Parasitoid Complex of the Gypsy Moth (*Lymantria dispar*) in the Increase-phase Populations in Korea

Lee, Jang-Hoon^{1*} and Robert W. Pemberton²

¹Research Institute for Natural Science, Dongguk University, Seoul 100-715, Korea ²Invasive Plant Research Laboratory, United States Department of Agriculture, Agricultural Research Service, 3225 College Ave., Ft. Lauderdale, Florida 33314 U.S.A.

ABSTRACT: The species composition of the parasitoid complex and the degree of parasitism by each species were analyzed for gypsy moth (*Lymantria dispar*) populations in the increasing phase. Total of 7,826 mid-late instar larvae and pupae were collected and reared from two collection sites in Gangwon Province, Korea. Two tachinid flies (*Blepharipa schineri* and *Parasetigena silvestris*), and the ichneumonid wasp (*Coccygomimus disparis*) were the most abundant parasitoids, in the order of decreasing importance. Other parasitoids occurring included *Coteisa melanoscelus*, *Cotesia scheaferi*, *Glyptapanteles liparidis*, *Brachymeria lasus*, and *Exorista* spp. The low incidence of the NPVirus is hypothesized to be an important factor in determining degree of parasitism rate by *P. silvestris* and *B. schineri*, and their relative dominance in the parasitoid complex.

Key words: Gypsy moth, Increase-phase population, Natural enemies, NPV, Parasitism

INTRODUCTION

Lymantria dispar L., gypsy moth (hereafter referred as to GM) populations usually experience a cyclic pattern of abundance, described to have the following phases: as innocuous (latent), increase (pre-culmination), outbreak (culmination), and post-outbreak phase (post-culmination) (Campbell 1978, Schonherr 1988, Elkinton and Liebhold 1990). Berryman (1996) reported that parasitoids are frequently involved in this cyclic population dynamics of this univoltine moth, and parasitoids invariably kill a consistently high proportion of lepidopteran immature stages during the decline phase than the increase phase.

Gypsy moth populations in the Republic of Korea (South Korea) are sporadic and usually very low levels where they did occur, making it difficult to study their natural enemies (Pemberton et al. 1993). At times, relatively high gypsy moth populations occur in a small area, but they collapse into the innocuous level, mainly due to infections of NPV (Nuclear Polyhedrosis Virus), within following year or two. For this reason, the phase related parasitoid mortality of GM populations can not be validly assessed, because density dependent pathogen infections masks parasitoid induced mortalities (Pemberton et al. 1993).

Larvae and pupae from GM populations in the increasing phases were collected from low NPV infection sites in Gangwon Province in 1993. The GM populations at these sites decreased to the innocuous phase two years later in 1995. Our objectives were to define components of parasitoid complex, and to determine the patterns of parasitism by the most abundant parasitoids in increasing GM populations.

MATERIALS AND METHODS

Season Long Collections

Collections were made from two different sites located in Gangwon Province, which are 50 km apart from each other. The Yongdaeri site (Book-Myeon, Injae-Gun, Gangwon Province), bounded by $128^{\circ} 21' 12''$ and $128^{\circ} 21' 16''$ E and by $38^{\circ} 11' 52''$ and $38^{\circ} 11' 30''$ N (elevation $340 \sim 370$ m), is located on the north west side of Mt. Surak near Highway 44. GM larvae and pupae were collected from this site weekly during from late May to early July 1993. Tree species composition in the Yongdae-ri sites consisted of *Prunus sargentii* Rehder and *P. persica* (L.) Batch, *Salix pseudo-lasiogyne* Lév, *Robinia pseudoacacia* L., and *Betula platyphylla* Sukatschev.

The Doochon site, the area between Yeoknae and Juan-ri (Doochon-Myeon, Hongchon-Gun (Highway 44), bounded by 37° 50' 16" and 37° 51' 19" N, 128° 00' 44" and 128° 01' 11" E (230~250 m), is of East side of Mt. Gari. GM larvae and pupae were collected from this site weekly and six samplings were made from May 27 to July 08. The tree species in Doochon-Myeon sites were *Populus seiboldii* Miquel, *Salix pseudo-lasiogyne* Lév, *Quercus* spp., *Larix gmelini* var. *principisruprechtii* (Mayr) Pilger *Robinia pseudoacacia*, and

* Corresponding author; Phone: +82-2-2260-3511, e-mail: ecojhl@dongguk.edu

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Morus bombycis Koidz.

Collections at all sites were made along roadside trees and overstory of neighboring forests and extended up to twenty meters into forests. The areas of collection were 2,000 m². Thirty trees of the species listed above each collection site spaced with 10 m interval were selected for each of the sampling sites. Burlap bands were set on trees at breast height to facilitate collections of larvae and pupae one week before initial collections. The bands provide refuges for larvae during the day and pupation sites, both of which concentrates the larvae and pupae, making them easier to collection. Generally, for any week's collection, larvae and pupae were collected by one collector for one hour for each collection sites. This procedure was followed until the end of the season. Eggs began to hatch in both areas after about early May. First collections were made during the week of May 27th and the last collections during the week of July 7.

Rearing

The collection and rearing procedures were similar to those followed by Pemberton and Lee (1996). The larvae and pupae collected from burlap bands, then taken to the laboratory where they were reared in screen-toped plastic boxes (20.5 by 28 by 16.5 cm in groups of up to 30 individuals and fed Quercus spp. leaves. To minimize mortality due to nuclear polyhedrosis virus (NPV), all leaves were disinfected in a sodium hypochlorite solution and well rinsed before placed in the rearing boxes. The containers were checked every other day for parasitoid emergence. Also noted were the numbers of gypsy moth larvae killed by disease including the Nuclear Polyhedrosis Virus, those that died from unknown causes, and those that successfully developed to adult stage. Parasitoid identifications were made by the authors, by comparison with authoritatively determined voucher material from the former USDA-ARS Asian Parasite Laboratory collection. Dead hosts were kept for ca. two weeks because some parasitoids emerge from dead hosts. If no parasitoids were observed to emerge, host material was dissected to determine the cause of death.

Gypsy Moth Population Estimation and Analysis

Gypsy moth population estimates were made for each site by calculating the hourly density (number of larvae and pupae collected per person per hour). Parasitism also was analyzed in terms of host population phase affinities. In order to determine the population phase, egg mass density (eggs masses are usually on tree trunks and major branches), the ratio of new to old egg masses, the ratio of adult female to males emerged during rearing, and hourly density of immature stages were used. The egg mass density and the ratio of new to old egg masses were determined by egg mass counts during five min long walks (n = 4) (Schneeberger 1987). Although five min walks are very practical and convenient for relative abundance of egg mass density, they are not recommended for estimation of absolute density (Liebhold et al. 1991).

Indices of parasitism for each parasitoid and each site to evaluate their importance were used in this study (see Pemberton et al. (1993) for details). The percentages of parasitism by each species were calculated by dividing the number of emerged individuals of each parasitoid species by the number of collected GM larvae and / or pupae. These parasitism percentages for individual parasitoid species were added to yield combined parasitism rates for collection dates, sites, and ultimately the whole study. Total parasitism (seasonlong parasitism) is the number of individuals parasitized by all parasitoids in the samples of a season-long collection at a particular site divided by the total individuals collected. Thus average seasonlong parasitism is the average parasitism in the two season long collections from the sites. Gregarious parasites emerging from a single larva (Cotesia schaeferi (Marsh) and Glyptapanteles liparidis Bouché) were counted as one parasite. Parasite-host associations were generally determined by the cocoon aggregations on or near the host cadavers.

Statistical analyses were performed using SAS 9.1 (SAS Institute 2004). Differences of relative frequencies were tested by cross table χ^2 analysis. Percent data were arcsin-transformed and tested for significance of difference by one-way ANOVA; means were compared using Tukey's studentized range (HSD) test [PROC GLM (SAS Institute 2004)].

RESULTS AND DISCUSSION

A list of common parasites we recovered from the larvae and pupae of L. dispar at increasing population sites in Gangwon Province is presented in Table 1. At Yongdae-ri, a total of 4,339 larvae and pupae were collected from May 27 to July 8 and at Doochon sites, a total of 3,487 larvae and pupae were collected at the same dates. The hourly collection of larvae and pupae per person averaged 361 at Yongdae-ri and and 303 at Doochon. The gypsy moth population at both Yongdae-ri and Doochon were both determined to be in the increasing phase. The sites had 57.5 and 41.3 egg masses per 5 min walk, and to the best our knowledge, GM population were not high in recent years. The determination of increasing phase was supported by the fact that old egg masses were rare at the sites and by female biased emergence with the rate of females to males, 1.2 and 1.6 in Yongdae and Doochon sites, respectively (Table 1). The predicted buildup of the populations actually took place at these sites during the following the year (1994), and then collapsed in 1995, when no new egg masses could be found during the post-season egg-mass counts. Pre-season egg-mass counts at the sites also failed to locate no new egg masses in 1996.

The total parasitism (season-long parasitism) recorded was 22.4 and 27.7% at Yongdae-ri and Doochon, respectively and these were not significantly different ($\chi^2 = 0.0256$, df = 1, p = 0.8728). 11 primary parasitoids, one unidentified tachinid, 2 unidentified sarcophagids and two diseases were found in the 7,826 collected larvae and

Table 1. Percentage season-long mortality of gypsy moth in increasing phase in Gangwon Province, Korea in 1993

Natural enemy species	Collection sites ^c			
or source of mortality	Yongdae-ri	Doochon		
Braconidae				
Cotesia melanoscelus	< 0.1	0.1		
Cotesia schaeferi	0.4	0.1		
Glyptapanteles liparidis	0.1	< 0.1		
Ichneumonidae				
Lymantrichneumon disparis	1.5	0.1		
Coccygomimus disparis	2.7	1.9		
Brachymeria lasus	0.3	0.0		
Brachymeria fiski	0.1	0.0		
Tachinidae				
Blepharipa schineri	12.0	18.0		
Compsilura concinnata	0.2	0.6		
Exorista spp.	1.5	1.3		
Parasetigena silvestris	1.3	4.3		
Unidentified sp.	1.0	0.2		
Sarcophagidae				
Sarcophagid spp.	1.3	1.0		
NPV	6.3	4.5		
Beauveria sp.	0.3	0.2		
Unknown causes ^a	7.1	10.3		
No. hosts examined	4,339	3,487		
Total percentage parasitism	22.4	27.7		
Total percentage dead ^b	36.1	42.7		
Adult emergence(\mathscr{Z} : $\stackrel{\circ}{+}$)	63.9 (28.6:35.3)	57.3 (22.0:35.5)		

^a Host killed by desiccation or unknown causes. ^b Denotes overall mortality induced by parasitoids, pathogens and unknown causes. ^c Mean percentage parasitism by parasites species did not differ between collection sites ($\chi^2 = 0.2684$, df = 1, p = 0.6044). pupae. Of these, *Blepharipa schineri* (Robineau-Desvoidy) (Diptera: Tachinidae) emerged from 1,150 (14.7%), *Parastigena silvestris* (Robineau-Desvoidy) (Diptera: Tachinidae) from 210 (2.7%), *Coccygominus disparis* (Hymenoptera: Ichneumonidae) from 181 (2.3%), *Exorista* spp. (Diptera: Tachinidae) from 109 (1.4%), Sarcophagid spp. (Diptera: Sarcophagidae) from 94 (1.2%), *Compsilura concinnata* (Meigen) from 29 (0.4), unidentified tachinid from 41 (0.5%), *Brachymeria lasus* (Walker) (Hymenoptera: Chalicididae) from 3 (0.04%), *Coteisa schaeferi* (Marsh) from 19 (0.24%), *Glyptapanteles liparidis* (Bouché) from 5 (0.06%), and *Coteisa melanoscelus* (Ratzeburg) (Hymenoptera: Braconidae) (0.03%) from 3 hosts. It is quite evident that *B. schineri*, *P. silvestris*, *C. disparis* are the dominant parasitoids of GM in these selected areas of Gangwon Province.

There was a similar parasitization pattern at the two sites. *Blepharipa schineri* caused the highest parasitism rates at both sites: Yongdae-ri with total parasitism rate (season-long rate) of 12%, compared to 18% at Doochon. *Blepharipa schineri* also induced the highest stage specific parasitism at each site (Table 2). Species of tachinids and ichneumonids accounted for > 94% of the parasitoid induced morality in the study. However, braconids had low levels (< $0.1 \sim 0.4\%$) of parasitism. These three families usually account for most of the parasitoid-induced mortality in the GM in previous studies (Pemberton et al 1993; Pemberton and Lee 1996; Lee et al. 2002).

Weekly data on percentage parasitism by dominant mortality agents is shown in Fig. 1. *Blepharipa schineri* was the dominant parasite at both collection sites (with peak parasitism 27.8 on 17 June at Yongdae-ri, and 27.8% on 24 June at Doochon). The parasitism rates by *B. schineri* were higher than those by other parasites during three collection periods at Yongdae-ri and during five collection periods at Doochon. The parasitism rates by this fly were significantly different from other mortality agents at both the Yongdae-ri site (Tukey's studentized range (HSD) test, F = 3.82, df = 5, p = 0.0086) and Doochon site (Tukey's studentized range (HSD) test, F = 6.4, df = 5, p = 0.004)

Table 2 shows the identified host stage mortality expressed as mean parasitism for each host stage grouping. Late instar larvae were more heavily parasitized than mid larvae (3 ~4th instars). *B. schineri* showed the highest parasitism rate in all age group in both study sites. Ichneumonid parasitoids were the second most dominant parasitoids, with *C. disparis* emerging from the pupal stage combined with parasitism by *Lymantrichneumon disparis* Poda in Yong-dae-ri yielding a similar level of the 8% caused by *B. schineri*.

Blepharipa schineri is an oligophagous, univoltine larval-pupal parasitoid which lays microtype eggs on foliage. Larvae of all ages can ingest these eggs as they consume the leaves and become



Fig. 1. Percentage parasitism during each collection period in two different sites in Gangwon Province, Korea in 1993.

 $BS = Blepharipa \ schineri$, $PS = Parasetigena \ silevstris$, NPV = NucleoPolyhedrosis virus, Unknown = Host killed by desiccation or unknown cause, $CD = Coccygominus \ disparis$.

Parasitism rate by *B. schineri* is significantly different from other mortality agents for both Yongdae-ri (Tukey's studentized range (HSD) test, F = 3.82, df = 5, p = 0.0086) and Doochon sites (Tukey's studentized range (HSD) test, F = 6.4, df = 5, p = 0.004).

parasitized. As shown in Table 2, as larvae grow older, the parasitism rate appeared to increases. As noted above, *B. schineri* was the most important larval and pupal parasitoid accounting for 15% of gypsy moth mortality in this study (Table 1). This total parasitism rate is much higher than the mean rates of 4.15% detected previously in Kyonggi Province (Pemberton et al. 1993). Pemberton et al. (1993) demonstrated that the impact of NPV on late instar larvae could have reduced the parasitoid population at the high density sites and masked the potential effects of *B. schineri*. This fly is common in Europe and in Northeastern Asia. In Europe, this *B. schineri* was assumed to be effective against late instar larvae and pupae, inducing high rates of parasitism in the first post culmination year (Fuester et al. 1988).

Parasetigena silvestris, an oligophagous, univoltine tachinid fly that lays eggs directly on the surface of host larvae, was recovered at both collection sites. It was the second important parasite at Doochon (4.3%) (Table 1) with the peak parasitism of 8.8% on 8

June (Fig. 1), but was less important at Yongdae-ri, where its season-long parasitism rate was only 1.3% (Table 1). It is a major parasitoid of *L. dispar* throughout much of Eurasia (Fuester et al. 1983, Drea & Fuester 1979, Fuester et al. 1988, Schaefer 1981, Schaefer et al. 1984, Kolomiets 1987), and Korea (Pemberton et al. 1993). Studies in Yougoslavia (Sisojević 1975), Austria (Fuester et al. 1983) and Lithuaia (Zolubas et al. 2001) indicate that the *P. silvestris* are a major factor in reducing populations during the second post-culmination year of the gypsy moth gradation (declining phase). This tachinid is considered important in the progradation (increasing phase) phase, disrupting the build-up of a gypsy moth population (in Austria, Hoch et al. 2001; in Germany, Maier 1990). Similarly it was the most important parasite in Korea, accounting for 22.1% of mortality of late instar larvae in increasing gypsy moth populations (Pemberton 1993 and Lee 2007).

Coccygomimus disparis is a polyphagous, multivoltine ichneumonid wasp. This wasp was recorded from host pupae collected from 24 June to 8 July. Pupae from the collection sites were parasitized by this wasp at average season-long rates (total parasitism rate) of 2.3 % (Table 1). It was the second most important pupal parasite at Yongdae-ri, where peak parasitism of 8.8% was recorded from 717 pupae collected on June 25 (Fig. 1). Generalist natural enemies such as C. disparis can remain abundant when a particular host species has become extremely sparse or locally extinct, and respond quickly when reinfestations of the host occurs (Murdoch et al. 1985). This seems to be what occurred in this study. Fuester et al. (1997) noted that levels of parasitism by this species were not affected by host density. A common moth host, such as Hyphatria cunea (Drury), in Korea may promote C. disparis, as indicated by a high level of parasitism often found in the overwintering pupae of this moth in Korea (Kim and Lee 1982).

Braconid wasps induced low levels (< $0.1 \sim 0.4\%$) of parasitism in this study, compared with previous studies in Korea, in which the braconid *Cotesia melanoscelus* was a major component of the gypsy moth parasitoid complex especially in augmented populations (Pemberton at al. 1993). Increased parasitism rate in augmented gypsy moth populations has also observed by other authors (Liebhold and Elkinton 1989, Hoch et al. 2001). These authors suggested that foraging behavior of this wasp is positively density dependent and it could be effective in controlling increasing phase of GM populations. *C. melanoscella* was found to be the most important hymenopteran species in the third post culmination year (Eichhorn 1996, Hoch et al. 2001).

Notably, disease infection, including NPV, was relatively low at all collection sites in this study. NPV frequently decimates high density GM populations in Korea (Pemberton et al. 1993, Lee et al. 2002). At Yongdae-ri, in the collection of 4,339 individuals, di-

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Table 2. Stage specific mortality of gypsy moth larvae and pupae in the increasing population phase in Gangwon Province, Korea in 1993

		Parasitism by host stage ^c						
		Yongdae-ri		Doochon				
Mortality agent	3 & 4th	5 & 6th ^a	Pupae	3 & 4th	5 & 6th	Pupae		
Cotesia melanoscelus	0.1	0.0	0.0	0.3	0.0	0.0		
Cotesia schaeferi	2.3	0.0	0.0	0.8	0.0	0.0		
Glyptapanteles liparidis	0.3	0.1	0.0	0.2	0.0	0.0		
Brachymeria lasus	0.1	0.1	0.4	0	0.0	0.0		
Brachymeria. fiski	0.0	0.0	0.1	0	0.0	0.0		
Coccygomimus disparis	0.0	0.1	5.2	0	0.0	4.5		
Lymantrichneumon disparis	0.0	0.1	2.8	0	0.0	0.3		
Blepharipa schineri	2.7	23.9	8.1	9.0	15.6	24.3		
Parasetigena silvestris	0.1	2.0	1.4	5.8	7.5	0.6		
Exorista spp. ^b	0.4	2.2	1.4	0.1	0.7	2.4		
Compsilura concinnata	0.0	0.4	0.1	0.5	1.2	0.2		
Tachinid unidentified	0.0	0.4	1.7	0.0	0.1	0.4		
Sarcophagid spp.	0.0	1.3	1.7	0.2	0.4	2.0		
NPV	1.0	2.3	10.5	1.3	5.1	5.2		
Beauveria sp.	0.0	0.0	0.7	0	0.2	0.3		
Unknown causes ^c	8.6	7.5	6.5	7.1	17.2	5.0		
No. hosts examined	709	1,341	2,231	635	1,398	1,452		
Total parasitoid-induced parasitism	5.9	30.6	23.1	16.9	25.5	34.7		
Total percentage dead ^d	15.5	40.4	40.7	25.3	48	45.2		
Host emergence rate (%) $(\mathcal{S}: \stackrel{\circ}{+})$	84.5	59.6	59.3	74.8	52.0	54.7		
	(49.5:35.0)	(22.5:36.1)	(24.1:35.2)	(32.1:42.7)	(12.7:39.3)	(26.5:28.2)		

^a This group separated contains prepupae. ^b Includes *Exorista japonica* and probably a few *E. larvarum* and *E. sorbillans*. ^c Host killed by desiccation or unknown cause. ^d Denotes overall mortality induced by parasitoids, pathogens and death from unknown cause.

^c Mean percentage parasitism by parasites species did not differ between collection sites for each host stage grouping ($\chi^2 = 0.375$, df = 1, p = 0.54 for 3 & 4th, $\chi^2 = 0.4139$, df = 1, p = 0.52 for 5& 6th, $\chi^2 = 0.10958$, df = 1, p = 0.2952).

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sease-induced mortality (largely NPV-induced) was only 1.0% for third to fourth instar larvae, 2.3% for the late larvae and prepupae, 10.5% for pupae (Table 2), and the season-long mortality (total mortality) of 6.3% (Table 1). The stage specific morality caused by disease at Doochon were 1.3, 5.1, and 5.2% respectively (Table 2), with the total mortality of 4.5% in the subsample of 3,487 (Table 1). One of the most conspicuous results in this study is the high level of parasitism by *B. schineri* and its relative dominance over *P. silvestris* (p<0.05). The reverse was frequently found from gypsy moth populations with high NPV incidence in Korea (Pemberton 1993, Lee 2007). This pattern probably results from the fact that *B.* schineri which emerges mainly from the pupal stage is more severely affected by disease infections than *P. silvestris* which emerges from larvae, the difference being that *B. schineri* is to be exposed to NPV infection for a longer period than *P. silvestris* and disease infected host larvae accordingly are not likely to develop to the pupal stage. Barbosa et al. (1975) reported that a virus-host interaction affecting feeding negatively affects the rate of parasitism by *B. scutellata*, the ecological homologue of *B. schineri* that also depends on host ingestion of its eggs. Negative effects of pathogen infection of gypsy moth on parasitoid development were also demonstrated for *Blephripa pratensis* (Godwin and Shields 1982, 1984), and for

Glyptapnteles liparidis (Hoch et al. 2000). On the contrary, there have been reports of a positive interaction between the incidence of pathogen attack and the degree of parasitism in the host. Incidence of the nuclear polyhedrosis virus disease (NPV) was found to be positively correlated with the occurence of the parasitoids *Apanteles melanoscelus* (Ratzeburg) and *Parasetigena silvestris* (Reardon and Podgwaite 1976). Because sublethal diseases can lengthen the development times of the gypsy moth, infected larvae may have longer periods of exposure to parasites and certain sublethal levels of NPV (Weseloh & Andreadis 1982) and *Bacillus thuringiensis* (Weseloh 1984) may therefore promote more parasitism.

As these results suggests, the interaction between pathogens and gypsy moth may be important determinants of change in the parasitoid community associated with the moth's population phase. These interactions are pronounced in Korea because the weather during the gypsy moth activity period is characterized high relative humidity and high summer rainfall, which promotes frequent NPV epizootics in the moth (Pemberton 1993).

Many studies have increasingly focused on population cycles of the gypsy moth (Johnson et al. 2005, Liebhold and Kamata 2000, Pernek et al. 2008), and on identifying the parasite communities associated with a particular population phase (Eichhorn 1996, Fuester et al. 1988, Hoch et al. 2001, Maier 1990, Lee 2007). Few studies have dealt with specific mechanisms determining the structure of parasite complex, suggesting the need for further investigation.

LITERATURE CITED

- Barbosa P, Capinera JL, Harrington ER. 1975. The gypsy moth parasitoid complex in western Massachusetts: a study of parasitoids in areas of high and low host density. Environ Entomol 4: 842-846.
- Berryman AA. 1996. What causes population cycles of forest Lepidoptera? Tree 11: 28-32.
- Campbell RW. 1978. Some effects of gypsy moth density on rate of development, pupation time, and fecundity. Ann Entomol Soc Am 71: 442-448.
- Drea JJ Jr, Fuester RW. 1979. Larval and pupal parasites of *Lymantria dispar* and notes on parasites of other Lymantriidae [Lep] in Poland, 1975. Entomophaga 24: 319-327.
- Eichhorn O. 1996. Experimental studies upon the parasitoid complex of the gypsy moth (*Lymantria dispar L.*) (Lep, Lymantriidae) in lower host populations in eastern Austria. J Appl Entomol 120: 205-212.
- Elkinton JS, Liebhold AM. 1990. Population dynamics of gypsy moth in North America. Annu Rev Entomol 35: 571-596.
- Fuester RW, Gruber F, Drea JJ Jr, H Hoyer. 1988. Parasites of Lymantria dispar in France and their relation to a biological control program. Acta Oecol Appl 9: 385-402.
- Fuester RW, Drea JJ Jr, Gruber F, Mercadier G. 1983. Larval parasites and other natural enemies of *Lymantria dispar* (Lepidoptera: Lymantriidae) in Burgenland, Austria, and Wurzburg, Germany. En-

viron Entomol 12: 724-737.

- Fuester RW, Sandridge PT, Dill NH, Mclaughlin JM, Peiffer RA, Taylor PB, Sigmon JOD, Newlon CJ. 1997. Parasitism of gypsy moth (Lepidoptera: Lymantriidae) pupae on the Delmarva Peninsula with emphasis on *Coccygomimus disparis* (Hymenoptera: Ichneumonidae). J Econ Entomol 90: 1551-1559.
- Godwin, PA, Shilds KS. 1982. Some interactions of Serratia marcescens, Nucleopolyhedrosis virus and Blepharipa pratensis (Dip: Tachinidae) in Lymantria dispar (Lep: Lymantriidae). Entomophaga 27: 189-196.
- Godwin PA, Odell TM. 1984. Laboratory study of competition between Blepharipa pratensis and Parasetigena silvestris (Diptera: Tachinidae) in Lymantria dispar (Lepidoptera: Lymantriidae). Environ Entomol 13: 1059-1063.
- Hoch G, Schopf A, Maddox JV. 2000. Interactions between an Entomopathogenic Microsporidium and the Endoparasitoid *Glyptapanteles liparidis* within their host, the gypsy moth larva. J Invert Pathol 75: 59-68.
- Hoch G, Zubrik M, Novotny J, Schopf A. 2001. The natural enemy complex of the gypsy moth, *Lymantria dispar* (Lep, Lymantriidae) in different phases of its population dynamics in eastern Austria and Slovakia - a comparative study. J Appl Entomol 125: 217-227.
- Johnson MD, Liebhold AM, Ottar NB, McManus ML. 2005. Circumpolar variation in periodicity and synchrony among gypsy moth populations. J Anim Ecol 74: 882-892.
- Kim OS, Lee HP. 1982. Studies on the biological control of *Hyphan-tria cunea* Drury (Lepidoptera: Arctidae). Korean J Entomol 12: 49-56 (in Korean, English abstract).
- Kolomiets NG. 1987. Insects-parasites and predators of the gypsy moth (Lymantria dispar L., Lepidoptera) from the Asiatic part of the USSR. Izvestiya Sibirskogo Otdeleniya Akademii Nauk SSSR (Seriya Biologicheskikh Nauk) 6: 83-89 (in Russian).
- Lee JH. 2007. The parasitoid complex of late instar gypsy moth (*Lymantria dispar* L.) in Kyonggi Province, Korea: a study of parasitoids attacking the populations of increasing phase with a high disease incidence. J Nat Sci RINS 8: 92-96.
- Lee JH, Lee HP, Schaefer PW, Fuester RW, Park JD, Lee BY, Shin CH. 2002. Gypsy moth parasite complex, Mt Halla National Park, Cheju Island, Korea .Entomol News 113: 103-112.
- Liebhold AM, Elkinton JS. 1989. Elevated parasitism in artificially augmented populations of *Lymantria dispar* (Lepidoptera: Lymantriidae). Environ Entomol 18: 986-995.
- Liebhold A, Kamata N. 2000. Are population cycles and spatial synchrony a universal characteristic of forest insect populations? Popul Ecol 42: 205-209.
- Liebhold AM, Twardus D, Buonaccorsi J. 1991. Evaluation of the timed-walk method of estimating gypsy moth, *Lymantria dispar* (Lepidoptera: Lymantriidae) egg mass densities. J Econ Entomol 84: 1774-1781.
- Maier K. 1990. Contribution to the biology of primary and secondary parasitoids of *Lymantria dispar* L. (Lep, Lymantriidae). J Appl Entomol 110: 167-182.
- Maier KJ. 1995. Der Einflu
 β der Parasitoide auf Lymantria dispar L (Lep, Lymantriidae) in W
 äldern mit unterschiedlich starkem Massenwechsel Mitt Dtsch Ges Allg Angew. Entomol 10: 129-134.

- Murdoch WW, Chesson J, Chesson PL. 1985. Biological control in theory and practice. Am Nat 125: 344-366.
- Pemberton RW, Lee JH. 1996. The influence of extrafloral nectaries on parasitism of an insect herbivore. Am J Bot 83: 1187-1194.
- Pemberton RW, Lee JH, Reed DK, Carlson RW, Han HY. 1993. Natural enemies of the Asian gypsy moth (Lepidoptera: Lymantriidae) in South Korea. Ann Entomol Soc Am 86: 423-440.
- Pernek M, Pilas I, Vrbek B, Benko M, Hrasovec B, Milkovic J. 2008. Forecasting the impact of the Gypsy moth on lowland hardwood forests by analyzing the cyclical pattern of population and climate data series Forest. Ecol Manag 255: 1740-1748.
- Reardon RC, Podgwaite JD. 1976. Disease-parasitoid relationships in natural populations of *Lymantria dispar* [Lep: Lymantriidae] in the northeastern United States. Entomophaga 21: 333-341.
- SAS Institute Inc. 2004. SAS/STAT 91 user's guide Cary, NC.
- Schaefer PW. 1981. Explorations in Japan and Korea by the ARS Asian Parasite Laboratory: 1975-77. In The Gypsy Moth; Research Towards Integrated Pest Management (Doane CC, McManus ML, Eds). USDA Tech Bull 1584. pp. 340-348.
- Schaefer PW, Yan J, Sun X, Wallner WE, Weseloh RM. 1984. Natural enemies of the gypsy moth, *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae), in China. Sci Silvae 20: 434-440.
- Schneeberger NF. 1987. Monitoring gypsy moth populations. In Coping

with the Gypsy Moth in the New Frontier West Virginia University, Morgantown, WV. pp 81-88.

- Schonherr J. 1988. Outbreak characteristics of Lymantriids. In Lymantriidae: a Comparison of Features of New and Old World Tussock Moths (Proceedings) (Waller WE, McManus KA, Eds). June 26-July 1, New Haven, Connecticut. pp 171-178.
- Sisojević P. 1975. Population dynamics of tachinid parasites of the gypsy moth (*Lymantria dispar* L.) during a gradation period (in Serbo-Croatian, English summary). Zast Bilja 26: 97-170.
- Weseloh RM. 1984. Effect of the feeding inhibitor Plictran and low Bacillus thuringiensis Berliner doses on Lymantria dispar (L.) (Lepidoptera: Lymantriidae): implications for Cotesia melanoscelus (Ratzeburg) (Hymenoptera: Braconidae). Environ Entomol 13: 1371-1376.
- Weseloh RM, Andreadis TG. 1982. Possible mechanism for *Bacillus thuringiensis* and gypsy moth (Lepidoptera: Lymantriidae) parasitoid, *Apanteles melanoscelus* (Hymenoptera: Braconidae). Ann Entomol Soc Am 75: 435-438.
- Zolubas P, Gedminas A, Shields K. 2001. Gypsy moth parasitoids in the declining outbreak in Lithuania. J Appl Entomol 125: 229-234.

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