

Preimaginal mortality of the black-veined white *Aporia crataegi* Linnaeus, 1758 (Lepidoptera: Pieridae) at different phases of an outbreak cycle

Преимагинальная смертность боярышницы *Aporia crataegi* Linnaeus, 1758 (Lepidoptera: Pieridae) в разных фазах динамики численности

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Key words: mortality, outbreak, population cycle, eruptive species, parasitoids, black-veined white, nuclear polyhedrosis virus.

Ключевые слова: смертность, вспышка массового размножения, градационный цикл, эруптивные виды, паразитоиды, боярышница, вирус ядерного полиэдроза.

Abstract. This study investigates the long-term dynamics of preimaginal mortality of the black-veined white at different stages of its life cycle (II–III instar larvae during the diapause and overwintering, V instar larvae, prepupae and pupae). The research was conducted in two locations: in the south of the Sverdlovskaya Oblast near Fomino village and in the suburban forests of the City of Novosibirsk. The mortality of black-veined white larvae during overwintering is shown to be independent of winter weather conditions and reaches maximum values (up to 89%) at the end of outbreaks. The decline of the black-veined white outbreak in the southern Sverdlovsk region was significantly contributed to by mass mortality of V instar larvae due to the nuclear polyhedrosis virus and II–III instar larvae during overwintering. In Novosibirsk, the infection rate of V instar larvae, prepupae, and pupae by tachinid flies (Diptera: Tachinidae) and the high mortality of larvae during diapause and overwintering were found to have a similar effect. The parasitoid hymenoptera *Cotesia* Cameron, 1891 sp. (Hymenoptera: Braconidae) (specialised parasitoids of larvae) and ichneumonids (Hymenoptera: Ichneumonidae) (pupal parasitoids) did not significantly contribute to reducing the density of the studied black-veined white populations.

Резюме. В работе изучены закономерности многолетней динамики преимагинальной смертности боярышницы на разных стадиях жизненного цикла: гусениц II–III возраста во время диапаузы и зимовки, гусениц V возраста, предкуколок и куколок. Исследования проводились в двух районах: на юге Свердловской области в окр. д. Фомино, и в пригородных лесах г. Новосибирск. Показано, что смертность гусениц боярышницы во время диапаузы и зимовки не зависит от погодных условий зимы и достигает максимальных значений (до 89 %) в годы окончания вспышек массового размножения. Значительный вклад в затухание вспышки массового размножения боярышницы на юге Свердловской области внесла массовая гибель гусениц V возраста от вируса ядерного полиэдроза и гусениц младших возрастов во время диапаузы и зимовки. В г. Новосибирск аналогичную роль играли увеличение заражённости гусениц V возраста, предкуколок и куколок тахинами (Diptera: Tachinidae) и высокая смертность гусениц во время диапаузы и зимовки. В то же время специализированные паразитоиды гусениц наездники *Cotesia*

Cameron, 1891 sp. (Hymenoptera: Braconidae) и паразитоиды куколок ихневмониды (Hymenoptera: Ichneumonidae) не оказали существенного влияния на снижение плотности изученных популяций боярышницы.

Introduction

The black-veined white *Aporia crataegi* Linnaeus, 1758 (Lepidoptera: Pieridae) is an eruptive butterfly species, that is widespread in the Palearctic [Gorbu-nov, Kosterin, 2003; Todisco et al., 2020]. Outbreaks of black-veined white have been recorded in Central and Eastern Europe [Stellwaag, 1924; Blunck, Wilbert, 1962; Osipenko, 1984; Anikin, 2015], the Urals and Pre-Urals [Turaev, 1964; Kulakova, Tatarinov, 2019], various regions of Siberia and the Russian Far East [Ammosov, 1966; Golutvin, 1972; Kopylov, Malkov, 2012; Kuznetsova, Palnikova, 2014; Ivonin et al., 2018]. During outbreaks, black-veined white caterpillars consume the foliage of wild and garden woody Rosaceous (bird cherry *Padus avium* Mill., apple tree *Malus* Mill., pear tree *Pyrus* L., blackthorn *Prunus spinosa* L., sour cherry *Prunus cerasus* L., sweet cherry *Prunus avium* L., quince *Cydonia oblonga* Mill., hawthorn *Crataegus* L., shadwood *Amelanchier* Medik., etc.) and can cause considerable damage to fruit and berry plantations and orchards [Krasnyuk, 1928; Babenko, 1982; Osipenko, 1984; Kuznetsov et al., 1999; Jugovic et al., 2017].

The causes of preimaginal mortality of the black-veined white are well described in the literature. Caterpillars are typically preyed upon by insectivorous birds, infected by parasitoid hymenoptera of the genus *Cotesia* Cameron, 1891 (Hymenoptera: Braconidae), or succumb to the nuclear polyhedrosis virus *Alphabaculovirus aporiae* (Krieg et Langenbuch, 1956) (Baculoviridae). Pupal mortality is usually caused by parasitoids, especially parasitoid hymenoptera of the tribe Pimplini (Hymenoptera: Ichneumonidae) and parasitoid tachinid flies (Diptera: Tachinidae) [Stellwaag, 1924; Krasnyuk, 1928; Kolomiets, 1956; Blunck, Wilbert, 1962; Turaev,

1964; Orlovskaya, 1968; Golutvin, 1972; Karpov, 1981; Osipenko, 1984; Zhang, Li, 1993; Kuznetsova, 2004]. However, the relative contribution of different factors to preimaginal mortality of black-veined white during different phases of the outbreak cycle is not well studied. In some cases, researchers have observed an increase in caterpillar mortality due to nuclear polyhedrosis virus or an increase in pupal infestation with parasitoids during the outbreak [Krasnyuk, 1928; Blunck, Wilbert, 1962]. In other cases, these patterns were absent [Osipenko, 1984; Kuznetsova, 2004]. The contradictory results obtained by different authors indicate the diversity of the ecological mechanisms involved in the decline of black-veined white outbreaks and suggest the necessity for further studies on the dynamics of preimaginal mortality factors during the outbreak cycles of this species. In this study we investigate the mortality of early instar black-veined white caterpillars during diapause and overwintering, and the rates and causes of mortality of pupae and V instar caterpillars.

Materials and methods

Study sites. The study was conducted at two distant sites with similar vegetation: in the south of Sverdlovskaya Oblast near Fomino village (56°36' N, 61°03' E), and in the floodplain pine forests of the City of Novosibirsk. The sampling site near Fomino is located in the subzone of pre-forest-steppe pine-birch forests [Kulikov et al., 2013], 14 km southeast of the large urban agglomeration of Ekaterinburg City. Pine berry and pine grass forests dominate near Fomino. These are dissected by paths and clearings and are surrounded by wet and dry meadows [Mukhin et al., 2003]. The sampling sites in Novosibirsk

are located in the northern forest-steppe subzone, in the Priobsky pine forest-steppe region, on the right bank of the Ob River. This area is mainly covered by berry, mossy-berry, bracken and grass pine forests, which have been modified to varying degrees by human activities [Krylov, 1961; Otmakhov et al., 2018].

Sampling. Samples were collecting from 2013 to 2022 in Fomino and from 2019 to 2022 in Novosibirsk. In order to estimate the population density of black-veined white near Fomino, we conducted transect counts of adults using the E. Pollard method [Pollard, 1977; Pollard, Yates, 1993] from 2015. Counts were carried out on a 1.6 km long and 10 m wide transect, which is part of an overgrown clearing under a power line, surrounded by a pine grass-shrub forest. In addition, we counted the wintering nests of the black-veined white in the autumn of 2019–2021, both near Fomino and in Novosibirsk. The nests were counted each year on the same randomly selected bird cherry, apple and rowan trees in the undergrowth of a pine forest. Near the Fomino 65 bird cherry trees, 34 rowan trees and 6 apple trees were selected for counting. In the pine forests of Novosibirsk, near Nizhnaya Eltsovka microdistrict (Нижняя Ельцовка), we counted wintering nests on 49 bird cherry trees (11 in 2019), 25 rowan trees (6 in 2019) and 8 apple trees. Host plant occupancy was calculated as the proportion of trees (in %) with wintering nests out of the total number of trees counted.

To estimate the mortality of early instar (II–III) caterpillars during diapause and overwintering, we collected wintering nests (near Fomino — from bird cherry and rowan trees, in Novosibirsk — from bird cherry and apple trees) in late March – early April, before the reactivation of caterpillars in nature, and kept them at room temperature (Table 1). Mortality was estimated

Table 1. Sample sizes of wintering nests and early instar larvae of the black-veined white
Таблица 1. Объём выборки зимовочных гнёзд и гусениц младших возрастов боярышницы

Sampling site	Year	Host plant	Number of trees	Number of nests	Number of dead larvae	Total number of larvae
Fomino	2013	Bird cherry	8	341	109	641
		Apple tree	3	77	21	367
	2014	Bird cherry	11	228	1172	1321
		Rowan	2	19	67	115
	2015	Apple tree	5	76	258	383
		Bird cherry	4	5	5	138
	2016	Rowan	2	3	0	68
		Bird cherry	28	104	80	2867
	2017	Rowan	20	65	37	1399
		Bird cherry	20	48	126	1144
	2018	Rowan	16	55	97	1123
		Bird cherry	8	17	16	304
	2019	Rowan	3	6	13	96
		Bird cherry	6	10	9	289
	2020	Bird cherry	14	23	67	580
		Rowan	3	4	4	115
2021	Bird cherry	5	9	17	334	
	Bird cherry	21	41	211	1404	
2022	Rowan	10	24	205	820	
	Bird cherry	15	107	717	2973	
Novosibirsk	2019	Apple tree	5	14	53	440
		Bird cherry	11	27	74	327
	2020	Apple tree	4	10	22	112
		Bird cherry	12	43	351	586
	2021	Apple tree	1	5	37	90
		Bird cherry	6	10	51	130
	2022	Apple tree	2	2	6	37
		Bird cherry				

by the number of caterpillars that were not reactivated and did not leave the wintering cocoons [Zakharova et al., 2015]. In the case of wintering nests destroyed by birds, it is not possible to determine the original number of caterpillars and, consequently, to calculate mortality. Therefore, we did not collect such nests.

In late May–early June we randomly sampled V instar caterpillars, prepupae and pupae from bird cherry, apple and rowan trees to determine the rate and causes of mortality of late instar caterpillars and pupae. Near Fomino, sampling started when the majority of the caterpillars in the population were in late V instar and continued until pupation was complete. Due to the extremely low density of the black-veined white population in 2014 and 2017–2019, insufficient samples of prepupae and pupae were collected (Table 2) and this material was therefore excluded from further analysis. For the same reason, it was not possible to collect a sample of caterpillars in 2019. In Novosibirsk, samples were collected over a shorter period when most individuals were in the prepupal or pupal stage (Table 2). Sampling was carried out in 2019–20 near Nizhnyaya Yeltsovka (54°53' N, 83°05' E) and in 2021 in the Zaeltzovskii Raion (55°04' N, 82°49' E).

Collected caterpillars and pupae were kept under natural light and temperature in individual 0.5 litre plastic containers covered with a cotton cloth until death or adult emergence. Caterpillars were supplied daily with fresh leaves of the host plant from which they were collected. Dead caterpillars, prepupae and pupae were left in the containers until the emergence of the parasitoids.

The death of caterpillars from nuclear polyhedrosis virus was determined by external specific signs of acute infection: softening and reddening of the body, liquefaction of internal organs, leakage of brownish fluid through ruptures in the cuticle [Polenogova, 2013]. In 2013, Dr. A.V. Ilyinykh confirmed the presence of polyhedra in caterpillars. We did not assess pupal mortality due to nuclear polyhedrosis virus or fungal and bacterial diseases, nor did we assess larval mortality due to fungal and bacterial diseases.

Statistical analysis. Caterpillar mortality during diapause and overwintering as a function of year, host plant and winter weather was analysed using a beta-binomial regression implemented in the glmmTMB package [Brooks et al., 2017]. A mixed effects beta-binomial model was applied (year was treated as a random factor) to analyse the influence of winter weather (mean and minimum temperatures). Mortality of V instar caterpillars, prepupae and pupae as a function of year and host plant was analysed using binomial logistic regression. The significance of the effect of categorical predictors was assessed via the Wald χ^2 test. A multinomial model in the nnet package was used to analyse the pattern of mortality causes of V instar caterpillars, prepupae and pupae as a function of year and host plant [Venables, Ripley, 2002], and the maximum likelihood ratio test was used to assess the influence of categorical predictors. The causes of mortality for V instar caterpillars differ significantly from those of the prepupae and pupae. Therefore, these groups were analysed separately. Specimens that died due to accidental injury or were lost during the study

Table 2. Sample sizes of V instar larvae, prepupae and pupae of the black-veined white collected from different host plants in 2013–2022

Таблица 2. Объем выборки гусениц старших возрастов, предкуколок и куколок боярышницы, собранных с разных кормовых растений в 2013–2022 гг.

Sampling site	Year	Sampling dates	Host plant	Number of larvae	Number of prepupae and pupae
Fomino	2013	1–15.06	Bird cherry	285	202
			Rowan	107	16
			Apple tree	11	0
	2014	22–26.05	Bird cherry	365	5
			Rowan	260	0
	2015	28.05–1.06.	Bird cherry	299	77
			Rowan	255	18
	2016	24–28.05	Bird cherry	249	202
			Rowan	217	16
	2017	31.05–11.06	Bird cherry	330	0
			Rowan	262	0
	2018	6–16.06	Bird cherry	174	0
			Rowan	30	0
	2020	21–23.05	Bird cherry	150	2
			Bird cherry	141	164
	2021	16–22.05	Rowan	48	3
Apple tree			16	0	
Bird cherry			341	325	
2022	1–12.06	Rowan	133	10	
		Apple tree	43	0	
		Bird cherry	105	385	
Novosibirsk	2019	6.06	Rowan	57	54
			Apple tree	113	109
			Bird cherry	97	851
	2020	20.05	Rowan	30	78
			Apple tree	0	44
			Bird cherry	41	128
	2021	29–31.05	Rowan	13	29
			Apple tree	56	561
			Bird cherry	13	29

Table 3. Abundance of adult black-veined whites near Fomino in 2015–2022
Таблица 3. Результаты маршрутных учётов имаго боярышницы в окр. д. Фомино (2015–2022 гг.)

Year	Number of counts	Abundance of adults, ind./km	95% confidence interval (under – upper)
2015	3	18.5	11.1 – 29.6
2016	11	40.3	28.6 – 51.8
2017	8	21.5	14.2 – 29.5
2018	8	12.2	7.5 – 16.7
2019	10	28.9	17.4 – 43.1
2020	12	35.8	24.9 – 47.2
2021	9	86.5	61.6 – 110.9
2022	8	381.1	204.2 – 574.8

were excluded from the analysis. Confidence intervals for means were calculated by basic non-parametric bootstrap, and confidence intervals for proportions were calculated using Wilson's method. All statistical analyses were performed in R [R Core Team, 2022].

The present work is registered in ZooBank (www.zoobank.org) under LSID urn:lsid:zoobank.org:pub:D510D638-5108-40FD-AEE2-A6FB5E82410A.

Results

Population dynamics. An outbreak of black-veined white was recorded from 2011 to 2013 in the Urals, north-eastern European Russia and the Trans-Urals [Vlasova et al., 2014; Bogacheva et al., 2018; Adakhovskiy, 2019; Kulakova, Tatarinov, 2019]. Near Fomino, the population density decreased significantly in 2014 [Zakharova и др., 2015]. According to the results of the adult counts, the abundance of adult black-veined whites near Fomino remained low between 2015 and 2020 (from 12 to 40 adults per 1 km of route). From 2021 onwards, adult abundance began to increase, reaching 380 individuals per 1 km of route in 2022 (Table 3). Wintering nest counts showed that the occupancy of bird cherry (the main black-veined white host plant in the Middle

Urals) increased from 25–35 % to 83 % between 2020 and 2022 (Fig. 1). Consequently, the black-veined white population near Fomino was in the latency (endemic) phase from 2014 to 2020, with a transition to increasing abundance and the start of a new outbreak in 2021–2022.

An outbreak of black-veined white started in 2017 in Novosibirsk and the surrounding area [Ivonin et al., 2018]. According to our observations, the outbreak continued in spring 2019 in Novosibirsk. Wintering nest counts revealed a decrease in host plant occupancy near Nizhnyaya Eltsovka from 100 % (autumn 2019) to 15 % between 2020 and 2022 (Fig. 1). In the spring of 2022, we did not find a single live caterpillar or pupa during a three-day search in the pine forests of Novosibirsk. Thus, the black-veined white population was in the outbreak phase in 2019, with declining abundance occurring in 2020–2022.

Mortality of early instar larvae during diapause and overwintering. Caterpillar mortality during diapause and overwintering near Fomino is independent of host plant (Wald $\chi^2 = 0.35$; $df = 1$; $p = 0.554$), but differs significantly between years (Wald $\chi^2 = 289.03$; $df = 9$; $p < 0.001$). In most cases, the mortality rate was low, ranging from 3 to 20 % (Table 4). A remarkably high mortality rate (89 % on bird cherry and 58 % on rowan) was observed in the autumn-winter period of 2013–2014 — at the end of the outbreak. Winter air temperature has no significant effect on the mortality of early instar caterpillars (in the case of average temperature Wald $\chi^2 = 0.12$; $df = 1$; $p = 0.724$; in the case of minimum temperature Wald $\chi^2 = 0.98$; $df = 1$; $p = 0.323$).

Autumn-winter caterpillar mortality in Novosibirsk was generally higher than near Fomino, ranging from 12 to 60 %. Caterpillar mortality in Novosibirsk is independent of the host plant (Wald $\chi^2 = 0.24$; $df = 1$; $p = 0.621$), but differs significantly between years (Wald $\chi^2 = 26.47$; $df = 3$; $p < 0.001$). The highest mortality (40 % on apple and 60 % on bird cherry) was recorded in the autumn-winter period 2020–2021, at the end of the outbreak (Table 4). Average and minimum winter temperatures in Novosibirsk, as well as near Fomino, do not significantly affect the autumn-winter mortality rate of caterpillars (in the case of average temperature Wald $\chi^2 = 0.34$; $df = 1$; $p = 0.561$; in the case of minimum temperature Wald $\chi^2 = 0.21$; $df = 1$; $p = 0.646$).

Mortality of V instar larvae and pupae. Tachinids (Diptera: Tachinidae) (in 21 % of the total number of

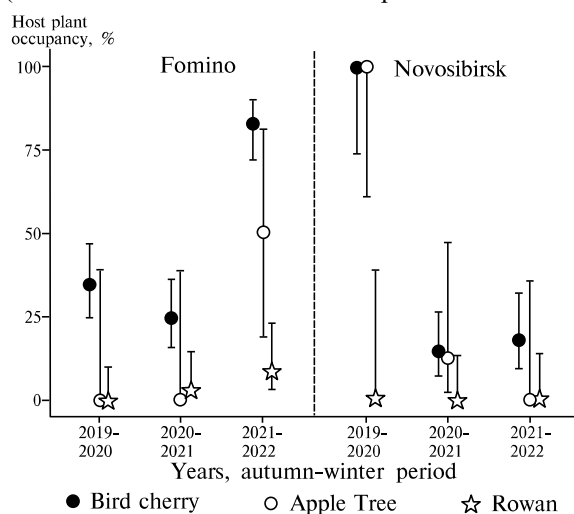


Fig. 1. Proportion of the host plants with winter nests (mean and 95 % confidence intervals by Wilson) near Fomino vill. and in the City of Novosibirsk.

Рис. 1. Заселённость кормовых растений (среднее и 95 % доверительные интервалы по Уилсону) в окр. д. Фомино и в г. Новосибирск.

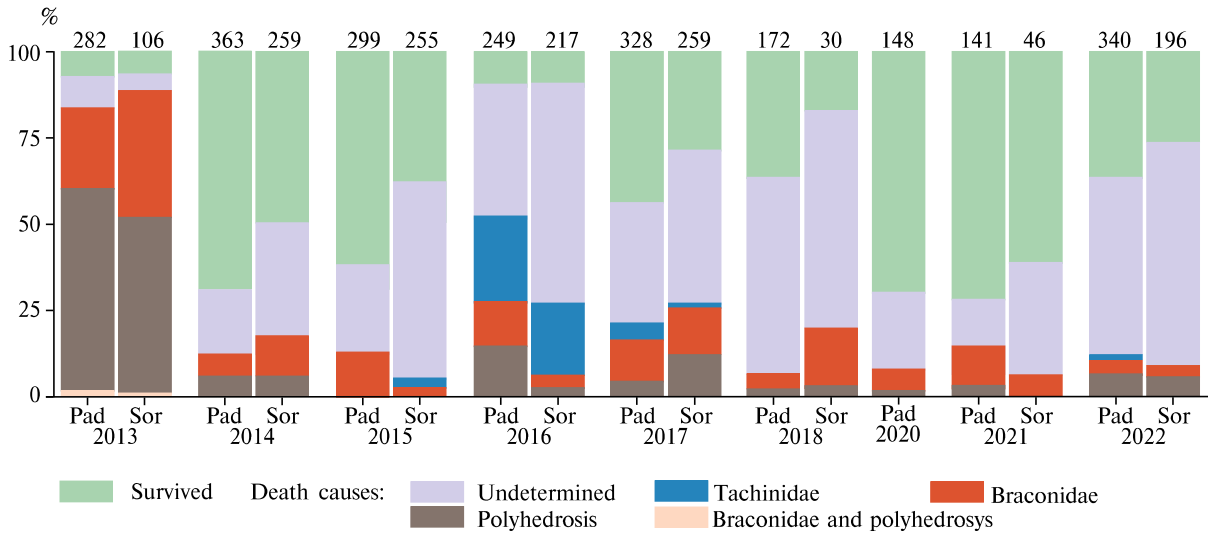


Fig. 2. Survival rate and pattern of mortality causes of the V instar larvae of the black-veined white near Fomino from 2013 to 2022. Designations: Pad — Bird Cherry, Sor — Rowan, sample sizes given above the columns.

Рис. 2. Доля выживших и структура причин смертности гусениц боярышницы V возраста в окр. д. Фомино (2013–2022 гг.). Обозначения: Pad — черёмуха, Sor — рябина; над столбцами указаны объёмы выборок.

dead individuals), parasitoid wasps *Cotesia* Cameron, 1891 sp. (Hymenoptera: Braconidae) (in 13 % of cases) and an acute form of polyhedrosis infection (in 11 % of cases) were the main causes of death of the black-veined white V instar caterpillars, prepupae and pupae near Fomino and in pine forests of Novosibirsk. In 51 % of cases, the cause of death could not be determined. These individuals may have died as a result of a latent form of polyhedrosis infection, a fungal or bacterial disease, or due to the stress associated with capture and rearing.

Mortality of V instar larvae near Fomino depended on host plant (Wald $\chi^2 = 71.6$; $df = 1$; $p < 0.001$) and year of study (Wald $\chi^2 = 507.0$; $df = 8$; $p < 0.001$). Caterpillar mortality was slightly higher on rowan than on bird cherry. The pattern of mortality causes differed significantly between years (LR $\chi^2 = 1052.3$; $df = 24$; $p < 0.001$) and on different host plants (LR $\chi^2 = 29.8$; $df = 3$; $p < 0.001$). In the year of the outbreak decline (2013), mortality was highest, reaching 93%, with acute polyhedrosis infection being the main cause of caterpillar death (in 61% of cases). In 2014–2015, after the outbreak termination, mortality decreased to 39–50 %. In 2016, a new peak in caterpillar mortality was recorded (up to 91 %), with tachinids being a significant factor in their deaths (Fig. 2). Mortality of V instar caterpillars was minimal (30 %) in 2020–2021, before the start of a new outbreak. It rose again in 2022, mainly due to an increase in the number of caterpillars dying from unknown causes (Fig. 2). Caterpillar infestation by *Cotesia* Cameron, 1891 sp. was generally low. It reached its maximum in 2013 (25 % for bird cherry and 37 % for rowan) and fluctuated between 2 and 17 % in other years.

Mortality of prepupae and pupae near Fomino was significantly dependent on the study year (Wald $\chi^2 = 81.5$; $df = 4$; $p < 0.001$), but not on the host plant species (Wald $\chi^2 = 2.4$; $df = 1$; $p = 0.12$). It reached a maximum in 2013 and 2016 (49–51 %), whereas it was relatively

low in 2015 and 2021–2022 (23–33 %, Fig. 3). The pattern of mortality causes differed significantly between years (LR $\chi^2 = 217.8$; $df = 8$; $p < 0.001$), but not between host plants (LR $\chi^2 = 1.6$; $df = 2$; $p = 0.44$). In 2013, the majority of individuals (92 % of all deaths) perished from undetermined causes. In 2016, the main drivers of pupal mortality were parasitoids: tachinids (43 % of all dead individuals) and ichneumonids (28 %). In 2015 and 2021, prepupae and pupae were most likely to die due to infection by ichneumonids, and in 2022 from undetermined causes (Fig. 3).

Caterpillar mortality in the Novosibirsk pine forests was significantly dependent on study year (Wald $\chi^2 = 17.2$;

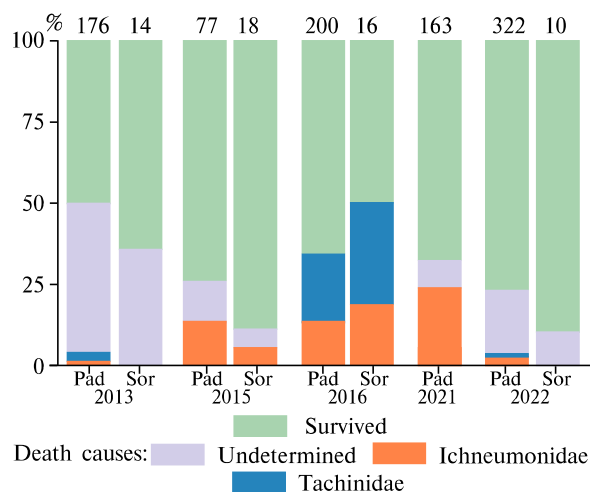


Fig. 3. Survival rate and pattern of mortality causes of the prepupae and pupae of the black-veined white near Fomino during 2013–2022. Designations: Pad — Bird Cherry, Sor — Rowan; sample sizes given above the columns.

Рис. 3. Доля выживших и структура причин смертности предкуколок и куколок боярышницы в окр. д. Фомино (2013–2022 гг.). Обозначения: Pad — черёмуха, Sor — рябина; над столбцами указаны объёмы выборок.

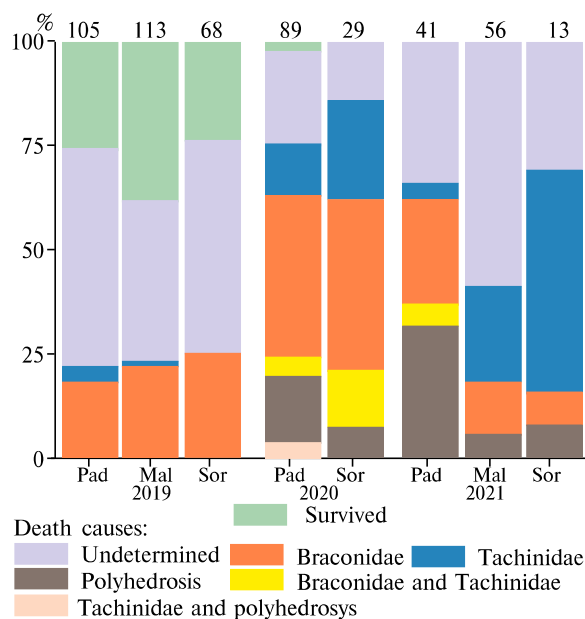


Fig. 4. Survival rate and pattern of mortality causes of the V instar larvae of the black-veined white in Novosibirsk City during 2019–2021. Designations: Pad — Bird Cherry, Mal — Apple tree, Sor — Rowan; sample sizes given above the columns.

Рис. 4. Доля выживших и структура причин смертности гусениц боярышницы V возраста в г. Новосибирск (2019–2021 гг.). Обозначения: Pad — черёмуха, Mal — яблоня, Sor — рябина; над столбцами указаны объёмы выборки.

$df = 2$; $p < 0.001$), but not on host plant (Wald $\chi^2 = 5.8$; $df = 2$; $p = 0.055$). The pattern of caterpillar mortality causes differed significantly between years (LR $\chi^2 = 130.7$; $df = 8$; $p < 0.001$) and on different host plants (LR $\chi^2 = 17.0$; $df = 8$; $p = 0.031$). In 2019, at peak population densities, caterpillar mortality ranged from 62 % on apple tree to 76 % on rowan, with parasitoid wasps *Cotesia Cameron*, 1891 sp. being the main cause of death. In 2020, the mortality rate increased to 98 %; in 2021, all collected caterpillars died (Fig. 4). At the same time, the proportion of tachinids among the parasitoids increased in 2020–2021.

Mortality of prepupae and pupae depended on both host plant species (Wald $\chi^2 = 30.7$; $df = 2$; $p < 0.001$) and year of study (Wald $\chi^2 = 264.0$; $df = 2$; $p < 0.001$). Prepupae and pupae developing on bird cherry died least often, while those feeding on apple trees died slightly more often. Prepupal and pupal mortality was highest (up to 86 %) on rowan (Fig. 5). Mortality increased steadily on all host plants from 2019 to 2021. The pattern of mortality causes differed significantly between years (LR $\chi^2 = 69.0$; $df = 4$; $p < 0.001$). Tachinids were the main driver of increased mortality in prepupae and pupae, as shown in Fig. 5.

Discussion

According to the available data, the mortality rate of black-veined white larvae during the diapause and overwintering is typically not high and varies between 5 % and 30 % [Krasnyuk, 1928; Kajgorodtsev, 1971; Osipenko, 1984]. An exception is the data of Yu.N. Ammosov

from Yakutia, according to which live caterpillars were found in only 21 % of the nests examined [Ammosov, 1966]. The results of this study are generally consistent with these observations: mortality of black-veined white caterpillars during diapause and overwintering did not usually exceed 25 %, but in some years it reached extremely high levels (60–89 %, Table 4). It should be noted that we only estimated caterpillar mortality in undisturbed nests and therefore did not take into account their mortality by insectivorous birds, which can be quite significant [Kuznetsova, Palnikova, 2014].

Black-veined white wintering nests are located outdoors and are directly exposed to wind and freezing temperatures. Diapausing caterpillars have been shown to be exceptionally frost tolerant and can survive freezing in liquid nitrogen [Asahina et al., 1972; Li, 2006]. Nevertheless, the experiment by N.G. Li [Li, 2012] revealed a direct dependence of caterpillar mortality on the ambient temperature: when diapausing caterpillars were kept at -22 °C for one hour, mortality was only 2 %, at -85 °C it was 44 % and at -85 °C for one day 59 % of the caterpillars did not survive. Previously, we suggested that the extremely high mortality of black-veined white caterpillars near Fomino in the winter of 2013–2014 was caused by a sharp decrease in air temperature to -35.7 °C [Zakharova et al., 2015]. However, statistical analysis of data from 2013–2022 near Fomino and 2019–2022 in Novosibirsk showed that mortality of black-veined white caterpillars during diapause and overwintering varied independently of winter air temperature. In the study areas, winter air temperatures did not fall below -41 °C (Table 4). This suggests that temperature drops to -30 °C to -40 °C are far from extreme for the black-veined white and do not lead to a statistically significant increase in caterpillar mortality.

Caterpillar mortality during diapause and overwintering reached its maximum in the year of the outbreak termination, both near Fomino and in the pine forests of Novosibirsk. It is known that the hardiness of black-veined white caterpillars to cold and freezing temperatures is caused by their ability to synthesise and accumulate a number of chemical compounds, primarily ice-nucleating proteins and intracellular glycerol [Li, 2006, 2012]. The main source of glycerol for diapausing insects is glycogen stores in the fat body [Storey, 1990]. It is thus possible that lack of or poor quality food, overcrowding and disease at the end of outbreaks may reduce the ability of caterpillars to withstand low or extremely low temperatures. It is likely that the mass mortality of caterpillars in the winter of 2013–2014 near Fomino and in 2020–2021 in Novosibirsk was caused by a combination of unfavourable conditions for caterpillar prediapause development and a frosty winter. High caterpillar mortality may also be caused by nuclear polyhedrosis virus. Infection of first instar caterpillars and subsequent mass mortality during overwintering have been observed in epizootics induced by this virus [Orlovskaya, 1968].

The long-term data presented in this study on mortality rates and factors of V instar caterpillars, prepupae and

Table 4. Mean and minimum winter air temperature and larval mortality during diapause and overwintering (means and 95% confidence intervals by Wilson) near Fomino and in Novosibirsk.

Таблица 4. Средние и минимальные значения температуры воздуха с декабря по февраль и смертность гусениц во время диапаузы и зимовки (среднее и 95% доверительные интервалы по Уилсон) в окр. д. Фомино и в г. Новосибирске

Sampling site	Years of winter	Mean temperature, °C	Minimum temperature, °C	Host plant	Mortality, %	95% confidence interval (under – upper)
Fomino	2012–2013	-12.5	-26.1	Bird cherry	17.0	14.3 – 20.1
	2013–2014	-12.2	-35.7	Bird cherry	88.7	86.9 – 90.3
				Rowan	58.3	49.1 – 66.9
	2014–2015	-8.8	-27.8	Bird cherry	3.6	1.6 – 8.2
				Rowan	0.0	0.00 – 5.4
	2015–2016	-9.2	-26.4	Bird cherry	2.8	2.3 – 3.5
				Rowan	2.6	1.9 – 3.6
	2016–2017	-13.3	-33.1	Bird cherry	11.0	9.3 – 13.0
				Rowan	8.6	7.1 – 10.4
	2017–2018	-11.0	-25.2	Bird cherry	5.3	3.3 – 8.4
				Rowan	13.5	8.1 – 21.8
	2018–2019	-11.2	-31.9	Bird cherry	3.1	1.7 – 5.8
Bird cherry				11.6	9.2 – 14.4	
2019–2020	-6.3	-22.7	Rowan	3.5	1.4 – 8.6	
			Bird cherry	5.1	3.2 – 8.0	
2020–2021	-14.2	-32.0	Bird cherry	15.0	13.3 – 17.0	
			Rowan	25.0	22.2 – 28.1	
2021–2022	-8.5	-23.3	Bird cherry	24.1	22.6 – 25.7	
			Apple tree	12.1	9.3 – 15.4	
Novosibirsk	2018–2019	-16.9	-40.1	Bird cherry	22.6	18.4 – 27.5
				Apple tree	19.6	13.3 – 28.0
	2019–2020	-9.3	-31.6	Bird cherry	59.9	55.9 – 63.8
				Apple tree	41.1	31.5 – 51.4
	2020–2021	-18.0	-41.0	Bird cherry	39.2	31.3 – 47.8
				Apple tree	16.2	7.7 – 31.1
2021–2022	-11.7	-30.0				

Примечание: The average and minimum temperature near Fomino are given by data from the Ekaterinburg weather station, in Novosibirsk — by data from the Novosibirsk weather station.

Note: Средние и минимальные температуры в окр. д. Фомино приведены по данным метеостанции г. Екатеринбург, в г. Новосибирск — по данным метеостанции г. Новосибирск.

pupae of the black-veined white near Fomino and in the pine forests of Novosibirsk significantly complement the data available in the literature [Krasnyuk, 1928; Blunck, Wilbert, 1962; Turaev, 1964; Golutvin, 1972; Osipenko, 1984; Kuznetsova, 2004]. At the end of the outbreak near Fomino, we observed mass mortality of caterpillars due to nuclear polyhedrosis virus and of prepupae and pupae from unidentified causes (Figs 2, 3). It is possible that the main cause of death of prepupae and pupae was also polyhedrosis infection [Orlovskaya, 1968]. Our results are in concordance with the data from other authors, according to which epizootics caused by this virus have in some cases led to the termination of outbreaks of black-veined white [Krasnyuk, 1928; Blunck, Wilbert, 1962].

We found no consistent increase in the infestation of the black-veined white caterpillars and pupae by Braconidae (genus *Cotesia* Cameron, 1891) and Ichneumonidae parasitoid wasps as the outbreak subsided in the pine forests of Novosibirsk (Figs 4, 5). Their contribution to the termination of the outbreak near Fomino in 2013 was also insignificant (Figs 2, 3).

The parasitoid wasps *Cotesia* Cameron, 1891 sp., particularly *C. glomerata* (Linnaeus, 1758) and *C. pieridis* (Bouche, 1834), parasitise predominantly the garden whites of the genus *Pieris* Hübner, 1819 [Osmolovsky, 1964; Alekseev et al., 2019]. *C. glomerata* (Linnaeus, 1758) has been shown to readily transition from black-veined whites to garden whites and vice versa [Osmolovsky, 1964; Sato, 1978]. During the period when *C. glomerata* (Linnaeus, 1758) adults emerge from V instar

black-veined white caterpillars, I-III instar black-veined white larvae are absent in nature, and accordingly the parasitoid female can only lay eggs in caterpillars of

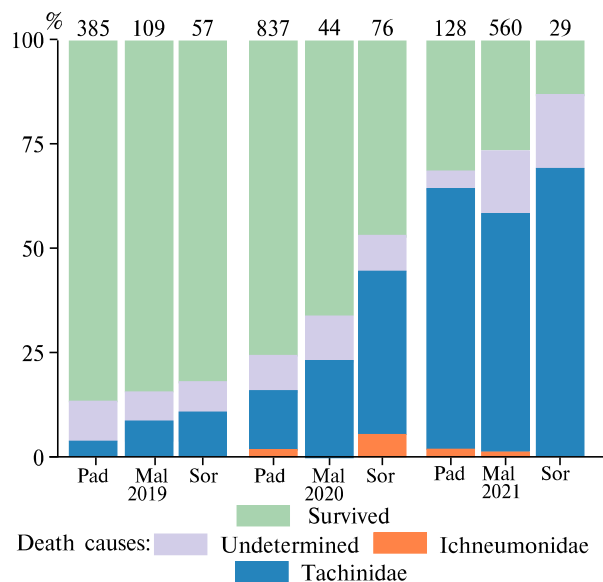


Fig. 5. Survival rate and pattern of mortality causes of the prepupae and pupae of the black-veined white in Novosibirsk City during 2019–2021. Designations: Pad — Bird Cherry, Mal — Apple tree, Sor — Rowan; sample sizes given above the columns.

Рис. 5. Доля выживших и структура причин смертности предкуколок и куколок боярышницы в г. Новосибирск (2019–2021 гг.). Обозначения: Pad — черёмуха, Mal — яблоня, Sor — рябина; над столбцами указаны объёмы выборок.

garden whites [Wilbert, 1959]. Therefore, the abundance of *Cotesia* Cameron, 1891 sp. depends not only on the population density of black-veined whites, but also on the abundance of whites of the genus *Pieris* Hübner, 1819 [Blunck and Wilbert, 1962]. This is probably the reason why these parasitoids do not play a significant role in suppressing outbreaks of black-veined whites, according to our results and data from other researchers [Krasnyuk, 1928; Osipenko, 1984; Kuznetsova, 2004].

Ichneumonidae infestation of pupae was generally low (12% near Fomino and 1% in Novosibirsk). It is known that all Ichneumonidae species parasitising the black-veined white are broadly oligophagous or polyphagous and can develop in pupae of different Lepidoptera families [Kolomiets, 1956; Alekseev et al., 2019]. Apparently, the black-veined white is not their main host, even in outbreak years. It is also possible that the abundance of these parasitoid wasps is effectively limited by secondary parasitoids [Kolomiets, 1956]. Previously, similar results were obtained for ichneumonids in Central Europe [Blunck, Wilbert, 1962] and in the northern steppe zone of Eastern Europe [Osipenko, 1984]. However, cases have been described where pupal infestation by ichneumonids increased towards the end of the outbreak and these parasitoids played an important role in terminating the outbreak [Krasnyuk, 1928; Telenga, 1955; Turaev, 1964].

It was found that the infestation of V instar larvae, prepupae and pupae by tachinids in the pine forests of Novosibirsk increased steadily as the outbreak subsided (Figs 4, 5). Thus, tachinid flies contributed significantly to the decline in black-veined white population density in this region in 2020–2021. The tachinid species that parasitise the black-veined white are known to be polyphagous, developing on caterpillars and pupae of different families of Lepidoptera [Tschorsnig, 2017]. Apparently, they are able to switch to parasitising black-veined white during outbreak years and increase their abundance following the phytophagous population. Other researchers [Krasnyuk, 1928; Blunck, Wilbert, 1962; Turaev, 1964; Golutvin, 1972; Osipenko, 1984] did not find a significant contribution of tachinids to the preimaginal mortality of black-veined white. Our data suggest that tachinids may play a more important role in regulating black-veined white population density and outbreak termination than previously recognised.

It has often been argued that predators and parasitoids effectively control fluctuations in the abundance of eruptive species during the latency phase of the outbreak cycle, eliminating a significant proportion of the population [Isaev et al., 2001; Klemola et al., 2002, 2010; Purewaran et al., 2016; Mlynarek et al., 2017]. However, the mortality of black-veined white larvae and pupae from parasitoids remained relatively low during the latency phase (2014–2020) near Fomino (with the exception of 2016, when an increase in tachinid infestation of caterpillars and pupae was observed, Figs 2, 3). Therefore, the low population density after the end of the outbreak in the studied population was not maintained by a high pressure of entomophages. This is probably related to the

fact that there are no narrowly specialised species among the parasitoids of the black-veined white, and when the phytophagous population density decreases, they immediately switch to parasitising other species of Lepidoptera.

Many significant variables were not taken into account in this study (e.g. nuclear polyhedrosis virus infection of early instar caterpillars, defoliation of host plants and foliage quality). Therefore, it is not possible to provide an exhaustive description of the mechanisms involved in the initiation and suppression of black-veined white outbreaks. Nevertheless, the results allow us to draw conclusions about the factors of preimaginal mortality, that played an important role in the decline of outbreaks of black-veined white in 2013–2014 near Fomino and in 2020–2021 in the pine forests of Novosibirsk. Near Fomino, the termination of the outbreak was associated with an epizootic of nuclear polyhedrosis virus and extremely high mortality of caterpillars during diapause and overwintering (possibly also caused by this virus). In Novosibirsk, the decline in population density was largely due to tachinids and, similar to Fomino, high winter caterpillar mortality. The factors influencing the decline of black-veined white therefore depend on the specific ecological conditions under which the outbreak cycle is realised.

Acknowledgements

The authors are obliged to [A.V. Ilyinykh](#) for the identification of the black-veined white nuclear polyhedrosis virus. We are also grateful to T.S. Oslina, [A.V. Ivanov](#), P.V. Rudoiskatel and K.I. Fadeev for their help in collecting material and growing preimaginal stages of black-veined white.

The study was supported by the state assignment of the Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences (№ 122021000091-2).

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Поступила в редакцию 13.2.2024