

Interactions between the introduced fungal pathogen *Entomophaga maimaiga* and indigenous tachinid parasitoids of gypsy moth *Lymantria dispar* in Bulgaria

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Abstract Interactions between the gypsy moth, *Lymantria dispar* L. (Lepidoptera: Erebidae), pathogenic fungus *Entomophaga maimaiga*, and the tachinid parasitoid (Diptera: Tachinidae) complex in gypsy

moth larvae were investigated in Bulgaria, where *E. maimaiga* was recently released as a biological control agent. Gypsy moth larvae were collected in oak stands where *E. maimaiga* was originally introduced (nine sites) and in sites where the pathogen has invaded by natural extension of the range (ten sites). In total, 4,375 host larvae were examined and 401 tachinid larvae emerged from parasitized hosts. Host mortality caused by tachinids varied from 0 to 48.5% among sites, with an overall average of 9.2%. Emerging adult tachinid parasitoids included 54 individuals belonging to six species: *Compsilura concinnata*, *Exorista larvarum*, *Senometopia separata*, *Senometopia excisa*, *Drino incospicua* and *Zenilia libatrix*; the remaining parasitoids (86.5%) died in the pupal stage. *E. maimaiga* azygospores were observed on puparia surfaces, an indication that the gypsy moth host larvae were infected with the fungus. No azygospores were observed in parasitoid tissues. The high parasitoid mortality may be the result of the competition with *E. maimaiga* during development in the same host.

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Introduction

The gypsy moth, *Lymantria dispar* (L.) (Lepidoptera: Erebidae), is one of the most deleterious insect pests in deciduous forests of Europe, Asia and Northern

Africa, and was accidentally introduced into North America in the late 1860's (McManus and McIntyre 1981). Although strongly polyphagous, the larvae feed primarily on foliage of oaks (*Quercus* spp.) and poplars (*Populus* spp.). European populations of the gypsy moth gradually increase over multiple seasons, resulting in outbreaks and defoliation events every 8–12 years in forested areas. The damage is most severe in southeastern Europe because of the abundance of oak forests and favorable climatic conditions for the development and survival of the pest. In outbreak years, gypsy moth defoliation in Hungary, Serbia, Bulgaria and Romania has ranged from 200,000–600,000 ha (Georgiev *et al.* 2011; McManus & Csóka 2007) per year.

Gypsy moth is an introduced and widely distributed pest in the northeast regions of the U.S., and integrated pest management programs include classical biological control via introduced natural enemies recovered from native habitats (Coulson 1981; Pilarska *et al.* 2010a, b; Reardon 1981b). Among them, the entomophthorous fungus *Entomophaga maimaiga* Humber, Shimazu & Soper (Entomophthorales: Entomophthoraceae), introduced from Japan where epizootics in *Lymantria dispar japonica* occur periodically (Hajek *et al.* 2005), the pathogen has proven to have significant effects on gypsy moth outbreaks (Solter & Hajek 2009).

Introductions of *E. maimaiga* to Europe were first made in Bulgaria in 1999–2001 with biological material from the U.S. (Pilarska *et al.* 2000). In 2005, strong epizootics in four gypsy moth populations were reported in forests at a distance of 30–90 km from the introduction sites (Pilarska *et al.* 2006). Currently, the fungus is widely distributed in all regions of Bulgaria where gypsy moth occurs (Georgiev *et al.* 2011). *E. maimaiga* was recently identified in Georgia (Kereselidze *et al.* 2011), the European part of Turkey (Georgiev *et al.* 2012) and Serbia (Tabaković-Tošić *et al.* 2012).

Among the natural enemies of *L. dispar* in Bulgaria, 20 species of parasitoids in the family Tachinidae have been reported (Hubenov 1985, 1991). Previous studies in Bulgaria showed that some tachinids are important in gypsy moth population dynamics with relatively high host mortality reported: *Compsilura concinnata* (Meigen), 11.5–36.1% (Keremidtschiev 1954); *Exorista larvarum* (Linnaeus), 2.6–22.0% (Gantschew 1975; 1972, thesis, Univ. of

Forestry, Sofia, Bulgaria); *Blepharipa pratensis* (Meigen), 1.6–46.2% (Karnožitcky 1957); and *Parasetigena silvestris* (Robinedau-Desvoidy), 3.3–23.5% (Gantschew 1975). The four species are one of the most effective gypsy moth tachinid parasitoids in Europe, and were introduced into North America (Reardon 1981c). These parasitoids are polyphagous on a variety of phytophagous host species (Cerretti & Tschorsnig 2010; Herting 1960; Nielsen 1912; Shima 2006; Tschorsnig & Herting 1994). They are typically multivoltine with two or more generations per year, the first of which parasitizes gypsy moth.

Entomophaga maimaiga is a host specific pathogen of gypsy moth in its natural range. In the U.S., only two non-target lepidopteran species were found to be weakly infected during *E. maimaiga* epizootics, *Malacosoma disstria* Hübner (0.3% of collected specimens) and *Catocala ilia* (Cramer) (1.0%) (Hajek 1999). The high level of host specificity of *E. maimaiga* limits negative impact on non-target species but in biological control programs it is also important to evaluate impact on other biological agents of the target host. This is especially true for the parasitoids in the family Tachinidae, which are strongly associated with late instar gypsy moth larvae in which *E. maimaiga* also develops, but no information has been reported on potential interactions. Here we report on mortality of tachinid parasitoids associated with the gypsy moth after the introduction of *E. maimaiga* in Bulgaria.

Material and methods

The studies were conducted in 2008–2011 in 19 sites in Bulgaria (Table 1). *E. maimaiga* was introduced in nine sites in 1999–2010, epizootics were documented in four additional sites, and the pathogen has invaded the remaining sites by natural range extension but epizootics have not yet occurred (Georgiev *et al.* 2011). No completely naïve gypsy moth populations have been identified in Bulgaria since 2008. Gypsy moth larvae were collected in oak stands or mixed forest stands dominated by different oak species (Table 1). Each study plot was 100×100 m (1 ha) in size and included a minimum of 25 oak trees: five groups of five trees each, one chosen as the center of the plot, and four additional trees located approximately 50 m distant from the center tree at approximately 90° angles. Gypsy moth larvae were collected one to four

Table 1 Characteristics of study localities

Locality	Altitude, m a.s.l.	Geographic coordinates		Tree species *
		N	E	
<i>E. maimaiga</i> introduction				
Sadievo	151	42°31.783'	026°08.901'	<i>Q.r.</i>
Gorni Domlian	375	42°33.150'	024°54.032'	<i>Q.f.</i>
Gabrovnitsa	481	43°05.331'	023°27.626'	<i>C.o.</i> , <i>Q.p.</i>
Striama	182	42°13.710'	024°51.659'	<i>U.m.</i> , <i>A.t.</i> , <i>Q.r.</i>
Assenovo	401	43°17.695'	026°04.051'	<i>Q.c.</i>
Slavyanovo	345	43°17.090'	026°08.834'	<i>Q.c.</i>
Dalgach	193	43°12.966'	026°42.478'	<i>Q.ru.</i> , <i>T.p.</i>
Ruets	312	43°12.119'	026°37.950'	<i>C.b.</i> , <i>Q.c.</i>
Solnik	202	42°54.268'	027°44.296'	<i>Q.f.</i> , <i>Q.c.</i>
<i>E. maimaiga</i> epizootics (not introduced)				
Elovitsa	345	43°19.850'	023°00.247'	<i>C.o.</i> , <i>Q.c.</i>
Skravena	516	42°57.420'	023°49.504'	<i>Q.f.</i> , <i>Q.c.</i>
Spahievo	451	42°00.978'	025°25.566'	<i>Q.f.</i>
Kremen	474	41°17.133'	025°19.868'	<i>Q.f.</i> , <i>Q.p.</i>
<i>E. maimaiga</i> reported (no epizootics)				
Ravna gora	40	43°02.217'	027°49.938'	<i>Q.c.</i> , <i>Q.pu.</i>
Zvezdets	336	42°06.541'	027°25.100'	<i>Q.p.</i> , <i>Q.f.</i> , <i>Q.c.</i>
Karlanovo	645	41°33.047'	023°25.228'	<i>Q.pu.</i>
Indzhe voyvoda	299	42°13.295'	027°27.007'	<i>Q.p.</i> , <i>Q.f.</i> , <i>Q.c.</i>
Obzor	97	42°47.547'	027°52.547'	<i>Q.c.</i> , <i>Q.pu.</i>
Fakia	362	42°13.428'	027°08.084'	<i>Q.f.</i> , <i>Q.c.</i> , <i>F.o.</i>

* Tree species: *A.t.* *Acer tataricum*; *C.b.* *Carpinus betulus*; *C.o.* *Carpinus orientalis*; *F.o.* *Fraxinus ornus*; *Q.c.* *Quercus cerris*; *Q.f.* *Quercus frainetto*; *Q.p.* *Quercus petraea*; *Q.pu.* *Quercus pubescens*; *Q.r.* *Quercus robur*; *Q.ru.* *Quercus rubra*; *T.p.* *Tilia platyphyllos*; *U.m.* *Ulmus minor*

times annually in each of the study sites. First and second instar larvae were collected manually from foliage in the lower parts of tree crowns and tree branches, and late instar larvae were collected from beneath burlap cloth bands that were tied around the tree trunks approximately 1.3 m above the ground (Reardon 1981a). All larvae found in burlap bands were collected for examination.

Collected larvae were transported to the laboratory and reared on fresh oak foliage in 15x10x8 cm plastic boxes, ten larvae per box. The foliage was changed daily. Larvae that were parasitized with braconid (Hymenoptera) puparia and those from which tachinid larvae emerged were separated and held individually in petri dishes for observation and microscopic examination. Individual gypsy moth pupae were placed in 50 cm³ plastic containers, one pupa per container, and mortality caused by parasitoids was recorded.

Tachinid pupae were maintained in sterile petri dishes containing sand moistened with sterile water.

Relative humidity of 75–80% was maintained in order to prevent drying of pupae. Tachinid adults emerging from pupae were identified to species using taxonomic keys (Mesnil 1944–1975; Richter 2004; Tschorsnig & Herting 1994; Tschorsnig & Richter 1998) using actual nomenclature (Tschorsnig *et al.* 2005). Microscopic analyses of dead pupae were conducted two or more months after pupation using the following procedures:

1. To determine if tachinids emerged from infected hosts, presence of *E. maimaiga* azygospores on the surface of puparia was determined by washing dead pupae in 1 ml sterile water and examining a 20- μ l droplet of the suspension under a cover slip.
2. After washing puparia with tap water a second time, the pupal tissues were extracted from puparia using forceps and microscopically examined for the presence of mycelia and azygospores of *E. maimaiga*. The pupal tissues were also evaluated for presence or absence of other parasites and pathogens.

Table 2 Mortality of tachinid parasitoids in pupal stage

Locality	Year	<i>L. dispar</i> larvae			<i>L. dispar</i> mortality caused by tachinids (%)	Number of tachinid pupae	Tachinid mortality (%)	Tachinid pupae with <i>E. maimaiga</i> azygospores (%)
		Number of collections	Collection dates	Number of larvae				
Sadievo	2008	1	29 May	128	42.2	54	100.0	100.0
	2009	2	8–19 June	126	22.2	28	100.0	96.4
Gorni Domlian	2009	3	26 May–22 June	79	0	0	-	-
	2010	4	18 May–29 June	160	0	0	-	-
	2011	3	18 May–1 July	92	0	0	-	-
Gabrovnitsa	2009	4	28 May–5 July	75	9.3	7	0.0	-
	2010	4	22 May–3 July	111	0.9	1	100.0	100.0
	2011	3	22 May–2 July	32	6.3	2	100.0	0.0
Striama	2009	3	26 May–23 June	77	1.3	1	0.0	-
	2010	4	17 May–29 June	95	0	0	-	-
	2011	3	19 May–30 June	41	0	0	-	-
Assenovo	2010	1	20 May	44	0	0	-	-
Slavyanovo	2010	1	4 June	59	5.1	3	100.0	100.0
	2011	1	2 June	34	5.9	2	100.0	100.0
Dalgach	2011	1	13 May	53	0	0	-	-
Ruets	2011	2	13 May–2 June	8	0	0	-	-
Solnik	2011	3	13 May–16 June	107	9.3	10	72.7	0.0
Elovitsa	2009	2	4–18 June	36	0	0	-	-
	2010	4	16 May–2 July	34	20.6	7	100.0	57.1
	2011	1	20 June	5	0	0	-	-
Skravena	2009	3	27 May–25 June	24	16.7	4	0.0	-
	2010	4	21 May–1 July	21	19.0	4	0.0	-
Spahievo	2009	2	2–22 June	302	12.3	37	70.3	81.1
	2010	3	17 May–23 June	144	17.4	25	100.0	80.0
	2011	4	14 May–24 June	208	12.5	26	100.0	0.0
Kremen	2009	2	2–22 June	89	9.0	8	100.0	75.0
	2010	3	17 May–23 June	23	8.7	2	100.0	100.0
	2011	4	14 May–24 July	374	6.1	23	95.7	21.7
Ravna gora	2009	2	9–23 June	214	2.8	6	66.7	33.3
	2010	3	19 May–24 June	144	2.1	3	66.7	66.7
	2011	3	2–30 June	158	0.6	1	0.0	-
Zvezdets	2009	2	8–23 June	33	48.5	16	37.5	75.0
	2010	3	18 May–24 June	56	5.4	3	100.0	66.7
	2011	4	14 May–1 July	449	3.8	17	64.7	0.0
Karlanovo	2010	4	19 May–18 July	87	2.3	2	100.0	100.0
	2011	3	17 May–27 June	93	0	0	-	-
Indzhe voyvoda	2010	2	17 May–5 June	30	3.3	1	0.0	-
	2011	1	17 June	49	10.2	5	60.0	0.0
Obzor	2011	2	17–30 June	138	22.5	31	100.0	29.0
Fakia	2011	4	14 May–1 July	343	21.0	72	98.6	4.2
Total				4375	9.2	401	86.5	53.6

Results

A total of 4,375 *L. dispar* larvae were collected and analyzed in 2008–2011 (Table 2). Host mortality due to tachinid parasitism in different localities varied from 0% to 48.5%; the overall average parasitism by tachinids was 9.2%. Mortality occurred in late stage (\geq fourth instar) gypsy moth larvae and pupae. Mortality due to the hymenopteran species *Protapanteles liparidis* (Bouché) and *Cotesia melanoscela* (Ratzeburg) (Hymenoptera: Braconidae) was recorded in earlier stage larvae (\leq third instar) (unpublished data). *E. maimaiga* was not observed in early instar larvae from which hymenopteran parasitoids emerged. No pathogens (*LdMNPV* or microsporidia) were observed in the parasitized larvae.

A total of 401 tachinid larvae and pupae were isolated from gypsy moth larvae and pupae (Table 2). Of these, 347 died as pupae, resulting in a high overall mortality of 86.5% (Table 2). No *E. maimaiga* azygospores were observed in internal tissues of dead pupae, but were detected on the surface of 186 (53.6%) of the dead pupae. No pathogens were noted in the tissues of the dead parasitoids.

Fifty-four tachinid adults emerged from pupae and six species were identified: *Compsilura concinnata* (Meigen), *Exorista larvarum* (L.), *Senometopia separata* (Rondani), *Senometopia excisa* (Fallén), *Drino inconspicua* (Meigen) and *Zenilia libatrix* (Panzer) (Table 3). Three species dominated in the parasitoid complex: *C. concinnata* (31 individuals), *S. separata* (12) and *E. larvarum* (8). The remaining species were represented by single individuals. It is likely that parasitism in this study is due partially to *B. pratensis* and *P. silvestris*, but the high tachinid mortality in the pupal stage did not allow identification of some species or evaluation of the role of different species in the regulation of gypsy moth density.

Discussion

Tachinids evidently do not become infected by *E. maimaiga* while parasitizing the infected host but the presence of *E. maimaiga* azygospores on the surface of more than half the tachinid puparia is evidence of development of the entomophthorous fungus in parasitized gypsy moth larvae. Although no azygospores

Table 3 Tachinid parasitoids reared to adult stage in the laboratory from field-collected *Lymantria dispar*

Parasitoid species	Locality	Parasitoid number	Date of emergence
<i>Compsilura concinnata</i>	Ravna gora	1 ♂, 1 ♀	22–24.06.2009
		1 ♀	03.07.2010
		1 ♀	04.07.2011
	Zvezdets	5 ♂♂, 5 ♀♀	19–25.06.2009
		6 ♀♀	24.06–05.07.2011
	Skravena	2 ♀♀	03.07.2009
	Gabrovnitsa	1 ♀	03.07.2009
	Striama	1 ♀	25.06.2009
	Kremen	1 ♀	27.06.2011
	Fakia	1 ♀	01.07.2011
	Indzhe voyvoda	2 ♀♀	01–04.07.2011
	Solnik	3 ♀♀	22.06.2011
	<i>Exorista larvarum</i>	Gabrovnitsa	3 ♂♂, 3 ♀♀
Skravena		2 ♀♀	13.06.2009
<i>Senometopia separata</i>	Spahievo	5 ♂♂, 5 ♀♀	06–17.06.2009
	Ravna gora	2 ♀♀	03–04.07.2010
<i>Senometopia excisa</i>	Indzhe voyvoda	1 ♂	16.06.2010
<i>Drino inconspicua</i>	Spahievo	1 ♀	12.07.2009
<i>Zenilia libatrix</i>	Ravna gora	1 ♂	06.07.2010
Total		16 ♂♂, 38 ♀♀	

were detected on the surfaces of the remaining dead pupae, it is possible that these tachinid larvae developed in gypsy moth larvae that were infected but in which no azygospores were formed prior to larval emergence. In previous laboratory bioassays, 23.3% of gypsy moth larvae died after exposure to *E. maimaiga* without azygospore formation (Pilarska *et al.* 2012).

Additional causes of tachinid mortality in this study are not clear and no other pathogens were observed, either in the parasitoids or in the *L. dispar* hosts. Although some tachinid mortality in the pupal stage may have been related to handling death in the laboratory, optimal humidity was provided during the relatively short development period (Georgiev 1996), approximately 10 days, reducing the possibility of desiccation. Prior to introduction of *E. maimaiga* in Bulgaria, three of the tachinid species found in this study, *C. concinnata*, *S. separata* and *D. incospicua*, were reared successfully from gypsy moth larvae in the laboratory using the same methods (Mirchev *et al.* 1999).

Mortality of tachinids during development in living gypsy moth larvae infected with *E. maimaiga* is likely a result of the competition between the parasitic species. We hypothesize that, during fungal development, nutritional resources available to the parasitoids decrease, limiting available energy for successful pupation and eclosion. Similar mortality of *B. pratensis* was reported in gypsy moth larvae infected with the baculovirus *LdNPV* (Godwin & Shields 1984). The authors observed significant reduction in survival of parasitoid larvae when host larvae were infected with three different dosages of *LdNPV*. Malakar *et al.* (1999) studied the interaction of *LdNPV* and *E. maimaiga* and showed that the number of the viral occlusion bodies produced in the cadavers of larvae infected with both pathogens was lower than those infected only with the virus. Studies also showed that *Vairimorpha disparis*, a relatively virulent microsporidium infecting *L. dispar* larvae, dramatically reduced trehalose, fatty acid and glycogen content in adipose tissue of the host (Hoch *et al.* 2004). Although no laboratory studies of competition between *E. maimaiga* and the microsporidia *V. disparis* and *Nosema lymantriae* have been conducted, neither microsporidian species appears to have persisted in field releases in the U.S. since 2008. Epizootics of *E. maimaiga* occurred in the sites where the microsporidia were released and the fungus may have reduced the survival of the microsporidia (LFS, unpublished data).

Entomophaga maimaiga has become the primary biological control agent in U.S. gypsy moth populations and is spreading rapidly in Bulgarian populations, but its impact on other natural enemies of gypsy moth in field populations is not known. Our studies suggest that *E. maimaiga* is a mortality factor for tachinid parasitoids but the scale of impact on these species and other natural enemies should be determined to evaluate the role of the fungus in gypsy moth control programs.

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