

Effect of Host Plants on the Viability of Black-veined White *Aporia crataegi* L. at Low Natural Population Density

E. Yu. Zakharova^{a, b, *}, A. O. Shkurikhin^a, I. A. Solonkin^a, and T. S. Oslina^a

^aInstitute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences, Yekaterinburg, 620144 Russia

^bUral Federal University, Yekaterinburg, 620002 Russia

*e-mail: zakharova@ipae.uran.ru

Received February 20, 2020; revised May 25, 2020; accepted May 29, 2020

Abstract—Patterns of interaction of an oligophagous insect, black-veined white *Aporia crataegi* L., with host plants in years with a low density of its natural population are analyzed. In years with low *A. crataegi* population abundance in the south of Sverdlovsk region (Sysertsky district), the species composition of caterpillar host plants gradually decreases from several woody rosaceous species of the genera *Padus*, *Sorbus*, *Malus*, and *Crataegus* to one species (*Padus avium* Mill.). It is shown that the mortality rate is higher for fifth-instar caterpillars developing on mountain ash than for those developing on bird cherry. Adult *A. crataegi* developing on bird cherry are not only larger but also grow faster than those developing on mountain ash, which may be an additional factor responsible for the observed chronographic variation during the emergence of *A. crataegi* generation in nature.

Keywords: variation, mortality rate, body weight, host plant, caterpillars, adults, oligophage, phytophage, *Aporia crataegi*

DOI: 10.1134/S1067413620060107

Different aspects of interaction between phytophagous insects and their host plants have been studied quite thoroughly both in terms of theoretical ecology of populations and communities [1–4, etc.] and in terms of applied disciplines (agricultural and forest entomology, plant protection and quarantine, etc. [5–7]). Special attention has recently been paid to studying the effect of climate change on the interaction of insects with plants [8]. Phytophagous insects and their relationships with host plants are a convenient model for studying ecological specialization and associated evolution of communities [9–12].

One of the most interesting problems concerns the choice of certain host plants by oligophages and polyphages. The literature discusses the hypothesis that phytophage females prefer to lay eggs on those host plants where the survival and productivity of their offspring prove to be higher (the preference-performance hypothesis). This hypothesis is confirmed in the two-component phytophage–host plant system (i.e., without regard to competition, predation, parasitism, mutualism, etc.) [10]. However, isolated phytophage–host plant pairs do not occur in nature; therefore, published data both in favor and against this hypothesis are available.

It seems interesting and relevant to consider some aspects of the ecology of phytophagous insects during their interaction with different host plants in a natural

environment. The black-veined white (*Aporia crataegi* L.) was chosen as a model object; according to our observations and literature data [13–16], its outbreak was recorded in the Middle Urals and neighboring regions in 2010–2013. In the following years (2014–2019), transition of the population into a low abundance state was observed. The study of insect populations at a low density level seems to be no less important than their study at the prodromal and eruptive levels [17].

The purpose of this study was to analyze the patterns of interaction between the oligophagous insect characterized by the eruptive type of population dynamics and its host plants in years with a low density of its natural population. To this end, we needed to identify the species composition of host plants for *A. crataegi* caterpillars and evaluate the viability of the caterpillars depending on their development on different host plants under natural conditions.

MATERIAL AND METHODS

Study object. The black-veined white is a polyphage on woody plants of the rose and heath families (Rosaceae and Ericaceae), but it is also characterized by well-manifested zonal oligophagy [18]. Currently available publications on this species provide not only a sufficiently detailed description of food specialization of its caterpillars in different parts of the range but

also data on some features of its physiology [7, 19–21], behavior, migratory abilities, expansion [22, 23], and population dynamics [24–26].

Bird cherry (*Padus avium* Mill.) is the main host plant for *A. crataegi* caterpillars on a significant part of the range (European Russia, the Urals, and Siberia). Its thickets serve as natural reservations from which the butterflies spread to gardens and parks [25–27]. In the Urals and adjacent regions, the preferred host plant for black-veined white caterpillars is apple tree (*Malus* spp.) growing in gardens, urban agglomerations, upland meadows, and near villages [13, 15].

The population under study lives near the biological station of the Ural Federal University in Sysertsky district, Sverdlovsk region (56°36' N, 61°03' E), in the subzone of pre-forest-steppe pine–birch forests. The prevalent plant communities in this area are south-taiga and pre-forest-steppe pine forest of herb–dwarf shrub and herb types and secondary birch and pine–birch forests of herb type [28]. The undergrowth in pine forests includes rosaceous tree and shrub species, mainly bird cherry *Padus avium* Mill. and mountain ash *Sorbus aucuparia* L.; there also occur apple tree *Malus baccata* (L.) Borkh. (sparse) and hawthorn *Crataegus sanguinea* Pall. (single plants).

Material. To determine the species composition of host plants, we searched for wintering nests with early-instar caterpillars in 2013–2019. The numbers of nests collected from different host plants in 2013–2018 are given in [16, 29]; in 2019, we continued to collect nests in early spring, before the emergence of overwintered caterpillars (April 6), and in autumn, after the onset of wintering (September 13).

Fifth-instar caterpillars were collected from two host plants (bird cherry and mountain ash) at the end of May in warm years (2014–2016) or during the first 10-day period of June (if the air temperature was low in May and caterpillars developed slowly) (2013 and 2017–2018)). A total of 2822 caterpillars were collected (Table 1). In addition, pupae were collected from bird cherry (202 spec.) and mountain ash (16 spec.) in 2016. In 2019, the population was in the phase of depression, and density of caterpillars was so low that we failed to collect a representative sample (only six caterpillars were found on bird cherry and three on mountain ash).

On the day of sampling, caterpillars and pupae were weighed on a Kern 440-21N balance with an accuracy of 1 mg and numbered. Each caterpillar was placed in an individual 0.5-L plastic container covered with cotton cloth and fed fresh foliage of the host plant from which it was collected. The containers were exposed on an open rack under tree crowns in uncontrolled conditions. Each container was checked daily until the emergence of adults or death of caterpillars or pupae. Records were kept of the dates and causes of their death and the dates of pupation and emergence of adults. The wet body weight of all adults on the day

of emergence was measured using the same balance with an accuracy of 1 mg.

The mortality rate of caterpillars was estimated in all study years; variation in the body weight of adults cultivated on different host plants was analyzed only for the period from 2014 to 2017, since we failed to collect representative samples from mountain ash in 2013 and 2018 (see Table 1).

Statistical analysis. Variation in body size (weight) during the emergence of adults was evaluated using regression analysis in PAST 2.17 [30]. The initial weighing results were averaged for each observation day. Each sample was analyzed independently, taking into account insect sex and sampling year. The date of emergence of the first adult individual was considered as the first observation day. These dates for 2013–2018 are given in Table 1. The mortality rates of late-instar caterpillars on different host plants were compared using the χ^2 test.

ANOVA with mixed effects was used to evaluate the effect of factors “food plant” and “caterpillar health” on caterpillar weight. The latter factor was understood as either successful pupation and adult emergence or caterpillar death of parasitoids or infections. The “host plant” and “caterpillar health” were fixed factors, and the year of sampling was a random factor. The effect of factors “host plant” and “sex” on the weight of adults was evaluated by the same method. These two factors were fixed, and the year of sampling was a random factor. Calculations were made in the R environment [31].

RESULTS AND DISCUSSION

During several years of observation on the state of the natural *A. crataegi* population near the biological station of the Ural Federal University, we revealed that caterpillars developed on different species of woody rosaceous plants (bird cherry, mountain ash, apple tree, and hawthorn) in the last year of their outbreak (2013) and the following year (2014). From 2015 to 2018, wintering nests with early-instar *A. crataegi* caterpillars were found mainly on bird cherry, less often on mountain ash, and very rarely on apple tree and hawthorn. In April 2018, several nests occurred on mountain ash, but all nests found in August–September of the same year (after the emergence of the following generation) and in 2019 were located exclusively on bird cherry. Therefore, our observations show that the species composition of *A. crataegi* caterpillar host plants in the study region is reduced from several to one species in years with low population abundance of the species.

Some fifth-instar caterpillars cultivated in individual containers died of different causes. In most cases, their death was caused by parasitoids of the family Braconidae or by viral and fungal infections. The most

Table 1. Sample size and caterpillar mortality during *A. crataegi* cultivation in 2013–2018 (Sverdlovsk region, Sysertsky district)

Caterpillar sampling dates	Host plant	Number of fifth-instar caterpillars	Caterpillar mortality rate, %	Emergence period of adults*	Number of adults
June 1–6, 2013	Bird cherry	285	93.0	June 19–23	<u>2</u>
				June 20–26	18
	Mountain ash	107	93.5	June 21–27	<u>5</u>
				June 21–23	2
May 22–24, 2014	Bird cherry	363	28.4	June 14–22	<u>63</u>
				June 15–24	184
	Mountain ash	260	48.8	June 14–21	<u>52</u>
				June 18–July 1	74
May 28–June 1, 2015	Bird cherry	310	23.9	June 14–19	<u>104</u>
				June 16–22	132
	Mountain ash	261	61.7	June 16–20	<u>52</u>
				June 16–21	52
May 24–26, 2016	Bird cherry	238	90.3	June 8–17	<u>56</u>
				June 9–20	66
	Mountain ash	202	90.6	June 10–21	<u>14</u>
				June 12–21	12
May 31–June 9, 2017	Bird cherry	330	59.4	June 26–July 9	<u>44</u>
				June 27–July 15	96
	Mountain ash	262	72.9	June 29–July 13	<u>31</u>
				June 29–July 17	39
June 6–11, 2018	Bird cherry	174	64.4	July 1–8	<u>26</u>
				July 2–10	36
	Mountain ash	30	83.3	July 8	<u>1</u>
				July 8–10	4

* Above the line, males; below the line, females.

prevalent infection was by nuclear polyhedrosis virus (det. by A.V. Il'inykh).

It is well known that the mortality rate of late-instar *A. crataegi* caterpillars and pupae can be very high in nature. Thus, the survival rate of adults was only 5.6% in Sverdlovsk region in 1962, which led to a sharp decrease in their abundance and stopped their outbreak [32]. According to our data, the mortality rate of fifth-instar caterpillars was also very high (93%) in the last year of their outbreak (2013). The mortality rate varied in a wide range during several years with consistently low population abundance (Table 1).

As a rule, the mortality rate was higher in caterpillars developing on mountain ash than in those on bird cherry. Comparison of the mortality rates of caterpillars on the two host plants showed a significant difference ($\chi^2 = 15.8$, d.f. = 5, $p = 0.008$). The average total

mortality rate of caterpillars was 59.9% on bird cherry and 75.1% on mountain ash for the period from 2013 to 2018. The fairly high average mortality rate of late-instar caterpillars is presumable one of the causes of their low population density in these years.

The growth and final body weight of last-instar caterpillars prior to their pupation in nature depend on many conditions such as the sum of accumulated degree–days, food consumption efficiency, biochemical (including antibiotic) foliage composition, etc. Therefore, it is incorrect to perform between-year comparisons of the weight of caterpillars during their growth process. In turn, comparison of caterpillars that were simultaneously collected from different host plants is quite informative.

According to the results of ANOVA, the effect of both factors under study (“host plant” and “caterpillar

Table 2. Results of ANOVA for the body weight of *A. crataegi* fifth-instar caterpillars

Factor	SS	d.f.	MS	F	p
Host plant	1499925	1	1499925	136.13	<0.001
Caterpillar health	7847349	1	7847349	741.90	<0.001
Host plant × caterpillar health	99519	1	99519	9.40	<0.01
Year	8344	4	2086		
Residual variance	27278083	2579	10577		

Table 3. Results of ANOVA for the body weight of adult *A. crataegi*

Factor	SS	d.f.	MS	F	p
Sex	374159	1	374159	180.78	<0.001
Host plant	161420	1	161420	77.99	<0.001
Sex × host plant	7257	1	7257	3.50	0.06
Year	4040	4	1010		
Residual variance	2051370	991	2070		

Table 4. Average body weights of adult *A. crataegi* that developed from caterpillars cultivated on different host plants in 2013–2018

Host plant	Sex	Year					
		2013	2014	2015	2016	2017	2018
Bird cherry	Males	166.0 ± 31.8	191.2 ± 5.6	159.9 ± 4.5	119.5 ± 31.8	128.3 ± 6.8	115.9 ± 17.3
	Females	223.2 ± 10.6	255.0 ± 3.3	187.5 ± 3.9	173.9 ± 10.1	159.9 ± 4.6	123.9 ± 14.1
Mountain ash	Males	139.3 ± 26.0	181.9 ± 6.2	129.0 ± 6.2	97.2 ± 15.0	120.8 ± 8.0	–
	Females	189.0 ± 31.8	206.4 ± 5.2	158.5 ± 6.2	167.7 ± 14.2	148.3 ± 7.2	131.8 ± 20.6

health”) and their interaction proved to be significant (Table 2). Naturally, the weight of the caterpillars affected by parasitoids and infections was significantly lower than that of healthy caterpillars. Thus, the average weight of the infected caterpillars collected from bird cherry over all study years was 260.1 ± 3.8 mg and that of the healthy ones was 393.7 ± 4.4 mg. The average weight was significantly lower for caterpillars that developed on mountain ash than for those on bird cherry: 217.5 ± 4.1 vs. 377.3 ± 6.2 mg.

According to the literature and our data [14, 24, 26], *A. crataegi* is characterized by sexual dimorphism in size: in general, females are larger than males. The results of ANOVA for the body weight of adults are given in Table 3: the “sex” and “host plant” factors have a statistically significant effect on variation in their size, while the interaction of these factors is insignificant. The effect of the random factor “year” is determined both by the growth rate and accumulation of degree-days (depending on weather conditions in a particular year) and by the fact that the caterpillars were weighed on the date of sampling (rather than prior to pupation) and then continued feeding and growing. Table 4 shows average body weights of adult

A. crataegi males and females cultivated on bird cherry and mountain ash in 2013–2018. As follows from these results, females that developed on bird cherry were the largest, while males that developed on mountain ash were the smallest. At the same time, the average body weight of males from bird cherry prove to be comparable with that of females fed on mountain ash (e.g., in 2015), which minimizes sexual size dimorphism.

Caterpillars probably use assimilated food energy more efficiently when they develop on bird cherry than on mountain ash. According to some authors [7], the environmental costs of food consumption by *A. crataegi* caterpillars and their food consumption efficiency can be compared with the experimental data on food consumption by gypsy moth caterpillars. Vshivkova [33, 34] showed that, compared to bird cherry, mountain ash is unfavorable for the growth of gypsy moth caterpillars, since its leaves contain secondary compounds that have influence on their use and consumption. In addition, the energy value of bird cherry leaves was higher than that mountain ash leaves. Adult *A. crataegi* adults developing on mountain ash are smaller and grow longer than those on bird cherry. Although caterpillars were always collected

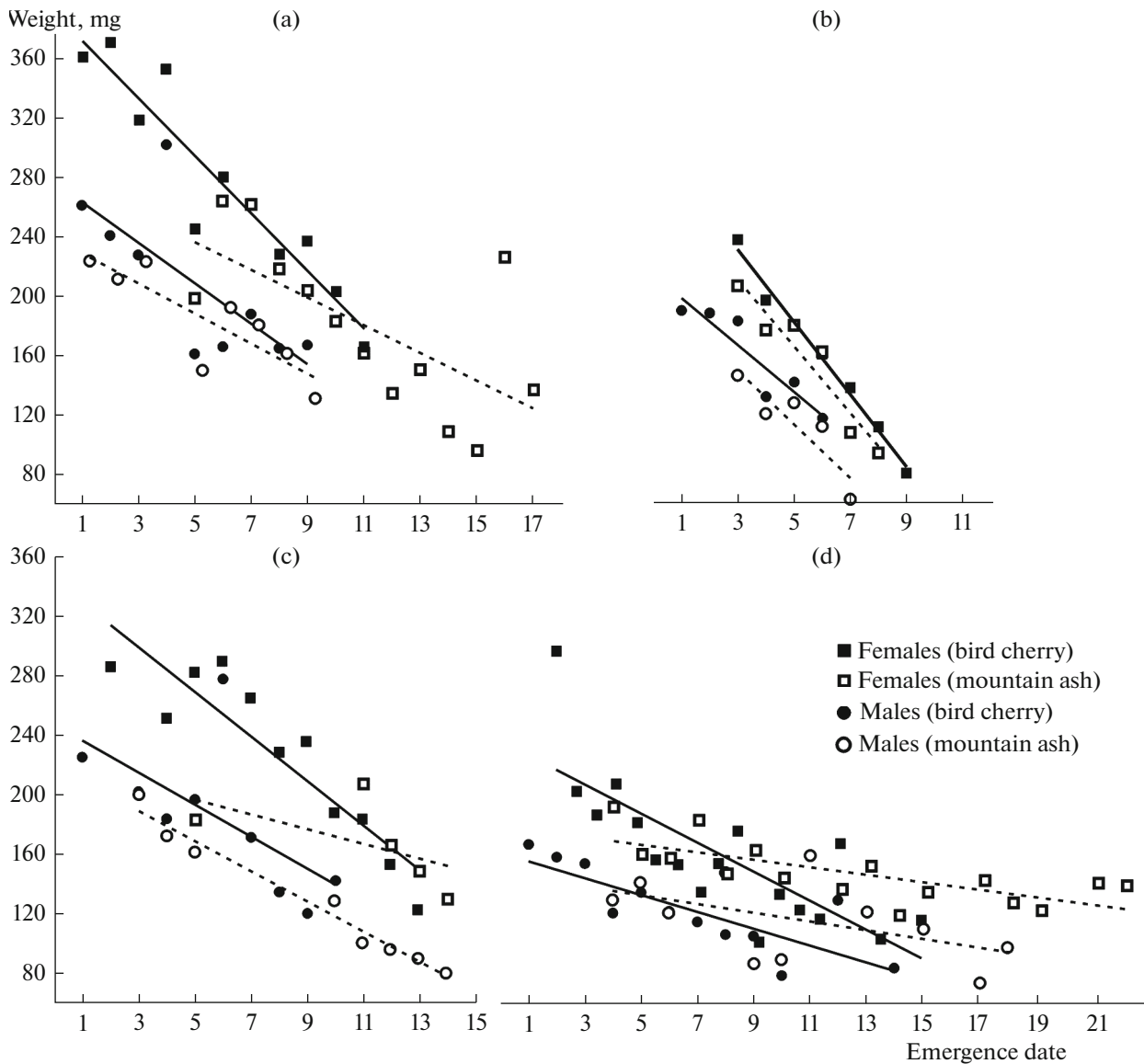


Fig. 1. Variation in the body weight of adult *A. crataegi* during the emergence of males and females cultivated on different host plants in (a) 2014, (b) 2015, (c) 2016, and (d) 2017.

simultaneously from both host plants, the emergence of adults from caterpillars was recorded one to several days later on mountain ash than on bird cherry (Table 1, Fig. 1). Regression analysis revealed a statistically significant dependence of the body size of adults on the date of emergence (except adult males cultivated on mountain ash in 2017 and adult females cultivated on mountain ash in 2016). These results are consistent with and complement the results of our previous studies [14]: the largest adults are the first to emerge, while the smallest ones are the last to appear, regardless of sex and caterpillar host plant. It was also shown for *A. crataegi* that the larger the size of a female, the higher its fertility [7, 21], which is generally typical for many insects [35–37].

Consequently, the chronographic variation of adult *A. crataegi* during the flight period in nature can be described as follows: the largest males that develop on bird cherry appear first, followed by the emergence of first large females from bird cherry and relatively small males from mountain ash, and females developing on mountain ash are the last to emerge. The smallest males and females that develop on mountain ash are the last to emerge from pupae. Therefore, not only the earlier emergence of large adults but also the asynchronous emergence of adults developing on different food species (large individuals from bird cherry and small individuals from mountain ash) is an additional factor accounting for the observed chronographic

variation during the flight period of *A. crataegi* generation in nature.

During the outbreak, *A. crataegi* in the study region developed on several host plants, with bird cherry being the preferred species. According to the preference–performance hypothesis, female insects prefer to lay eggs on the host plant on which the survival and productivity of the offspring is higher [10]. However, there is no instant transition from oligophagy to monophagy on the most preferred host plant under conditions of reduced population density and, consequently, reduced competition for food. On the contrary, female *A. crataegi* under conditions of low population density continue to lay eggs on mountain ash over several years, despite higher mortality rate of late-instar caterpillars, prolonged period of preimaginal development, and lower fecundity of adults due to their small size. Our results indicate that *A. crataegi* gradually changes its diet from oligophagy to almost complete monophagy during several years after its outbreak, i.e., with decrease in its population density.

ACKNOWLEDGMENTS

The authors are grateful to Dr. A.V. Il'inykh (Institute of Systematics and Ecology of Animals, Siberian Branch, Russian Academy of Sciences, Novosibirsk) for identifying nuclear polyhedrosis virus in *A. crataegi* and to A.V. Ivanov, P.V. Rudoiskatel, and K.I. Fadeev (Ural Federal University, Yekaterinburg) for their assistance in experimental research at the biological station.

FUNDING

The long-term collection of field material, its laboratory processing, analysis, and interpretation of the results were performed under the state assignment of the Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences (no. AAAAA19-119031890087-7) and the Integrated Basic Research Program of the Ural Branch, Russian Academy of Sciences (project no. 18-4-4-28).

COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interest. The authors declare that they have no conflict of interest.

Statement on the welfare of animals. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

REFERENCES

- Chernyshev, V.B., *Ekologiya nasekomykh* (Insect Ecology), Moscow: Mosk. Gos. Univ., 1996.
- Whitman, D. and Ananthkrishnan, T.N., *Phenotypic Plasticity of Insects: Mechanisms and Consequences*, Boca Raton, FL: CRC Press, 2009.
- Schowalter, T., *Insect Ecology. An Ecosystem Approach*, Cambridge, MA: Academic, 2011.
- Sot, T., Kagata, H., Ando, Y., et al., *Species Diversity and Community Structure: Novel Patterns and Processes in Plants, Insects, and Fungi*, Tokyo: Springer, 2014.
- Nadzor, uchet i prognoz massovykh razmnozhenii khvoe-i listogryzushchikh nasekomykh v lesakh SSSR (Monitoring, Inventory, and Prediction of Population Outbreaks of Needle- and Leaf-gnawing Insects in Forests of the Soviet Union), Moscow: Lesnaya Promyshlennost', 1965.
- Nasekomye i kleshchi - vrediteli sel'skokhozyaistvennykh kul'tur (Insect and Arachnid Pests of Agricultural Crops), vol. 3: *Cheshuekrylye* (Lepidoptera), part 2, St. Petersburg: Nauka, 1999.
- Isaev, A.S., Pal'nikova, E.N., Sukhovol'skii, V.G., and Tarasova, O.V. *Dinamika chislennosti lesnykh nasekomykh-fillofagov: modeli i prognozy* (Population Dynamics of Forest Phytophagous Insects: Models and Predictions), Moscow: KMK, 2015.
- Utkina, I.A. and Rubtsov, V.V., Modern views on the effect of climate change on the interaction of forest trees and phytophagous insects, *Lesnoi Vestnik*, 2017, vol. 21, no. 6, pp. 5–12. <https://doi.org/10.18698/2542-1468-2017-6-5-12>
- Rundle, H.D. and Nosil, P., *Ecological speciation*, *Ecol. Lett.*, 2005, vol. 8, pp. 336–352.
- Gripenberg, S., Mayhew, P.J., Parnell, M., and Roslin, T., A meta-analysis of preference–performance relationships in phytophagous insects, *Ecol. Lett.*, 2010, vol. 13, pp. 383–393.
- Matsubayashi, K.W., Ohshima, I., and Nosil, P., Ecological speciation in phytophagous insects, *Entomol. Exp. Appl.*, 2010, vol. 134, pp. 1–27.
- De la Masseliere, M.C., Facon, B., Hafsi, A., and Duyck, P.-F., Diet breadth modulates preference–performance relationships in a phytophagous insect community, *Sci. Rep.*, 2017, vol. 7, 16934. <https://doi.org/10.1038/s41598-017-17231-2>
- Bogacheva, I.A., Zamshina, G.A., and Nikolaeva, N.V., Dominant and abundant phytophagous insect pests of trees and shrubs in Yekaterinburg, *Fauna Urala i Sibiri*, 2018, no. 1, pp. 46–73.
- Shkurikhin, A.O., Zakharova, E.Y., Oslina, T.S., and Solonkin, I.A., Variation in morphophysiological traits of male and female *Aporia crataegi* L. (Lepidoptera: Pieridae) depending on the timing of adult emergence, *Russ. J. Ecol.*, 2018, vol. 49, no. 4, pp. 356–361. <https://doi.org/10.1134/S1067413618040124>
- Adakhovskii, D.A., New data on intraspecific ecological strategies of diurnal lepidopterans (Lepidoptera: Hesperioidea, Papilionoidea) in Udmurtia, *Tr. Stavropol. Otd. Russ. Entomol. O-va*, no. 15, Stavropol: Paragraf, 2019, pp. 64–67.
- Zakharova, E.Yu., Shkurikhin, A.O., Oslina, T.S., Solonkin, I.A., Effect of ecological factors on the ratio of early-instar larvae of *Aporia crataegi* L. (Lepidoptera: Pieridae) at the onset of wintering, *Evrz. Entomol. Zh.*, 2019, vol. 18, no. 4, pp. 292–300.
- Isaev, A.S., Ovchinnikova, T.M., Pal'nikova, E.N., et al., Abundance dynamics and stability of populations of forest insects at a low density level (the example of *Bupalus piniarius* L.), *Lesovedenie*, 2014, no. 4, pp. 3–11.

18. Baranchikov, Yu.N. *Trophic Specialization of Lepidoptera*, Krasnoyarsk: Sib. Otd. Akad. Nauk SSSR, 1987.
19. Baranchikov, Yu.N., Trophic specialization of larvae in two lepidopteran species and efficiency of their feeding on leaves of Rosaceae shrubs, *Zool. Zh.*, 1986, vol. 65, no. 3, pp. 361–368.
20. Li, N.G., Physiobiochemical adaptations of *Aporia crataegi* L. (Lepidoptera, Pieridae) to the cold and dry climate of Central Yakutia, *Evr. Entomol. Zh.*, 2006, vol. 5, no. 2, pp. 173–180.
21. Tarasova, O.V., Kalashnikova, I.I., and Kuznetsova, V.V., Energy balance of food consumption by phytophagous insects: Optimization model, *Sib. Lesnoi Zh.*, 2015, no. 3, pp. 83–92.
22. Jugovic, J., Črne, M., and Lužnik, M., Movement, demography and behaviour of a highly mobile species: A case study of the black-veined white, *Aporia crataegi* (Lepidoptera: Pieridae), *Eur. J. Entomol.*, 2017, vol. 114, pp. 113–122.
23. Jugovic, J. and Kržič, A., Behavior and oviposition preferences of a black-veined white, *Aporia crataegi* (Lepidoptera: Pieridae), *J. Entomol. Acarol. Res.*, 2019, vol. 51, no. 2, pp. 51–59.
24. Kuznetsova, V.V., Black-veined white (*Aporia crataegi* L.) in suburban tree stands near the city of Krasnyarsk: Biology, population dynamics, and interactions with food plants, *Extended Abstract of Cand. Sci. (Biol.) Dissertation*, Krasnoyarsk, 2001.
25. Kuznetsova, V.V. and Pal'nikova, E.N., Analysis of basic population parameters of black-veined white (*Aporia crataegi* L.) in suburban tree stands near the city of Krasnyarsk, in *VII chteniya pamyati O.A. Kataeva. Vrediteli i bolezni drevesnykh rastenii Rossii: Mat-ly mezhdun. konf. (Pests and Diseases of Woody Plants in Russia: VII Lectures in Memory of O.A. Kataev, Proc. Int. Conf.)*, St. Petersburg, 2013, pp. 51–52.
26. Kuznetsova, V.V. and Pal'nikova, E.N., Factors of black-veined white (*Aporia crataegi* L.) population dynamics in suburban tree stands near the city of Krasnyarsk, *Izv. S.-Peterb. Lesotekh. Akad.*, 2014, no. 34, pp. 49–59.
27. Babenko, Z.S., *Nasekomye-fitofagi plodovykh i yagodnykh rastenii lesnoi zony Priob'ya* (Phytophagous Insect Pests of Fruit- and Berry-bearing Plants in the Forest Zone of Ob Region), Tomsk: Tomsk. Gos. Univ., 1982.
28. Kulikov, P.V., Zolotareva, N.V., and Podgaevskaya, E.N., *Endemichnye rasteniya Urala vo flore Sverdlovskoi oblasti* (Endemic Plants of the Urals in the Flora of Sverdlovsk Oblast), Yekaterinburg: Goshchitskii, 2013.
29. Zakharova, E.Yu., Shkurikhin, A.O., Oslina, T.S., and Klyuchereva, I.D., Wintering success of different instar larvae of black-veined white *Aporia crataegi* L. (Lepidoptera: Pieridae) in the Middle Urals, *Evr. Entomol. Zh.*, 2015, vol. 14, no. 2, pp. 144–148.
30. Hammer, O., Harper, D.A.T., and Ryan, P.D., PAST: Paleontological statistics software package for education and data analysis, *Palaeontol. Electron.*, 2001, vol. 4, no. 1.
31. R Core Team, *R: A Language and Environment for Statistical Computing*, Vienna: R Foundation for Statistical Computing, 2019. <https://www.R-project.org/> Cited February 15, 2020.
32. Turaev, N.S., Parasites and their role in suppression of black-veined population outbreaks, *Tr. Sverdlovsk. S-kh. Inst.*, 1964, vol. 11, pp. 331–335.
33. Vshivkova, T.A., Feeding and growth energetics of gypsy moth larvae of different instars, *Zh. Obshch. Biol.*, 1989, vol. 50, no. 1, pp. 108–115.
34. Vshivkova, T.A., Biochemical components determining the quality of food plants for gypsy moth larvae (*Lymantria dispar* L.) of different instars, *Izv. S.-Peterb. Lesotekh. Akad.*, 2009, no. 187, pp. 87–96.
35. Blanckenhorn, W.U., The evolution of body size: What keeps organisms small?, *Q. Rev. Biol.*, 2000, vol. 75, pp. 385–407.
36. Tammaru, T., Esperk, T., and Castellanos, I., No evidence for costs of being large in females of *Orgyia* spp. (Lepidoptera, Lymantriidae): Larger is always better, *Oecologia*, 2002, vol. 133, pp. 430–438.
37. Flatt, T. and Heyland, A., *Mechanisms of Life History Evolution: The Genetics and Physiology of Life History Traits and Trade-offs*, Oxford: Oxford Univ. Press, 2011.

Translated by D. Zabolotny