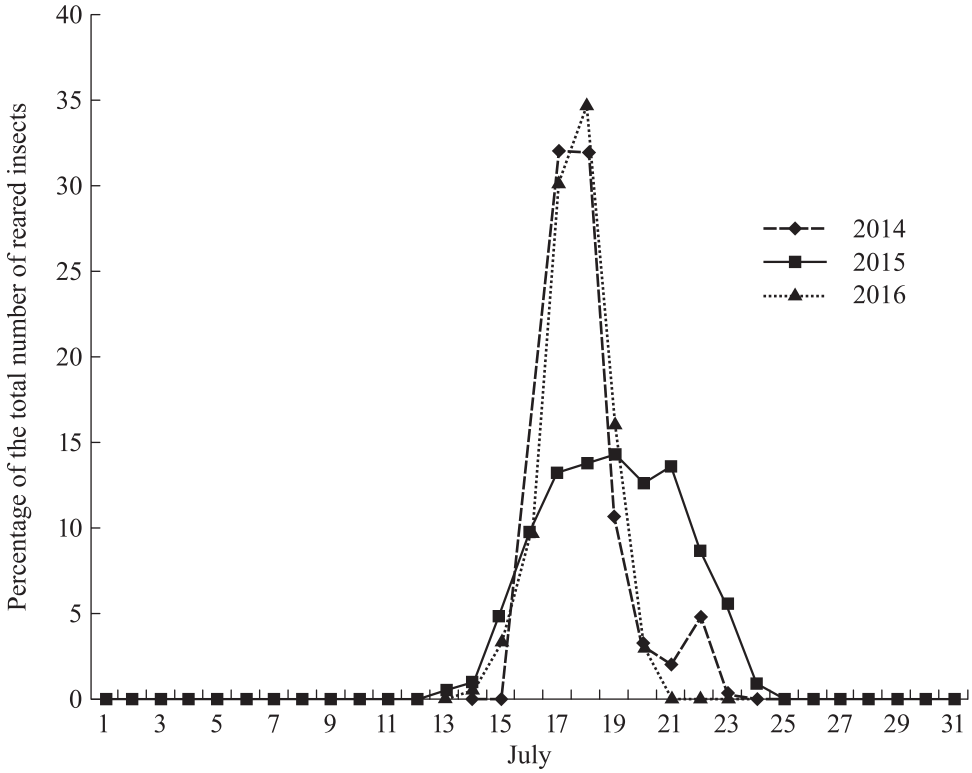

Fig. 3. Emergence dynamics of *Ph. apparella* in the field laboratory in 2014–2016 (n = 2504 in 2014; n = 2287 in 2015; n = 1009 in 2016).

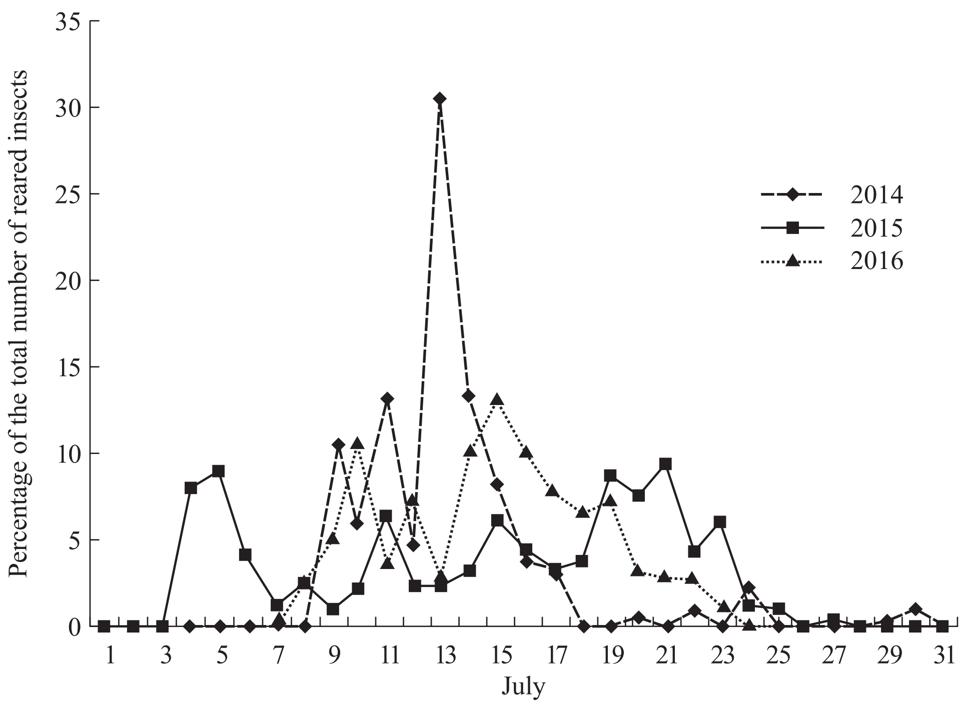

Fig. 4. Emergence dynamics of parasitoids of *Ph. apparella* in the field laboratory in 2014–2016 (n = 228 in 2014; n = 312 in 2015; n = 782 in 2016).

Table 3. Structure of the parasitoid complex of the aspen leafminer *Ph. apparella* in the sample plot

No.	Species	Share in the total number of specimens, %		
		2014	2015	2016
	Eulophidae			
1	*Pnigalio mediterraneus**	0	0.2 ± 0.2	0
2	*P. soemius**	0	0	0.6 ± 0.2
3	*Sympiesis acalle**	0	0	1.0 ± 0.4
4	*S. dolichogaster**	0	0	1.5 ± 0.5
5	*S. gordius**	1.6 ± 1.6	0.3 ± 0.2	7.8 ± 1.7
6	*S. sericeicornis**	3.1 ± 3.1	4.1 ± 1.7	5.4 ± 1.1
7	*Cirrospilus pictus**	0.2 ± 0.2	0	**13.6 ± 2.3**
8	*C. vittatus**	0	0	0.1 ± 0.1
9	*Hyssopus geniculatus**	0	0	0.6 ± 0.3
10	*Closterocerus trifasciatus*	0	**20.5 ± 3.6**	**33.4 ± 2.7**
11	*Chrysocharis laomedon*	1.8 ± 1.1	1.6 ± 0.7	6.4 ± 1.1
12	*Ch. nephereus*	0	0	2.7 ± 0.7
13	*Ch. pentheus*	0	0.5 ± 0.4	0
14	*Ch. phryne*	0	0	1.8 ±0.5
15	*Ch. viridis*	0	0	2.0 ± 0.6
16	*Neochrysocharis formosus*	0.9 ± 0.8	12.8 ± 2.5	0
17	*Minotetrastichus frontalis**	0	**45.1 ± 5.0**	**12.5 ± 2.2**
18	*Achrysocharoides* sp.	0	0	0.9 ± 0.4
	Braconidae			
19	*Pholetesor circumscriptus*	**92.4 ± 3.7**	14.9 ± 3.6	9.7 ± 1.4
	Total number of specimens	228	312	782

The shares of the dominant species are shown in bold. * ectoparasitoid.

of species and in the dominance pattern was observed. In particular, only six species of parasitoids were recorded in 2014 (Table 3). The dominant species was *P. circumscriptus* which comprised 92.4 ± 3.7% of the total specimen number. The number of larvae and pupae infested with this parasitoid was negatively and significantly correlated with the density of aspen infestation with the leafminer: $r = -0.32$, $n = 40$, $P < 0.05$.

Nine species of parasitoids were recorded in 2015. The dominant species were *M. frontalis* (45.1 ± 5.0%) and *C. trifasciatus* (20.5 ± 3.6%), which together comprised 65.6% of the total abundance; at the same time, the share of the previous dominant *P. circumscriptus* was only 14.9 ± 3.6%. The rate of *Ph. apparella* infestation with the two former parasitoid species was not correlated with the leafminer density on aspen: $r = 0.05$, $n = 40$, $P > 0.05$ and $r = 0.25$, $n = 40$, $P > 0.05$, respectively. Similar to the preceding year, infestation of the leafminer larvae and pupae with *P. circumscriptus* decreased significantly as the density of host plant infestation with the leafminer increased: $r = -0.33$, $n = 40$, $P < 0.05$.

The dominant species *M. frontalis* is a gregarious larval and pupal ectoparasitoid. Up to five larvae of *M. frontalis* may develop on one larva or pupa of a *Phyllonorycter* host (Yefremova and Mishchenko, 2012); therefore, the calculated rate of *Ph. apparella* infestation with this parasitoid may be somewhat overestimated.

Sixteen species of parasitoids were recorded in 2016. Three species were dominant: *C. trifasciatus* (33.4 ± 2.7%), *C. pictus* (13.6 ± 2.3%), and *M. frontalis* (12.5 ± 2.2%). The total share of the dominants was 59.5%. As compared with the preceding year, the share of *P. cir-*

cumscriptus in the complex decreased from 14.9 to 9.7%; that of *M. frontalis* also decreased. The rate of *Ph. apparella* infestation with *C. trifasciatus* was positively and significantly correlated with the density of aspen infestation with the leafminer: $r = 0.39$, $n = 40$, $P < 0.05$. No such correlation was observed for *C. pictus* and *M. frontalis*: $r = 0.27$, $n = 40$, $P > 0.05$ and $r = -0.24$, $n = 40$, $P > 0.05$, respectively.

The dominant species *C. trifasciatus* is a primary (less frequently secondary) larval and pupal endoparasitoid of mining insects (Bouček and Askew, 1968; Hansson, 1994). Its development from egg to adult takes about 20 days (Sundby, 1957). This species was previously recorded in the study territory as a parasitoid of *Ph. populifoliella* (Treitschke, 1833) on the balsam poplar *Populus balsamifera* L. (Ermolaev et al., 2016). An increase in the share of *C. trifasciatus* from 20.5 to 33.4% of the total specimen number of parasitoids probably facilitated a decrease in the density of aspen infestation with *Ph. apparella* from 7.8 ± 0.4 mines per leaf in 2016 to 1.0 ± 0.1 mines per leaf in 2017.

As can be seen from these data, development of the parasitoid complex in the persistent outbreak area of *Ph. apparella* during 2014–2016 was marked by an annual increase in the number of species (from 6 to 9 to 16), a change in the composition of dominants: *P. circumscriptus* → (*M. frontalis* + *C. trifasciatus*) → (*C. trifasciatus* + *C. pictus* + *M. frontalis*), and a decrease in the share of each species in the subsequent years. These changes occurred simultaneously with the density of *Ph. apparella* on aspen rising from 4.3 ± 0.4 mines per leaf in 2014 to 7.4 ± 0.4 and 7.8 ± 0.4 mines per leaf in 2015 and 2016, respectively.

Appearance of an abundant trophic resource, first of all, facilitates primary parasitism. An increase in the number of alternative hosts (the leafminer and its primary parasitoids) positively affects both primary and secondary parasitism. It is possible that in this case, *P. circumscriptus* acts as a kind of edificator, or habitat forming species, allowing other dominant species to join the parasitoid complex. For instance, *M. frontalis* is a hyperparasitoid (Domenichini, 1966; Herting, 1977; LaSalle, 1994; Yefremova and Mishchenko, 2009) attacking both the leafminer larvae and pupae and other parasitoids, including *P. circumscriptus*. Another factor of an abrupt increase in the abundance of *M. frontalis* near Izhevsk in 2015 may be the growing density of its alternative host, the lime leafminer *Ph. issikii* (Lepidoptera, Gracillariidae), since *M. frontalis* was the prevalent member of its parasitoid complex (Ermolaev et al., 2018). Endoparasitoids comprised 95.1, 50.3, and 56.9% of the total specimen number in 2014, 2015, and 2016, respectively. The role of endoparasitoids in controlling the leafminer population seems to be somewhat greater than that of ectoparasitoids. Besides, the total rate of *Ph. apparella* infestation with parasitoids increased from 7.4 ± 1.4% in 2014 to 19.6 ± 1.6% in 2016. As the result of combined effect of the control factors, the leafminer density decreased from 7.8 ± 0.4 mines per leaf in 2016 to 1.0 ± 0.1 mines per leaf in 2017.

ACKNOWLEDGMENTS

We are grateful to S.V. Baryshnikova (Zoological Institute, Russian Academy of Sciences, St. Petersburg) for confirming the species identification of the leafminer, and to S.Yu. Sinev (ZIN) and A.V. Selikhovkin (St. Petersburg State Forest Technical University) for support at different stages of our work.

FUNDING

This research was carried out within the framework of Project 1.1.2404 of the Russian Ministry of Education and Science.

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