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Abundance and impact of egg parasitoids on the pine processionary moth (*Thaumetopoea pityocampa*) in Bulgaria

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We collected 2297 egg batches of the pine processionary moth (*Thaumetopoea pityocampa*) during the period 1991-2018 from 44 sites in Bulgaria. The sampling sites were classified into three groups according to *T. pityocampa* phenological form (early, late and both forms) as well as in two groups of its range (historical and newly colonized areas). Seven primary egg parasitoids were identified: *Ooencyrtus pityocampae*, *Baryscapus servadeii*, *Pediobius bruchicida*, *Anastatus bifasciatus*, *Eupelmus (Macroneura) vesicularis*, *Eupelmus (Macroneura) vladimiri* and *Trichogramma* sp., and one hyperparasitoid, *Baryscapus transversalis*. The average impact of egg parasitoids (the percentage of parasitized host eggs) on *T. pityocampa* in Bulgaria was 13.8%. The two main parasitoids, *O. pityocampae* and *B. servadeii*, parasitized about 90% of the host eggs. The remaining parasitoids were of insignificant consequence to the parasitism of the *T. pityocampa* eggs, but in areas recently colonized by the pest, *A. bifasciatus* and *Trichogramma* sp. had a noticeable share (up to 33% of the impact). In old habitats of the host (areas colonized more than 10 years), the impact was almost two times higher than in new ones (15.3% *vs*. 8.6%). This could be attributed to *B. servadeii*, which was rare in newly colonized areas of *T. pityocampa* (impact 0.5%), but strongly dominant in old habitats (impact 7.2%). In contrast, *O. pityocampae* had a significant impact in new habitats (4.9%), which increased only slightly over time, reaching 6.0% in old habitats. There was no significant difference between the percentage of parasitism of the early and late form of the pine processionary moth (14.8% *vs*. 15.9%). However, there was a significant difference in the share of separate species in the parasitoid complex: in the early form, *B. servadeii* definitely dominated (63% of the infested eggs), while in the late form *O. pityocampae* dominated, although not so strongly (52% of the infested eggs). This difference is most likely due to the phenological characteristics of the parasitoids and the two forms of *T. pityocampa*. *B. transversalis* secondarily infested about 5% of the eggs of *O. pityocampae* and *B. servadeii*. This percentage was slightly lower for new habitats and habitats of the early form of pine processionary moth (3% and 4%, respectively). The impacts of the main parasitoids *O. pityocampae* and *B. servadeii* as well as the total impact of the parasitoid complex as a whole decreased with altitude. Conversely, the impacts of *A. bifasciatus* and *Trichogramma* sp. slightly increased with altitude probably due to the reduced competition of the main parasitoids.

Keywords: *Thaumetopoea pityocampa*, Distribution, Habitats, Expansion, Phenological Forms, Egg Parasitism, Bulgaria

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Introduction

The pine processionary moth, *Thaumetopoea pityocampa* Denis & Schiffermüller, 1775 (Lepidoptera: Notodontidae) is among the most dangerous insect pests in pine forests. The northern border of its distribution passes through Bulgaria where two phenological forms of the species are widespread: the summer (early developing) and the winter (late developing – Tsankov et al. 1996, Mirchev al. 2019). The abundance of *T. pityocampa* has been highly influenced by human activities. Since 1978, the annual size of its attacks in Bulgaria has increased five times as a consequence of the large-scale afforestation with black pine (*Pinus nigra* Arn.) and Scots pine (*P. sylvestris* L.) in the period 1950-1980 (Mirchev et al. 2011). Until the 1990s, the pest attacks remained limited to its historical range, where it has been known since the 1910s – southwestern and south central Bulgaria, both traditionally assigned to the Continental-Mediterranean and the European-Continental climatic zones (Sabev & Stanev 1959). In 1991, economically significant attacks began in Central Bulgaria, northeast of the historical range. As a result, a stable expansion zone of *T. pityocampa* developed in Central Bulgaria, despite all control measures (Mirchev et al. 2018). The front of expansion is steadily moving east at a speed of about 2.5 km per year on the southern slope of the Balkan Range and in Sredna Gora Mt. Currently, the expansion zone coincides with Stara Zagora region (Zaemdzhikova et al. 2018).

The egg parasitoids are the most signifi-

Tab. 1 - Characteristics of the studied localities of *T. pityocampa* and sampled biological material. (OH): old habitats; (NCA): newly colonized areas (new habitats).

Habitat	N	Locality, District	Altitude (m a.s.l.)	No. sampling years		*T. pityocampa* range	Sampling (n)	
				N	Year of collection		Egg batches	Eggs
Early phenological form	1	Dobrostan, Plovdiv	850	1	2018	NCA	8	1740
	2	Dyulitsa, Kardzhali	390	1	2016	OH	7	1815
	3	Domishte, Kardzhali	420	1	2016	OH	30	7164
	4	Drangovo, Kardzhali	440	1	2016	OH	6	1348
	5	Dzherovo, Kardzhali	460	1	2016	OH	20	4535
	6	Fotinovo, Kardzhali	450	1	2018	OH	180	38202
	7	Kandilka, Kardzhali	450	1	2018	OH	17	3780
	8	Kardzhali, Kardzhali	400	1	1995	OH	67	13560
	9	Kayaloba, Kardzhali	490	1	2016	OH	18	3337
	10	Medevtsi, Kardzhali	470	1	2016	OH	30	6832
	11	Yanino, Kardzhali	410	1	2016	OH	26	5428
	12	Hvoina, Smolyan	950	1	1995	NCA	14	2350
Late phenological form	13	Asenovgrad, Plovdiv	400	2	2016, 2017	OH	41	9455
	14	Banya, Plovdiv	340	4	1992, 1993, 1996, 1999	OH	93	20565
	15	Garmen, Blagoevgrad	700	2	2016, 2017	OH	42	8839
	16	Gega, Blagoevgrad	856	2	2017	OH	38	8226
	17	Gotse Delchev, Blagoevgrad	830	2	2016, 2017	OH	51	11935
	18	Dikchan, Blagoevgrad	900	3	2016, 2017, 2018	OH	107	24814
	19	Dupnitsa, Blagoevgrad	725	2	1994, 1995	OH	56	13732
	20	Ivailovgrad, Haskovo	285	5	2009-10, 2012, 2016, 2018	OH	145	39252
	21	Marikostinovo, Blagoevgrad	180	6	1991-1996	OH	329	76868
	22	Parvomai, Blagoevgrad	450	3	2016, 2017, 2018	OH	90	20978
	23	Plosky, Blagoevgrad	515	3	1991, 1992, 1994	OH	73	16211
	24	Satovcha, Blagoevgrad	950	4	1994, 2000, 2002, 2008	OH	74	15890
	25	Sandanski, Blagoevgrad	450	3	1994, 1997, 2017	OH	57	12792
	26	Maglizh, Stara Zagora	365	2	2016, 2017	NCA	25	6529
	27	Klisura, Plovdiv	710	3	2016, 2017, 2018	OH	96	22000
	28	Kurtovo, Plovdiv	500	3	1991, 1995, 1996	OH	41	8979
	29	Kyustendil, Kyustendil	1045	6	1994-95, 1997-99, 2014	NCA	96	14057
	30	Rilski Ðœanastir, Kyustendil	700	1	2016	OH	6	1478
	31	Vetren, Kyustendil	680	3	2013, 2014, 2016	NCA	85	20950
Common (both early and late phenological forms)	32	Hisaria, Plovdiv	415	2	2016, 2018	OH	59	15009
	33	Karlovo, Plovdiv	535	1	2016	OH	8	2183
	34	Chirpan, Stara Zagora	480	1	2017	NCA	13	2894
	35	Kazanlak, Stara Zagora	475	1	2016	NCA	71	18010
	36	Dolno Sahrane, Stara Zagora	450	2	2016, 2018	OH	40	9247
	37	Sladak kladenets, Stara Zagora	400	1	2016	NCA	36	8279
	38	Lesichevo, Pazardzhik	460	1	2016	NCA	11	2686
	39	Panagyurishte, Pazardzhik	650	1	2016	OH	5	1418
	40	Peshtera, Pazardzhik	640	1	2016	OH	10	2724
	41	Rakitovo, Pazardzhik	1000	1	2016	OH	5	1242
	42	Momchilgrad, Kardzhali	400	1	2018	OH	17	3639
	43	Zelenikovo, Plovdiv	425	1	2016	NCA	20	5331
	44	Zhenda, Kardzhali	400	2	2016, 2017	OH	34	8421
-	-	*Total*			-		*2297*	*509642*

cant biological factor regulating the numbers of the pine processionary moth (Mirchev 2005, Schmidt et al. 1999, Tsankov 1990). According to Masutti (1964), temperature is the major factor determining the favorable ecological niche of the main primary egg parasitoids – *Ooencyrtus pityocampae* Mercet (Hymenoptera: Encyrtidae) and *Baryscapus servadeii* Domenichini (Hymenoptera: Eulophidae). In addition to temperature, a number of other biotic and abiotic factors are known to affect the impact of primary egg parasitoids: the hyperparasitoid *Baryscapus transversalis* Graham (Hymenoptera: Eulophidae – Bellin et al. 1990, Bellin 1995, Mirchev 2005), the vegetation diversity near the studied sites (Mirchev 2005), etc. Long-term studies have shown that adaptation time (*i.e.*, the time after colonization of the area by the pine processionary moth) is also important for the development of host-specific parasitoids (Mirchev et al. 2017).

The present work summarizes the case studies on *T. pityocampa* egg parasitoids made in Bulgaria. It is focused on the relative share and abundance of different species in the parasitoid complex, their impact on the pest and the peculiarities of the parasitism in new and old habitats, as well as on the two different phenological forms.

Material and methods

The present work summarizes case studies made during 1991-2018 in 44 sites all over the range of the pine processionary moth in Bulgaria (Tab. 1, Fig. 1). The studied sites are located in an area of approximately 20,000 km^2. The distance between the southernmost site (Dzherovo) and the northernmost one (Klisura) is about 160 km, and between the westernmost and easternmost sites (Kyustendil and Maglizh, respectively) is 240 km.

The current range of the pine processionary moth in Bulgaria is outlined by the studied sites (Fig. 1). In the Sofia valley, the pine processionary moth occurs latently, in small numbers and without making attacks, due to the continental climate of the place. In the continental North of Bulgaria (*i.e.*, the Danube plain, where pine plantations are rare) and on the northern slope of the Balkan Range, the pine processionary moth has not yet been reported. The pest is also absent to the east of the zone of expansion in South Bulgaria, including Burgas district on the Black Sea coast, strongly influenced by Mediterranean climate.

The biological material (2297 egg batches containing 524,724 eggs) included both single and multiple samples, with up to six generations of *T. pityocampa* (in Kyustendil and Marikostinovo). The egg batches collected at the individual sites ranged from 5 (Panagiurishte, Rakitovo) to 329 (Marikostinovo). The number of eggs in different sites varied from 1242 (Rakitovo) to 76,868 (Marikostinovo). Over the years, the material has been collected for different purposes. The predominant part of the studied biological material was collected in the historical range of *T. pityocampa* in Bulgaria. After the beginning of pest expansion, additional biological material was collected in the expansion zone. After establishing the early form, a number of studies were focused in these localities.

All sites were divided into three groups according to *T. pityocampa* phenological form: (i) early form habitats; (ii) late form habitats; (iii) both form habitats (*i.e.*, where both early and late forms are present in the same area, sometimes on the same tree). In addition, in order to take into account the dynamics of the processes, the sampling sites were divided into: (i) old habitats (most of them), *i.e.*, areas where *T. pityocampa* had been present for more than 10 years at the time of sampling; and (ii) new habitats, *i.e.*, newly occupied areas where the pest had penetrated less than 10 years ago. For the same purpose, the sites were also divided into two other groups: (i) habitats from the historic range, where the pine processionary had been reported before 1991; and (ii) habitats from its expansion zone, which emerged in the Stara Zagora region in 1991 (Kazanlak, Sladak Kladenets, Chirpan, Dolno Sahrane, Maglizh). As the species has been expanding since the 1990s, it is important to note that there are new and old habitats in both the historic area and the area of expansion. The above subdivisions of the sampling sites were introduced to test for differences in the dynamics of the host and parasitoids in the different habitats.

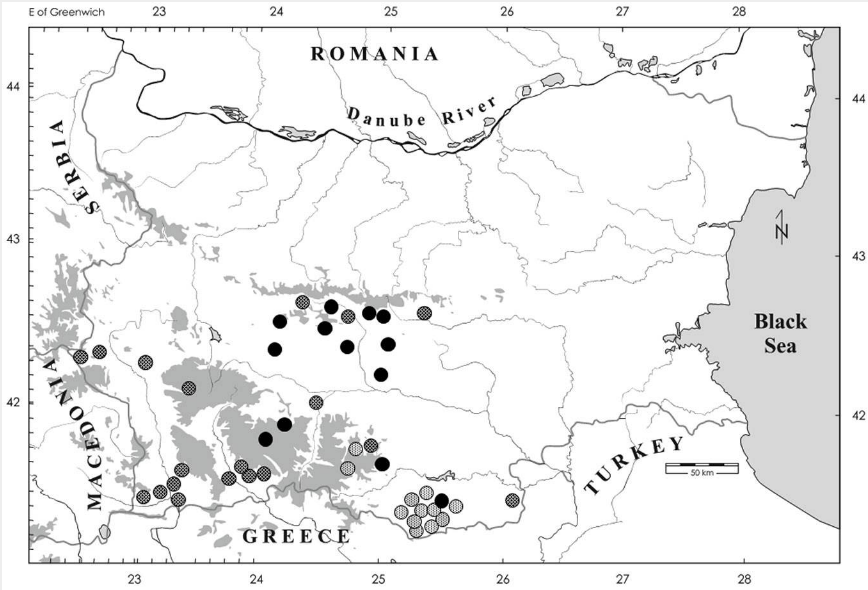

Fig. 1 - Studied habitats of *Thaumetopoea pityocampa* in Bulgaria. Early phenological form habitats are indicated by light grey dots, late phenological form habitats by dark grey dots, while black dots indicate both early and late phenological forms habitats.

Collected egg batches were transported to the laboratory of entomology at the Forest Research Institute in Sofia. The scales of the egg batches were removed, and the samples were analysed according to Tsankov et al. (1996). The egg batches were placed individually in test tubes covered by cotton stoppers and kept at room temperatures (20-22 °C). The samples were checked periodically and the emerged parasitoids were separated and identified under a stereomicroscope (40×). At the end of the experiments (10-12 months after sampling), the eggs were dissected and analyzed in detail.

The parasitoids that had emerged before sample collection were determined by their meconia and remains, according to Schmidt & Kitt (1994), Tanzen & Schmidt (1995) and Tsankov et al. (1996). The parasitoids emerged in the test tubes were identified by the following keys, according to the taxonomic group: Encyrtidae (Trjapitzin 1978b, 1989); Eulophidae (Trjapitzin 1978c, Graham 1987, 1991); Eupelmidae (Trjapitzin 1978a, Fusu 2017); Trichogrammatidae (Nikolskaya & Trjapitzin 1978). A part of the collected biological material was identified or confirmed by Dr. P. Boyadzhiev and Dr. M. Antov (Plovdiv University "P. Hilendarski", Bulgaria) and Dr. E. Yegorenkova (Ulyanovsk State Pedagogical University, Russia).

In order to allow the comparison among different datasets, the average impact of the parasitoids (*i.e.*, the rate of parasitism on *T. pityocampa* eggs) was chosen as the main indicator. In this way, the influence of different intensity of the research and the different number of repetitions in the different datasets is largely eliminated.

Statistical analysis was made using the package Statistica® v. 12.0 for Windows (StatSoft Inc., Tulsa, OK, USA). To compare the means, the *t*-test for independent samples was applied, with normality control.

Results

Seven primary egg parasitoids of the pine processionary moth were established in Bulgaria: *Ooencyrtus pityocampae* Mercet, 1921 (Hymenoptera: Encyrtidae); *Baryscapus servadeii* Domenichini, 1965; *Pediobius bruchicida* Rondani, 1872 (Hymenoptera: Eulophidae); *Anastatus bifasciatus* Fonscolombe, 1832; *Eupelmus* (*Macroneura*) *vesicularis* Retzius, 1783; *Eupelmus* (*Macroneura*) *vladimiri* Fusu, 2017 (Hymenoptera: Eupelmidae) and *Trichogramma* sp. (Hymenoptera: Trichogrammatidae), and one hyperpasitoid, *Baryscapus transversalis* Graham, 1991.

The majority of the studied sites were dominated by *O. pityocampae* (19 sites, 43.2% – Tab. 2), followed by *B. servadeii* (17 sites). *A. bifasciatus* was the dominant species in six localities (Dyulitsa, Hvoina, Garmen, Chirpan, Rakitovo, Vetren), and *Trichogramma* sp. in two (Dobrostan, Asenovgrad).

O. pityocampae had the highest impact (5.77%) on pine processionary moth, followed by *B. servadeii* (5.69%), *A. bifasciatus* (1.23%) and *Trichogramma* sp. (0.52% – Tab. 3). The other three species of primary parasitoids (*P. bruchicida, E. vladimiri* and *E. ves-*

Tab. 2 - Relative share and impact (in parentheses) of egg parasitoids of *T. pityocampa* in studied localities in Bulgaria. (Op): *Ooencyrtus pityocampae*; (Bs): *Baryscapus servadeii*; (Bt): *Baryscapus transversalis*; (Ab): *Anastatus bifasciatus*; (Tsp): *Trichogramma* sp.; (Pb): *Pediobius bruchicida*; (Ev1): *Eupelmus vladimiri*; (Ev2): *Eupelmus vesicularis.*

Habitats	Locality	Total impact (%)	Relative share (impact) of parasitoids (%)							
			Op	Bs	Bt	Ab	Tsp	Pb	Ev1	Ev2
Early phenological form	Dobrostan	9.4	0.6 (0.1)	3.1 (0.3)	0.6 (0.1)	-	95.7 (8.9)	-	-	-
	Dyulitsa	10.2	19.6 (2.0)	-	-	80.4 (8.2)	-	-	-	-
	Domishte	18.2	16.2 (3.0)	83.6 (15.2)	0.2 (0.04)	-	-	-	-	-
	Drangovo	34.6	2.6 (0.9)	97.4 (33.7)	-	-	-	-	-	-
	Dzherovo	7.1	6.2 (0.4)	90.0 (6.4)	-	3.8 (0.3)	-	-	-	-
	Fotinovo	4.5	33.3 (1.5)	41.4 (1.8)	17.8 (0.8)	0.4 (0.02)	1.5 (0.1)	0.6 (0.02)	5.0 (0.3)	-
	Hvoina	0.3	-	-	-	100.0 (0.3)	-	-	-	-
	Kandilka	14.1	30.4 (4.3)	52.1 (7.3)	6.1 (0.9)	9.2 (1.3)	1.9 (0.3)	-	-	-
	Kardzhali	25.7	4.9 (1.3)	86.3 (22.2	2.6 (0.7)	5.6 (1.4)	0.6 (0.1)	0.02 (0.01)	-	-
	Kayaloba	24.0	46.5 (11.2)	47.3 (11.4)	3.1 (0.7)	3.0 (0.7)	0.1 (0.03)	-	-	-
	Medevtsi	8.8	35.0 (3.1)	45.5 (4.0)	6.0 (0.5)	13.4 (1.2)	-	-	-	0.1 (0.03)
	Yanino	20.4	47.7 (9.7)	45.5 (9.3)	5.1 (1.1)	1.5 (0.3)	0.2 (0.04)	-	-	-
Late phenological form	Asenovgrad	6.4	29.4 (1.9)	14.3 (0.9)	6.3 (0.4)	13.8 (0.9)	36.2 (2.3)	-	-	-
	Banya	20.2	74.5(15.1)	19.4 (3.9)	0.3 (0.1)	1.1 (0.2)	4.6 (0.9)	0.1 (0.01)	-	-
	Dikchan	14.6	24.8 (3.6)	51.0 (7.5)	10.2 (1.5)	12.6 (1.8)	1.4 (0.2)	-	-	-
	Dupnitsa	11.4	78.2 (8.9)	13.3 (1.5)	3.6 (0.4)	4.4 (0.5)	0.5 (0.1)	-	-	-
	Garmen	13.0	31.9 (4.2)	23.1 (3.0)	8.5 (1.1)	35.5 (4.6)	1.0 (0.1)	-	-	-
	Gega	11.5	13.3 (1.2)	75.4 (8.9)	5.5 (0.7)	3.7 (0.4)	2.1 (0.2)	-	-	-
	Gotse Delchev	8.4	25.5 (2.1)	30.4 (2.6)	16.6 (1.4)	24.4 (2.0)	3.1 (0.3)	-	-	-
	Ivailovgrad	18.2	27.7 (5.0)	57.7 (10.5)	5.2 (0.9)	9.2 (1.7)	-	0.2 (0.1)	-	-
	Kurtovo	20.5	91.2 (18.7)	2.8 (0.6)	3.9 (0.8)	0.2 (0.1)	1.8 (0.4)	-	-	0.1 (0.1)
	Klisura	22.2	23.7 (5.3)	66.4 (14.7)	2.2 (0.5)	1.4 (0.3)	6.2 (1.4)	0.1 (0.02)	-	-
	Maglizh	13.6	88.2 (12.0)	1.7 (0.2)	4.0 (0.5)	4.1 (0.6)	2.0 (0.3)	-	-	-
	Marikostinovo	23.3	91.4 (21.3)	0.5 (0.1)	0.7 (0.2)	7.0 (1.6)	0.1 (0.01)	0.2 (0.05)	-	0.1 (0.001)
	Kyustendil	5.9	44.4 (2.6)	12.5 (0.7)	0.1 (0.01)	6.8 (0.4)	36.2 (2.2)	-	-	-
	Parvomay	25.9	13.3 (3.4)	81.7 (21.2)	2.3 (0.6)	1.6 (0.4)	1.1 (0.3)	-	-	-
	Ploski	22.8	55.5 (12.7)	34.3 (7.8)	8.0 (1.8)	1.5 (0.3)	0.7 (0.2)	-	-	-
	Rilski manastir	13.9	83.4 (11.6)	-	11.7 (1.6)	1.5 (0.2)	3.4 (0.5)	-	-	-
	Sandanski	13.8	72.4 (10.0)	9.9 (1.4)	2.2 (0.3)	14.9 (2.0)	0.6 (0.1)	-	-	-
	Satovcha	21.2	45.1 (9.5)	38.4 (8.2)	12.8 (2.7)	3.3 (0.7)	0.4 (0.1)	-	-	-
	Vetren	14.9	54.2 (8.1)	13.5 (2.0)	4.6 (0.7)	23.3 (3.5)	4.4 (0.6)	-	-	-
Common (both early and late phenological forms)	Chirpan	8.8	34.1 (3.0)	-	-	65.9 (5.8)	-	-	-	-
	Hisar	4.1	57.2 (2.3)	22.1 (0.9)	2.3 (0.1)	11.4 (0.5)	7.0 (0.3)	-	-	-
	Kazanlak	11.3	77.1 (8.7)	1.5 (0.2)	0.1 (0.01)	14.3 (1.6)	7.0 (0.8)	-	-	-
	Karlovo	3.0	19.7 (0.6)	66.7 (2.0)	-	10.6 (0.3)	3.0 (0.1)	-	-	-
	Lesichevo	13.1	68.8 (9.0)	14.5 (1.9)	5.7 (0.7)	11.0 (1.5)	-	-	-	-
	Momchilgrad	4.5	0.6 (0.02)	93.8 (4.2)	1.9 (0.1)	3.7 (0.2)	-	-	-	-
	Panagyurishte	7.8	90.9 (7.1)	1.8 (0.1)	7.3 (0.6)	-	-	-	-	-
	Peshtera	6.7	52.7 (3.5)	-	1.6 (0.1)	45.7 (3.1)	-	-	-	-
	Rakitovo	3.5	39.5 (1.4)	-	-	53.5 (1.9)	7.0 (0.2)	-	-	-
	Dolno Sahrane	31.6	15.9 (5.0)	75.9 (24.0)	1.6 (0.5)	1.7 (0.6)	4.9 (1.5)	-	-	0.03 (0.01)
	Sladak kladenets	4.3	65.7 (2.8)	-	-	34.3 (1.5)	-	-	-	-
	Zelenikovo	4.0	71.6 (2.9)	3.3 (0.1)	-	25.1 (1.0)	-	-	-	-
	Zhenda	24.8	52.0 (12.9)	39.0 (9.7)	6.4 (1.5)	1.4 (0.4)	1.2 (0.3)	-	-	-

icularis) had a negligible impact on the host. They were found only in old habitats of *T. pityocampa* (Tab. 3).

The impact of egg parasitoids on the numbers of the pine processionary moth varied within a fairly wide range in different localities, from 0.3% (Hvoina) to 31.6% (Dolno Sahrane – Tab. 2).

In old habitats, the greatest impact on *T. pityocampa* was due to *B. servadeii* (7.20% – Fig. 2B), followed by *O. pityocampae* (6.02% – Fig. 2A), *A. bifasciatus* (1.12% – Fig. 2D) and *Trichogramma* sp. (0.30% – Fig. 2E). In newly occupied habitats, the most important was *O. pityocampae* (4.92% – Fig. 2A), followed by *A. bifasciatus* (1.62% – Fig. 2D), *Trichogramma* sp. (1.28% – Fig. 2E) and *B. servadeii* (0.54% – Fig. 2B). The differences in the parasitoid impact in these two type of areas are statistically significant for *B. servadeii* ($p = 0.017$) and *Trichogramma* sp. ($p = 0.045$), as well as for the hyperparasitoid *B. transversalis* (0.67% and 0.20%, respectively; $p = 0.013$ – Fig. 2C).

Significant differences of impact between early and late phenological forms of *T. pityocampa* were observed for two polyphagous species: *O. pityocampae* (3.12% and 8.27%, respectively; $p = 0.012$ – Fig. 3A) and *A. bifasciatus* (1.14% and 1.17%; $p = 0.033$ –

Tab. 3 - Average impact (%) of egg parasitoids of *T. pityocampa* in different zones of its range in Bulgaria.

Species	Total (n=44)	Early form habitats (n=12)	Late form habitats (n=19)	Both early and late form habitats (n=13)	Old habitats (n=34)	New habitats (n=10)
O. pityocampae	5.77 ± 0.78	3.12 ± 1.06	8.27 ± 1.34	4.56 ± 1.06	6.02 ± 0.94	4.92 ± 1.32
B. servadeii	5.69± 1.16	9.30 ± 2.95	5.04 ± 1.32	3.32 ± 1.88	7.20 ± 1.40	0.54 ± 0.24
B. transversalis	0.56 ± 0.09	0.40 ± 0.12	0.85 ± 0.16	0.28 ± 0.12	0.67 ± 0.11	0.20 ± 0.10
A. bifasciatus	1.23 ± 0.25	1.14 ±0 .66	1.17 ± 0.28	1.42 ± 0.44	1.12 ± 0.27	1.62 ± 0.56
Trichogramma sp.	0.52 ± 0.21	0.79 ± 0.74	0.54 ± 0.16	0.25 ± 0.12	0.30 ± 0.09	1.28 ± 0.87
P. bruchicida	0.0048 ± 0.0026	0.0025 ± 0.0018	0.0095 ± 0.0058	0	0.0062 ± 0.0033	0
E. vladimiri	0.0068 ± 0.0068	0.0250 ± 0.0250	0	0	0.0088 ± 0.0088	0
E.vesicularis	0.0032 ± 0.0024	0.0025 ± 0.0025	0.0053 ± 0.0053	0.0008±0.0008	0.0041 ± 0.0031	0
All species	13.79 ±1.25	14.79 ± 2.89	15.89 ± 1.35	9.81 ± 2.45	15.33 ± 1.46	8.56 ± 1.52

Fig. 3D). The data on habitats colonized by both early and late forms are difficult to interpret, so statistical evaluation was only carried out for pure habitats (either early or late form habitats).

The relationship between the impact of parasitoids and the altitude of studied sites was analysed for five parasitoid species of *T. pityocampa* (Fig. 4). The rare parasitoids *P. bruchicida*, *E. vladimiri*, and *E. vesicularis* were excluded because only single specimens were found in a limited number of sites. The correlation between the impact of parasitoids and habitat elevation was not significant, with R^2 varying between 0.022 (*A. bifasciatus*) and 0.203 (*O. pityocampae*). In addition, no differences in altitude distribution trends of the two main parasitoids of *T. pityocampa* (*O. pityocampae* – Fig. 4A; *B. servadeii* – Fig. 4B) were established.

The studies on the parasitoids were conducted with comparable fertility and habitat characteristics of pine processionary moth. We found a small but significant difference in the average number of eggs per batch between early and late forms of *T. pityocampa* (209.16 ± 10.06 *vs.* 228.26 ± 5.79, respectively; p = 0.23), and between the new and old habitats of the species (225.64 ± 12.56 *vs.* 230.36 ± 4.80, respectively; p = 0.46 – Fig. 5). However, there was a significant difference in the average number of eggs of sites with both forms of pine processionary moth (249.35 ± 5.82), compared to the early form (p = 0.001) and the late form (p = 0.02) habitats.

The average altitude of the habitats in the expansion zone of *T. pityocampa* (429.00 ± 21.99 m a.s.l.) was lower than that of the habitats in its historical range (569 ± 35.28 m a.s.l.). This was expected, given that the

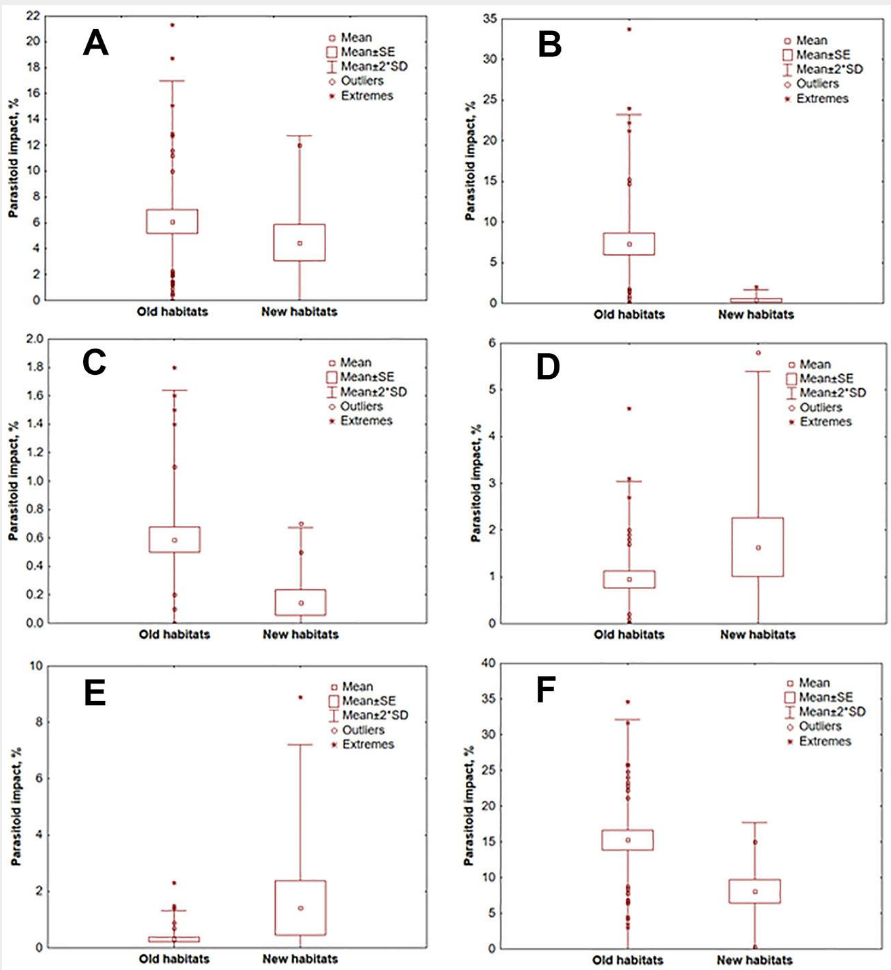

Fig. 2 - Impact of egg parasitoids in different zones of *T. pityocampa* range. (A): *O. pityocampae*; (B): *B. servadeii*; (C): *B. transversalis*; (D): *A. bifasciatus*; (E): *Trichogramma* sp.; (F): All parasitoid species.

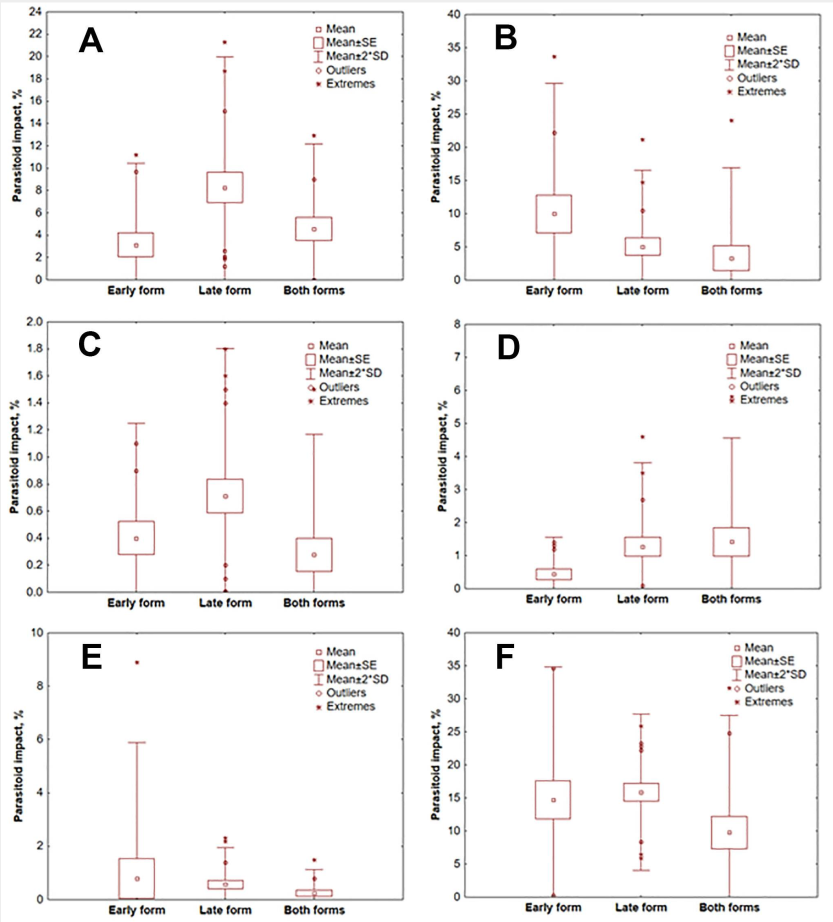

Fig. 3 - Impact of egg parasitoids on different phenological forms of *T. pityocampa*. (A): *O. pityocampae*; (B): *B. servadeii*; (C): *B. transversalis*; (D): *A. bifasciatus*; (E): *Trichogramma* sp.; (F): All parasitoid species.

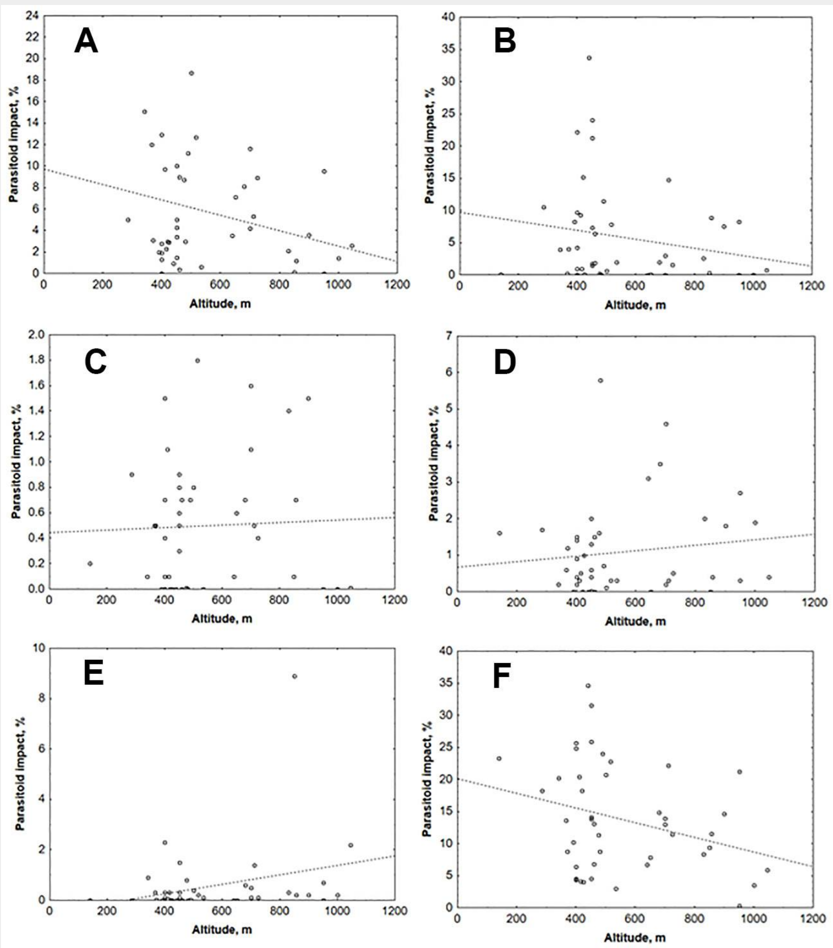

Fig. 4 - Influence of altitude on impact of egg parasitoids of *T. pityocampa*. (A): *O. pityocampae*; (B): *B.servadeii*; (C): *B. transversalis*; (D): *A. bifasciatus*; (E): *Trichogramma* sp.; (F): All parasitoid species.

expansion zone is located more northwards than the historical zone, on average (Fig. 1). Such difference seems unlikely to be explained by the lack of sampling sites at high altitudes, as the expansion develops on the southern slope of Stara Planina, whose main ridges reach elevations not suitable to this pest.

The hyperparasitoid *B. transversalis* developed on *O. pityocampae* and *B. servadeii*. Among the studied habitats, *B. transversalis* was not detected in nine locations (20.5%): four in sites with early form, and five in sites with both early and late forms (Tab. 2). The impact on primary parasitoids varied widely among sites from 0% up to 29.6% (Gotse Delchev). In nine localities, the impact on the number of primary parasitoids was above 10.0%, while it was between 5.1% and 10.0% in further nine localities, and below 5.0% in the remaining 26 localities. As for the relative share of *B. transversalis* in the total egg parasitoid complex of *T. pityocampa* in Bulgaria, it varied between 1.1% and 4.8%, with the lowest value in the new habitats (Tab. 3).

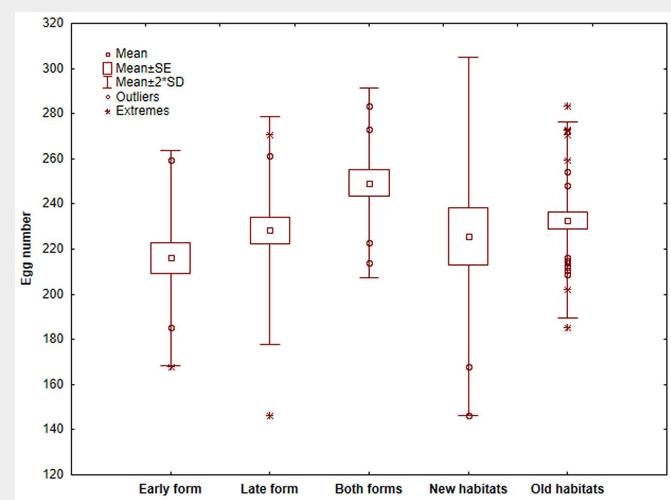

Fig. 5 - Average number of eggs in egg batches of pine processionary moth in Bulgaria.

Discussion

The results of this study showed that *B. servadeii* and *O. pityocampae* are the two most important egg parasitoids of pine processionary moth in Bulgaria. Both species are major egg parasitoids of the host in all its range (Battisti et al. 2005, Jactel et al. 2015, Roques et al. 2015), as well as of *Thaumetopoea bonjeani* Powell, 1922 and *Thaumetopoea wilkinsoni* Tams, 1926 (Lepidoptera: Notodontidae) in cedar forests (Battisti et al. 2005, Auger-Rozenberg et al. 2015a, Rahim et al. 2016).

Generally, the specialist *B. servadeii* is dominant in old habitats and habitats of the early phenological form of *T. pityocampa,* while the generalist *O. pityocampae* is dominant in new habitats and in habitats of the late form, as well as in habitats of both phenological forms. In new habitats, the polyphagous species *A. bifasciatus* and *Trichogramma* sp. can be also dominant in some cases. Such characteristics of distribution and impact of egg parasitoids of *T. pityocampa* have been recently recorded in case studies in Bulgaria and France (Mirchev et al. 2017, 2021, Georgiev et al. 2021).

The percentage of parasitism caused by *O. pityocampae* and *B. servadeii* does not depend on location of *T. pityocampa* egg batches on pine needles (Hezil et al. 2018). Masutti (1964) pointed out that *B. servadeii* is more resilient and develops successfully in areas with temperatures above 30 °C, *i.e.*, in conditions that suppress *O. pityocampae* development. According to Tiberi (1990), in Italy *B. servadeii* is most abundant in the warmer regions of the central and southern part of the country. However, the abundance and importance of the parasitoids depend not only on the temperature conditions of the habitats. In Algeria, the maximum summer temperature frequently exceeded 40 °C during the period of adult activity of *O. pityocampae* and *B. servadeii*, but no correlation with parasitism rates on *T. pityocampa* has been observed (Bouzar-Essaidi et al. 2021). Mirchev (2005) suggested that the rich floral diversity of habitats contributes to successful survival of the generalist *O. pityocampae* by creating favourable conditions for the presence and development of alternative hosts. This hypothesis could explain the drastic differences in parasitism rates of *O. pityocampae* and *B. servadeii* in Marikostinovo and Parvomay, which are nearby sites in southwestern Bulgaria with a strong Mediterranean influence. This assumption is supported by the results of studies carried out in Algeria, where a positive correlation between the proportion of agricultural areas and the parasitism by *O. pityocampae* was established (Bouzar-Essaidi et al. 2021). In support of this, in the region of Marikostinovo the share of agricultural land is significantly higher than in Parvomay, where forests predominate. On the other hand, Marikostinovo is 270 m lower in elevation than Parvomay (Tab. 1), and the average temperatures there should be quite higher, *i.e.*, more favorable for *B. servadeii*. Nevertheless, in Marikostinovo it is *O. pityocampae* that definitely dominates (91% of the infested eggs), while in Parvomay *B. servadeii* predominates (82% of the infested eggs – Tab. 2).

A higher relative abundance of *B. servadeii* has been reported in the Eastern Rhodopes, where the early phenological form is widespread (Mirchev et al. 2019). In this form, the female moths lay eggs about two months earlier than the typical late form. In laboratory conditions, the emergence of *B. servadeii* begins well before the period of laying eggs of *T. pityocampa* late ("winter") phenological form (Tsankov et al. 1996). With this in mind, the higher parasitism of the specialist *B. servadeii* in the early ("summer") phenological form of the host was expected. The significantly higher impact of *B. servadeii* in old habitats was also expected due to the time required for this specialized parasitoid to colonize the site after the host penetration. Indeed, it is known that *B. servadeii* tracks the host in the expansion range, ensuring a relatively quick density-dependent control (Auger-Rozenberg et al. 2015b). However, the reduced genetic diversity of *B. servadeii* could negatively affect its ability to adapt to the new environments colonized by its host, thus reducing the efficiency of biological control (Simonato et al. 2019).

The higher impact of the polyphagous polyvoltine generalist *O. pityocampae* and *A. bifasciatus* in late phenological form of *T. pityocampa*, as well as *Trichogramma* sp. in newly colonized areas, could be explained with the possibility of gradual multiplication on alternative hosts in the studied habitats.

In recent decades, the expansion of *T. pityocampa* range to higher latitude and elevation due to climate change has been observed (Battisti et al. 2005, Auger-Rozenberg et al. 2015b). As for the two main parasitoid species of pine processonary moth (*O. pityocampae* and *B. servadeii*), a decrease in parasitism rate with elevation has been established in a mountain range of Sierra Nevada (South-eastern Andalusia, Spain), with more severe decline for the specialist *B. servadeii* (Hódar et al. 2021). In Bulgaria, the impact of *O. pityocampae* and *B. servadeii* also decreases at higher altitude, however it is not entirely negligible even near the upper limits of the host elevation range (about 1200 m a.s.l.). Conversely, the effectiveness of the other two significant parasitoids (*A. bifasciatus* and *Trichogramma* sp.) increases with increasing altitude, probably due to the reduced competition from *O. pityocampae* and *B. servadeii*. This demonstrates their resilience and their ability to develop over a wider range of ambient temperatures.

In some habitats, the hyperparasitoid *B. transversalis* severely limits (up to 29.6%) the number of primary parasitoids *O. pityocampae* and *B. servadeii*. The species is known from Greece (Schmidt et al. 1997, Tsankov et al. 1999) and other countries on the Balkan Peninsula: Bulgaria (Tsankov et al. 1996), Albania (Mirchev et al. 2000) and Bosnia and Herzegovina (Boyadzhiev et al.

2015). It was also established on the Iberian Peninsula (López-Sebastián et al. 2003) and the Asiatic part of Turkey (Mirchev et al. 2004). The information that *B. transversalis* prefers *B. servadeii* (Bellin et al. 1990, Bellin 1995) is not supported by other studies where no clear host selectivity has been established (Mirchev 2005). The impact of the hyperparasitoid on the two primary parasitoids is known to vary widely, from 0.5-3.0% (Tsankov et al. 1996, Schmidt et al. 1997) to 23.6% (Mirchev et al. 2000). These data are fully consistent with the results of the present study and confirm the conclusion that there is great variability in the impact of the hyperparasitoid on the numbers of *O. pityocampae* and *B. servadeii* in different habitats.

Conclusions

Our results confirmed *O. pityocampae* and *B. servadeii* to be the two main egg parasitoids of pine processionary moth in Bulgaria. All the other parasitoids, mainly *A. bifasciatus* and *Trichogramma* sp., have a noticeable share (up to 33% of the parasitised eggs) only in areas recently colonized by *T. pityocampa*.

In old habitats of *T. pityocampa* (colonized more than 10 years ago), the impact of parasitoids is almost 2 times higher (15.3%) than in newly colonized areas (8.6%). This is due to the specialist *B. servadeii*, which is rare in newly colonized areas (0.54%), but strongly dominates in long-established ones (7.2%). In new habitats of the host, the generalist *O. pityocampae* dominates (4.9%). *B. servadeii* definitely dominates in the habitats of *T. pityocampa* early form (>50% of the parasitised eggs), while in the late form of the host, *O. pityocampae* dominates (>50% of the parasitised eggs). This difference is likely due to the phenological characteristics of the parasitoids and the host. The impact of the two most important species, *O. pityocampae* and *B. servadeii*, and the parasitoid complex as a whole decreases with altitude. On the contrary, the impact of *A. bifasciatus* and *Trichogramma* sp. slightly increases with altitude, which might indicate their suppression by the main parasitoids.

In general, the parasitism of *T. pityocampa* eggs is a complex process that depends not only on the time of adaptation and the coincidence of the phenology of parasitoids to the phenology of the host, but also on many other factors such as population density of the pest, age and density of pine stands, local plant biodiversity, exposure, temperature conditions of the habitats, etc. Clarifying the complex influence of these factors is extremely important for the choice of silvicultural activities that would contribute to increasing the effectiveness of the parasitoids.

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