
CHAPTER 14. DETERMINING THE HOST RANGE OF *APHANTORHAPHOPSIS SAMARENSIS*, A SPECIALIZED TACHINID INTRODUCED AGAINST THE GYPSY MOTH

R. W. Fuester,¹ K. S. Swan,¹ M. Kenis,² and F. Hérard³

¹USDA-ARS Beneficial Insects Introduction Research Laboratory, Newark, Delaware, USA
rfuester@biir.ars.usda.gov

²CABI Bioscience Center, Delémont, Switzerland

³USDA-ARS European Biological Control Laboratory, Montpellier, France

BACKGROUND OF SYSTEM

DESCRIPTION OF PEST INVASION AND PROBLEM

One of the consequences of the Civil War was the collapse of the cotton industry in the South. Ultimately, this led to idle textile mills in the New England states. A Franco-American scientist, Étienne Léopold Trouvelot, sought to capitalize on this situation by using giant silkworm moths native to North America to develop a sericulture industry (Liebhold *et al.*, 1989). Because a disease caused by a protozoan (*Nosema bombycis* Naegeli) had a devastating impact on the silk industry in Europe (Leggett, 1949), Trouvelot sought to negate this problem by crossing the European gypsy moth, *Lymantria dispar* (Linnaeus), with American silkworm moths, hoping to develop a pathogen-resistant silkworm (Howard, 1930). During the course of his experiments, conducted at his home at 27 Myrtle Street, Medford, MA, some immature stages escaped (Forbush and Fernald, 1896), and the moth began its colonization of North America in 1868 or 1869 (Liebhold *et al.*, 1989). Since that time, literally millions of dollars have been expended in attempts to eradicate, retard the spread, or suppress this invasive pest.

The gypsy moth is probably the most destructive forest and shade tree pest in the northeastern United States, defoliating a record 13 million acres in 1989. It attacks primarily hardwood trees, especially oak, although after the larvae are half-grown they will attack conifers. They usually do not infest ash, black walnut, catalpa, or yellow-poplar (tulip tree). The range of this introduced pest is primarily the northeastern United States, from Maine south to North Carolina and west to Wisconsin. Small, isolated infestations have been reported from California, Tennessee, and Iowa. Male moths have been trapped in a number of other states.

The eggs hatch in late April or early May, with the larvae completing feeding in late June or early July. After feeding, the larvae pupate within loose silken cradles and emerge as adult moths in about two weeks. Shortly after the female emerges, she mates and begins laying eggs on trees, rocks, or other nearby objects. The female, too heavy with eggs to fly, deposits buff-colored clusters of 100 to 1,000 eggs. The current year's egg masses can be found from late July or August until April or May of the following year. The gypsy moth has one generation per year.

When populations reach outbreak levels, gypsy moth defoliation produces adverse ecological effects and economic impacts in both forests and urban-suburban settings (McManus and McIntyre, 1981). Because it defoliates numerous species of shade trees and becomes a severe nuisance pest in urban environments, gypsy moth can be characterized as a "people pest" of the first order. This factor has afforded gypsy moth a high political profile and has driven many of the decisions made in efforts to eradicate or suppress the pest, including efforts at its biological control, which began shortly after the start of the 20th century, when biological control as a discipline was in its infancy (Clausen, 1978). As in the case of most pest problems, there was considerable pressure to obtain a quick solution, and the gypsy moth was no exception; consequently, the overall strategy was to introduce many species of control agents in the hope that one or more of them would suppress the pest. Before 1980, the host specificity of natural enemies introduced against pest insects was not a major consideration. In fact, the polyphagous nature of *Compsilura concinnata* Meigen, a tachinid fly established between 1907 and 1909 (Howard and Fiske, 1911) and now believed to have adverse effects on native giant silkworm moths (Boettner *et al.*, 2000), was considered desirable by early workers because this fly would attack the imported cabbageworm, *Pieris rapae* (L.); browntail moth, *Euproctis chrysorrhoea* (L.); and satin moth, *Leucoma salicis* (L.) (Howard and Fiske, 1911; Burgess and Crossman, 1929). A detailed description of earlier (pre-1990) work on classical biological control of the gypsy moth is beyond the scope of this chapter, and the interested reader is referred to the reviews provided by Hoy (1976), Reardon (1981), and Van Driesche *et al.* (1996).

A total of 16 introduced natural enemies became established as a result of these efforts: three predators – *Calosoma sycophanta* (L.), *Carabus auratus* L., and *Carabus nemoralis* Müller (Coleoptera: Carabidae) (Clausen, 1978); 11 parasitoids – *Ooencyrtus kuvanae* (Howard) (Hymenoptera: Encyrtidae), *Anastatus disparis* Ruschka (Hymenoptera: Eupelmidae), *Cotesia melanoscelus* (Ratzeburg) (Hymenoptera: Braconidae), *Phobocampe uncinata* (Gravenhorst) and *Pimpla* (= *Coccygomimus*) *disparis* (Viereck) (Hymenoptera: Ichneumonidae), *Brachymeria intermedia* (Nees) (Hymenoptera: Chalcididae), *Monodontomerus aereus* Walker (Hymenoptera: Torymidae), *Compsilura concinnata* (Meigen), *Exorista larvarum* (L.), *Parasetigena silvestris* (Robineau-Desvoidy), and *Blepharipa pratensis* (Meigen) (Diptera: Tachinidae) (Howard and Fiske, 1911; Burgess and Crossman, 1929; Hoy, 1976; Schaefer *et al.*, 1989); and two pathogens – gypsy moth nuclear polyhedrosis virus (*LdNPV*) (Glaser and Chapman, 1913) and *Entomophaga maimaiga* Humber, Shimazu and Soper (Zygomycetes: Entomophthorales) (Andreadis and Weseloh, 1990). The latter species has produced dramatic epizootics in gypsy moth populations in the years after its initial recovery in 1989 (Hajek *et al.*, 1995, 2000; Webb *et al.*, 1999). In addition, *E. maimaiga* appears to have had adverse effects on the guild of larval parasitoids, particularly the univoltine tachinid flies *P. silvestris* and *B. pratensis*, both of which attack late instars of the gypsy moth (Blumenthal and Wilt, 1998). There is some

evidence that *E. maimaiga* might not be as effective in the Great Lakes region as in other parts of the gypsy moth distribution (McCullough *et al.*, 2001).

DESCRIPTION OF AGENT PROPOSED FOR INTRODUCTION

Biology of the parasitoid Two independent evaluations of biological control work on gypsy moth were made during the 1990s (Delfosse *et al.*, 1994; Van Driesche *et al.*, 1996). Both recommended that further overseas exploration for natural enemies be focused in non-outbreak or low density populations of gypsy moth. This need prompted us to re-examine *Aphantorhaphopsis* (= *Ceranthia*) *samarensis* as a potential candidate for importation, study, and possible release. This fly, originally described from Russia in 1921 (Sabrosky and Reardon, 1976), was first recovered from gypsy moth in Austria (Fuester *et al.*, 1983). Because only a few puparia were recovered from *L. dispar* during our two-year study, we concluded that it was an occasional parasitoid of gypsy moth. However, a 10-year study conducted by Mills and Nealis (1992) suggested that this species had substantial potential for biological control of gypsy moth. In brief, they experimentally exposed gypsy moth larvae in areas where local gypsy moth populations were at low densities, recollected the hosts, and returned them to the laboratory to rear out the parasitoids. They concluded that *A. samarensis* represented a promising candidate for biological control of gypsy moth in Canada for the following reasons: (1) This parasitoid is able to persist in areas where gypsy moth populations are low and thus presumably has good host searching ability. (2) It responds quickly to local increases in gypsy moth density. (3) It was by far the main parasitoid attacking sentinel larvae exposed in the field, with very high rates of parasitism. (4) Based on photoperiod and temperature conditions in central Europe (same latitude as southern Ontario), if established in the United States, most of the parasitoid's population would be univoltine and not require alternate hosts. (5) Puparia in diapause could be shipped to Canada and overwintered in quarantine. (6) Post-storage emergence rates could be determined under a variety of environmental conditions. Releases were made in Canada (Nealis and Quednau, 1996)

Quednau (1993) worked out the biology of *A. samarensis*, which is briefly summarized as follows. This species hibernates as a pharate adult in the puparium. Newly emerged females mate with older (5-6 day old) males. There is a 10-12 day pre-oviposition period. The egg is deposited directly on the host; hatching occurs immediately, and the neonate maggot rapidly bores into the host (ovolarviposition). The average number of progeny produced by a female over its lifetime is 55. Females live an average of 41 days and deposit their eggs on second and third instars of *L. dispar*. The parasite develops internally, forming a respiratory funnel that produces a characteristic circular scar on the host cuticle. Development in the host takes 6-14 days, and the full grown maggot generally emerges from third or fourth instars, or less frequently, fifth instars. Because *A. samarensis* attacks earlier larval stages than the other univoltine tachinids associated with gypsy moth, interspecific competition with *E. maimaiga* might be less intense.

Source of agent This Palearctic species has a wide distribution in northern and central Europe: Austria (Fuester *et al.*, 1983), France (Mills and Nealis, 1992), Germany (Maier, 1990), Hungary (Mihalyi, 1986), Poland (Sukovata, 2000), and Sweden, as well as the Leningrad and Kubyshev regions of Russia (Herting, 1984). All of the material used in our laboratory tests

with North American Lepidoptera came from eastern France (Haute-Saône, Bas-Rhine, and Côte d'Or provinces) and had been reared from *L. dispar*.

Host range in native range of agent Prior to our host range studies, *A. samarensis* only had been recorded from two hosts in Europe, both lymantriids: *L. dispar* (Fuester *et al.*, 1983; Maier, 1990; Mills and Nealis, 1992; Kenis and López-Vaamonde, 1998) and *Orgyia recens* (Hübner) (Mihalyi, 1986). However, this parasitoid has not been reported from other destructive European lymantriids that have been studied extensively: nun moth, *Lymantria monacha* Linnaeus (Komarek, 1937; Fahringer, 1941; Thompson, 1944-1950; Thompson and Simmonds, 1964-1965; Herting, 1976; Mills and Schoenberg, 1985); browntail moth (Burgess and Crossman, 1929; Sisojeviæ *et al.*, 1976); satin moth (Pawlowicz, 1936; Pisica *et al.*, 1978; Drea and Fuester, 1979); rusty tussock moth, *Orgyia antiqua* (L.) (Wellenstein and Fabritius, 1973; Drea and Fuester, 1979; Mills and Schoenberg, 1985); and pale tussock moth, *Elkneria pudibunda* (L.) (Herting, 1960; Wellenstein, 1978).

THE RECEIVING LOCATION

DESCRIPTION OF FAUNA IN AREA OF PROPOSED AGENT INTRODUCTION

Area of proposed release Prior to the completion of our studies (Fuester *et al.*, 2001), *A. samarensis* already had been released in Canada (Mills and Nealis, 1992; Nealis *et al.*, 2002), but permanent establishment of the parasitoid there had not been documented (nor has it been to date). We wished to make releases of this species against gypsy moth in the northeastern United States, but the possibility that *C. concinnata* may have contributed to the reported decline of several saturniid moths in New England (Boettner *et al.*, 2000) and recent recoveries of *P. disparis*, a parasitoid of gypsy moth from the Far East introduced during the 1970s, from non-target species (Schaefer *et al.*, 1989) prompted us to look at the host range of *A. samarensis* more closely before taking action.

Species closely related to target pest There are only seven genera of Lymantriidae in North America, all of which fall in the subfamily Lymantriinae (Ferguson, 1978). Three of the genera (*Lymantria*, *Leucoma*, and *Euproctis*) fall in the tribe Lymantriini but are monotypic, represented solely by introduced species from Europe (gypsy, brown-tail, and satin moths), all of which can be considered legitimate target pests. The remaining genera fall in the tribe Orgyiini. Two of these are alpine or boreal: *Acsala*, known only from Alaska and the Yukon, and *Gynaephora*, widely distributed in the Arctic but occurring only above the tree line in the Rocky Mountains and northern Appalachians (New Hampshire, Maine, and Quebec). The likelihood of a temperate, sylvan species such as *A. samarensis* attacking species in these genera seems very remote indeed. This leaves two genera of interest – *Dasychira* (16 spp.) and *Orgyia* (10 spp.). At least 11 spp. of *Dasychira* occur in the northeastern United States – *tephra* Hübner, *dorsipennata* (Barnes and McDunnough), *vagans* (Barnes and McDunnough), *basiflava* (Packard), *meridionalis* (Barnes and McDunnough), *cinnamomea* (Grote and Robinson), *leucophaea* (J. E. Smith), *obliquata* (Grote and Robinson), *plagiata* (Walker), *pinicola* (Dyar), and *manteo* (Strecker). About half are minor forest and shade tree pests (Baker, 1972): *basiflava* (dark tussock moth) on a variety of hardwoods; *cinnamomea* on elm; *vagans*, *meridionalis*, and *tephra* on oaks; and *pinicola* and *plagiata* (pine tussock moth) on conifers. None are consid-

ered rare, and all are broadly distributed (Ferguson, 1978). Most of the North American *Orgyia* are western species, and only four occur in the northeastern United States – *antiqua* (L.) (rusty tussock moth), *detrita* Guérin-Méneville, *definita* Packard (definite-marked tussock moth), and *leucostigma* (J. E. Smith) (white-marked tussock moth). All of these except *O. detrita* are considered to be pests of forest and shade trees (Baker, 1972; Drooz, 1985; Johnson and Lyon, 1988; Wallner, 1989). Though not considered a pest and rare in collections, *O. detrita* is widely distributed (Ferguson, 1978), and at least one outbreak has been reported from coastal North Carolina (Drooz *et al.*, 1986).

Species of value as biological control agents Lepidoptera attacking aquatic weeds were not considered to be at risk of attack by *A. samarensis*. A number of Lepidoptera attack common reed, *Phragmites australis* Cavanilles, but all bore within shoots, roots, or rhizomes (Blossey *et al.*, 2002), and it is unlikely that they would be exposed to attack by *A. samarensis*. Two key natural enemies of spotted knapweed (*Centaurea maculosa* L.), the gelechiid *Metzneria paucipunctella* (Zeller) and the cochyliid *Agapeta zoegana* L., feed in flower heads and roots (Story, 2002), respectively, and are probably thus protected from attack by *A. samarensis*. The sphingid *Hyles euphorbiae* L., a defoliator of leafy spurge (*Euphorbia esula* L.) (Nowierski and Pemberton, 2002) and cypress spurge (*Euphorbia cyparissias* L.) (Faubert and Casagrande, 2002), occurs in New York state and is not sequestered within the plant, so it might be subject to attack by *A. samarensis*.

Species of marked conservation value Two endangered butterflies, the Karner blue (*Lycaeides melissa samuelis* Nabokov) and Mitchell's satyr (*Neonympha mitchelli mitchelli* French), occur in the northeastern United States. The first species inhabits meadows and prairies, and the second species, sphagnum bogs. Whereas the known hosts of *A. samarensis* are forest insects, it is expected that this fly will be limited to forest habitats. Because neither of the endangered butterflies occurs in forests, it is anticipated that they will be ecologically separated from *A. samarensis*. While no Saturniidae appear on the United States Fish and Wildlife Threatened and Endangered species list, Boettner *et al.* (2000) have provided evidence that *C. concinnata* can destroy large numbers of several species in the field, and a number of saturniids appear on state lists. For example, buck moth, *Hemileuca maia* (Drury); imperial moth, *Eacles imperialis pini* Mitchener; and Columbia silk moth, *Hyalophora columbia* (S. I. Smith) are listed among the endangered, threatened, and special concern Lepidoptera of Michigan. The monarch butterfly, *Danaus plexippus* L., while rather common in the eastern United States, has precarious overwintering sites in Mexico and has been the subject of recent studies concerning possible hazards presented by genetically modified corn pollen (containing toxins derived from *Bacillus thuringiensis* Berliner) landing on its food plant, milkweed. Therefore, it surely can be considered an icon species.

THE TESTING PLAN: ANALYSIS OF METHODS

SEARCH FOR OTHER HOSTS IN EUROPE

Our study differed from most other host range studies in that it was not confined to challenging the candidate parasitoid with non-target species in the laboratory; but, in addition, an effort was made to field collect other hosts that might be parasitized by *A. samarensis* in its region of

origin. We felt that this would be useful because of the possibility that *A. samarensis* could have been overlooked by previous investigators. Therefore, we made extensive collections of gypsy moth and other Lepidoptera at localities in Europe where *A. samarensis* was abundant (see Fuester *et al.* [2001] for a detailed account of the methodologies employed and results obtained).

TEST LIST FOR HOST RANGE TESTING

The test list of U.S. Lepidoptera selected for host range testing of *A. samarensis* in quarantine appears in Table 1. It was compiled by one of us (RWF) with input from Dale Schweitzer (The Nature Conservancy). The table includes the reasons why the various species were selected. In brief, the lymantriids were selected because they are closely related to the gypsy moth. The Noctuoidea exclusive of Lymantriidae (Noctuidae, Notodontidae, and Arctiidae) were considered somewhat related to gypsy moth. The rest were forest species that belonged to a sensitive group (Saturniidae) or were considered icon species (monarch butterfly). Unfortunately, only about half of the desired species were actually tested, generally because no mated females of *A. samarensis* were available when we had the caterpillars in hand. This was the case for *Amphipyra pyramidoides* Guenee, *Chaetoglaea sericea* (Morrison), *Sericaglaea signata* (French), *Malacosoma disstria* (Hübner), *Datana ministra* (Drury), *Biston betularia cognataria* (L.), and *Hemileuca maia* Drury. For four other species, we were unable to obtain material to rear – *Ceratonia hageni* Grote, *Pachysphinx modesta* Harris, *Prochoerodes transversata* (Drury), and *Closteria inclusa* (Hübner).

In addition, laboratory tests on host suitability of European Lepidoptera were carried out by inoculating caterpillars with young neonate maggots of *A. samarensis*. No special list of hosts was developed in advance, but inoculations were made on an *ad hoc* basis as host larvae became available.

DESCRIPTION AND RATIONALE OF TESTS RUN

Choice tests We relied mostly on choice tests for our laboratory studies with North American Lepidoptera. We used a choice test format because not all mated females of *A. samarensis* laid eggs when exposed to larvae even though all flies had been held long enough to become gravid. We feared that false negatives could occur if female flies that were not gravid (or were not behaviorally ready to lay eggs) were the ones chosen to be exposed to a non-target species. Quednau and Lamontagne (1998), found that the gestation period of mated females of *C. samarensis* ranges from 7-8 days at 22°C to 17 days at 10-15 °C (12:12 L:D) and, because of variation in the time of day when mating occurs and the metabolism of individual females, not all females in a cohort begin oviposition on the same day. We conducted these tests in a rearing room of the quarantine facility at the United States Department of Agriculture, Agricultural Research Service's Beneficial Insect Introduction Research Unit at Newark, Delaware, at 25°C, 50-60% RH, and a photoperiod of 14:10 (L:D). Screened cages (46 x 33 x 40 cm) with sliding plexiglas doors were used as test arenas. Flies were provided with sponges soaked in distilled water for moisture, and sugar cubes and jelly (Quednau and Lamontagne, 1998) for food. During tests, we exposed 15 gypsy moth larvae (second or early third instars) on a bouquet of red oak and 15 larvae of a nontarget species of similar size on a bouquet of a preferred host plant to two females of *A. samarensis*. Tests lasted 48 h and cages were gently

Table 1. U.S. species proposed for host range tests with *Aphantorhaphopsis samarensis*

Family/Scientific Name	Common Name	Reason Chosen
Danaidae		
* <i>Danaus plexippus</i> L.	Monarch Butterfly	Icon species
Sphingidae		
<i>Ceratomia hageni</i> Grote	Hagen's Sphinx	Forest species
<i>Pachysphinx modesta</i> Harris	Modest Sphinx	Forest species
Saturniidae		
* <i>Eacles imperialis</i> (Drury)	Imperial Moth	Sensitive group
* <i>Actias luna</i> (L.)	Luna Moth	Sensitive group
* <i>Automeris io</i> (Fabricius)	Io Moth	Sensitive group
* <i>Citheronia regalis</i> (Fabricius)	Regal Moth	Sensitive group
<i>Hemileuca maja</i> (Drury)	Buck Moth	Sensitive group
Noctuidae		
<i>Amphipyra pyramidoides</i> Guenee	Copper Underwing	Somewhat related
<i>Chaetagnaea sericea</i> Morrison	Silky Sallow	Somewhat related
* <i>Heliothis virescens</i> (Fabricius)	Tobacco Budworm	Readily available
<i>Sericagnaea signata</i> (French)	Variable Sallow	Somewhat related
* <i>Spodoptera exigua</i> (Hübner)	Beet Armyworm	Readily available
* <i>Trichoplusia ni</i> (Hübner)	Cabbage Looper	Readily available
Lymantriidae		
* <i>Orgyia leucostigma</i> (J. E. Smith)	White-marked Tussock	Closely related
* <i>Dasychira vagans</i> (Barnes and McDonnough)	Variable Tussock	Closely related
<i>Dasychira basiflava</i> (Packard)	Yellow-Based Tussock	Closely related
Lasiocampidae		
<i>Malacosoma disstria</i> (Hübner)	Forest Tent Caterpillar	Forest species
Geometridae		
<i>Biston betularia cognataria</i> (L.)	Pepper & Salt Moth	Forest species
<i>Prochoerodes transversata</i> (Drury)	Large Maple Spanworm	Forest species
Notodontidae		
<i>Datana ministra</i> (Drury)	Yellow-necked Caterpillar	Somewhat related
<i>Clostera inclusa</i> (Hübner)	Angle-lined Prominent	Somewhat related
Arctiidae		
* <i>Pyrharctia isabella</i> (J. E. Smith)	Isabella Tiger Moth	Somewhat related
* <i>Spilosoma virginica</i> (Fabricius)	Yellow Woolly Bear Moth	Somewhat related
* <i>Hyphantria cunea</i> (Drury)	Fall Webworm	Somewhat related
* <i>Grammia virgo</i> (L.)	Virgin Tiger Moth	Somewhat related
* <i>Estigmene acrea</i> (Drury)	Salt Marsh Caterpillar	Somewhat related

*Species actually tested

atomized with distilled water at least twice a day. When test periods were completed, larvae were reared to determine if parasitism had occurred. Caterpillars were reared in ventilated plastic cages (12 [h] x 12 [dia] cm) with false bottoms similar to those described by Loan and Holdaway (1961) so that any maggots of *C. samarensis* that emerged would drop to the bottom

and not be injured by any unparasitized caterpillars. After test exposures, larvae of gypsy moth were fed with an artificial diet while non-target species larvae were fed small bouquets of their usual host plant (or artificial diet if the species came from a laboratory culture). Hosts were reared to the pupal stage or until death occurred and categorized as parasitized, unparasitized (healthy), diseased, desiccated, or dying of unknown causes. Hosts dying before reaching the pupal stage were dissected to see if parasitization had occurred.

No-choice tests A limited number of no-choice tests were run by Philip Kingsley in the quarantine facility at the United States Department of Agriculture, Animal and Plant Health Inspection Service's Methods Development Center at Otis Air National Guard Base in Massachusetts. In each case, only five test larvae per species per trial were offered to females of *A. samarensis*. The oviposition cages (arenas) were similar to those described by Quednau (1993).

Host Suitability Tests Tests on host suitability were performed on several European species of macrolepidoptera by artificially inoculating larvae of *L. dispar* and non-target species with mature eggs of *C. samarensis* that had been dissected from uteri of gravid females three weeks or more in age and then placed on potential hosts with a watercolor brush. Females of butterflies and moths were netted or caught by light trapping and caged to obtain eggs. Many females were caught and some of them laid eggs, but most of the eggs did not hatch. Thus, very few caterpillars were available for testing. Inoculations were performed by restraining a host larva with pins, removing the hairs from the 9th and 10th body segments, and placing a freshly eclosed maggot on the host integument with a moistened brush. Maggots were kept damp with Ringer's solution while they searched for an entry site. Once a site was chosen, entry through the integument took 30 seconds. All larvae were reared on a natural host plant until *A. samarensis* emerged or pupation occurred. One month after oviposition, live larvae that had not pupated were dissected.

TEST RESULTS AND INTERPRETATIONS

RESULTS OF FIELD COLLECTIONS IN EUROPE

In addition to some 20,360 larvae of *L. dispar*, over 850 larvae in at least 54 other species in 11 families were collected and reared over a five-year period from field sites in Europe. Out of 103 larvae in five species of other Lymantriidae, only two, one of *L. monacha* and one of *O. antiqua*, yielded puparia that could not be distinguished from those of *A. samarensis*, but no adults emerged, so new host records could not be claimed with certainty. No *A. samarensis* was obtained from any of the remaining centrifugal groupings, which included the Noctuoidea other than Lymantriidae (492 specimens in 22 species), Heterocera other than Noctuoidea (135 specimens in 26 species), or Rhopalocera (121 specimens in seven species). Even if one assumes that the puparia recovered from *L. monacha* and *O. antiqua* were *A. samarensis*, overall parasitization rates across all years and sites for gypsy moth, other lymantriids, and Lepidoptera other than lymantriids would be 8, 2, and 0%, respectively. Thus, gypsy moth was obviously the chief, if not the only, host utilized by *A. samarensis* at our field sites. We feel that this is an important finding because the results reflected what was actually going on in the field in habitats favorable to *A. samarensis*.

RESULTS OF LABORATORY TESTING IN NORTH AMERICA

Assessment of overall testing success A summary of the trials (=replicates) pairing *L. dispar* with North American species of Lepidoptera appears in Table 2. Choice and no-choice tests were conducted with 14 and two native species, respectively.

In the choice tests, 1-5 trials were run for each species, depending upon the numbers of caterpillars and parasitoids available. Unfortunately, females of *A. samarensis* failed to attack any hosts (including the *L. dispar* control) whatsoever in nearly 40% of all trials, rendering the results inconclusive. We did not anticipate this high rate of failure of *A. samarensis* to attack *L.*

Table 2. Numbers of successful and unsuccessful laboratory trials attempted for native species of North American Lepidoptera exposed with *L. dispar* to two females of *A. samarensis*, 1997-1998.

Native species tested	No. of trials attempted	No. of trials unsuccessful ^a	No. of trials successful ^b
Choice tests			
<i>D. plexippus</i>	2	1	1
<i>A. luna</i>	2	0	2
<i>E. imperialis</i>	1	1	0
<i>C. regalis</i>	1	1	0
<i>P. isabellaa</i>	1	0	1
<i>S. virginica</i>	5	3	2
<i>H. cunea</i>	5	0	5
<i>G. virgo</i>	4	0	4
<i>E. acrea</i>	2	2	0
<i>Dasychira</i> sp. prob. <i>vagans</i>	1	0	1
<i>O. leucostigma</i>	4	0	4
<i>S. exigua</i>	1	0	1
<i>H. virescens</i>	5	3	2
<i>T. ni</i>	4	4	0
Totals	38	15	23
No-choice tests			
<i>A. io</i>	3	0	3?
<i>A. luna</i>	1	0	1

^aNeither the test (native) or control (*Lymantria dispar*) species were parasitized

^bEither the test, control species, or both were parasitized

dispar because we were using two female flies instead of just one, as per Quednau and Lamontagne (1998) in their rearing protocol. In 10 of the 14 species tested, one or more trials were successful in that at least some control hosts (*L. dispar*) were attacked, and it was possible to draw inferences as to whether the non-target larvae were likely to be acceptable hosts for *A. samarensis*. In those cases where no hosts were parasitized, we concluded that either the females were not gravid or not behaviorally ready to lay eggs. The four species in which all trials were inconclusive were the saturniids *Citheronia regalis* (Fabricius) and *Eacles imperialis* (Drury), the arctiid *Estigmene acrea* (Drury), and the noctuid *Spodoptera exigua* (Hübner).

In the no-choice tests, none of the non-target species were parasitized in any of the trials, but at least some of the *L. dispar* in each trial (as evidenced by the production of puparia) had been attacked by the females of *A. samarensis*. However, even in these cases, the results cannot be considered conclusive because of the possibility that the female flies used in nontarget species cages might not have been gravid or might not have been behaviorally ready to eggs

Assessment of host range The results of those trials that we considered successful are presented in Table 3. Successful choice and no-choice tests were run with ten and two native species, respectively. In one case, *Actias luna* (L.), both choice and no-choice trials were run. In every choice test between gypsy moth and non-target species except one, *A. samarensis* attacked the gypsy moth but not the non-target species (Table 3). We concluded that all of these species were outside of the host range of *A. samarensis*. Females of *A. samarensis* attacked only one non-target species, the white-marked tussock moth, *Orgyia leucostigma* (J. E. Smith), another lymantriid. In this case, substantial numbers of hosts were attacked, yielding about two puparia per parasitized host, so we concluded that *O. leucostigma* lies within the host range of *A. samarensis*. The only other lymantriid tested, *Dasychira* sp., probably *vegans* (Barnes and McDunnough), was not parasitized.

Concerning the no-choice tests, three paired trials were run with *Automeris io* (Fabricius) and *L. dispar*. The results were similar in all trials: no larvae of *A. io* yielded puparia of *A. samarensis*, but 10 puparia were obtained from gypsy moth (Table 3). At least one female fly in each trial and arena with gypsy moth was gravid, attacking the target pest. Although it is conceivable that all females exposed to *A. io* were not gravid, it seems unlikely. Therefore, we suspect that *A. io* does not lie within the host range of *A. samarensis*. In the remaining test, one trial was run with test larvae of *A. luna* and *L. dispar*, each species in a different arena. No larvae of *A. luna* yielded puparia of *A. samarensis*, but three puparia were obtained from gypsy moth. Although it is possible that the *A. samarensis* exposed to *A. luna* were not gravid, the results are at least consistent with the results in the choice test with the same species (Table 3), so we believe that *A. luna* does not lie within the host range of *A. samarensis*.

RESULTS OF HOST SUITABILITY TESTS IN EUROPE

Successful development of fly larvae implanted in field-collected caterpillars occurred only in gypsy moth (Table 4). Dead parasitoid larvae were found in three arctiids, one nemeobid, and one noctuid. No maggots successfully penetrated *H. euphorbiae*, a sphingid, which was the only biological control agent tested.

Table 3. Results of successful tests involving exposures of *L. dispar* with selected native species of North American Lepidoptera to two gravid females of *A. samarensis*, USDA-ARS, Newark, Delaware, 1997-1999

Native species tested	Host plant of native species tested ^a	Hosts attacked (puparia recovered)		Native species within or outside host range
		Native species	<i>L. dispar</i>	
Choice tests				
<i>D. plexippus</i>	<i>Asclepias syriaca</i> L.	0	5(6)	outside
<i>A. luna</i>	<i>Juglans nigra</i> L.	0	9(10)	outside
<i>P. isabella</i> ^b	Mixed Graminaceae	0	4(14)	outside
<i>S. virginica</i>	<i>Betula populifolia</i> Marshall	0	2(2)	outside
<i>H. cunea</i>	<i>Prunus serotina</i> Ehrhart	0	40(73)	outside
<i>G. virgo</i>	<i>Lactuca sativa</i> L.	0	30(72)	outside
<i>Dasychira vagans?</i>	<i>Quercus prinus</i> L.	0	4(4)	outside
<i>O. leucostigma</i>	<i>Acer rubrum</i> L.	20(45)	5(5)	within
<i>S. exigua</i>	<i>Pyrus malus</i> L.	0	1(1)	outside
<i>H. virescens</i>	<i>Rosa multiflora</i> Thunberg	0	5(6)	outside
Totals		20(45)	105(193)	
No-choice tests^c				
<i>A. io</i>	<i>Quercus</i> sp.	0	?(12)	outside?
<i>A. luna</i>	<i>Quercus</i> sp.	0	?(3)	outside

^aAll exposures of control species, *L. dispar*, made on *Quercus rubra* Linnaeus.

^bOnly four test larvae per species instead of 15.

^cIn no-choice tests, only five test larvae per species instead of 15.

SUMMARY EVALUATION

OVERALL SYNTHESIS

The results of all four approaches used—review of the literature, field collections of Lepidoptera in a favorable habitat for the candidate natural enemy within its native range, laboratory host range tests on North American species, and artificial inoculations to assess host suitability—led us to the conclusion that the host range of *A. samarensis* is restricted to the family Lymantriidae,

Table 4. Lepidopterous larvae inoculated with young *A. samarensis* maggots and results of rearings or dissections.

Species and Family	No. larvae inoculated	No. of <i>A. samarensis</i> reared	No. of dead maggots found by dissection
<i>Agriades glandon</i> (Prun.) - Lycaenidae	3	0	0
<i>Hamearis lucina</i> (L.) - Nemeobidae	2	0	0
<i>Macrothyacia rubi</i> (L.) - Lasiocampidae	1	0	0
<i>Hyles euphorbiae</i> (L.) - Sphingidae	2	0	0
<i>Peridea anceps</i> (L.) - Notodontidae	1	0	0
<i>Callimorpha dominula</i> (L.) - Arctiidae	17	0	3
<i>Eilema deplane</i> (Esper) - Arctiidae	4	0	4
<i>Lithosia quadra</i> (L.) - Arctiidae	3	0	1
<i>Lymantria dispar</i> (L.) - Lymantriidae	38	20	— ^a
<i>Mamestra brassicae</i> (L.) - Noctuidae	2	0	7

^aNon-parasitized *Lymantria dispar* were not dissected.

probably only to the genera *Lymantria* and *Orgyia*. Because the only *Lymantria* species in North America is the pest *L. dispar*, and all four species of *Orgyia* in the eastern United States are native pests (Baker, 1972; Drooz, 1985; Drooz *et al.*, 1986; Johnson and Lyon, 1988; Wallner, 1989), the host range of *A. samarensis* seemed specific enough to justify release, and an Environmental Assessment was submitted by USDA-APHIS to the State of Pennsylvania. This resulted in a finding of no significant impact, and releases of *A. samarensis* were made by personnel from the Pennsylvania Department of Environmental Resources, Bureau of Forestry. The technical results of our studies were published in a peer-reviewed journal (Fuester *et al.*, 2001).

COMPLETENESS OF ASSESSMENT

It would have been desirable to do more tests on North American Lepidoptera, especially in the genus *Dasychira* and possibly of other Noctuoidea. We only did a few no-choice tests with *A. samarensis*, but to have relied on such tests exclusively could have given rise to false negative tests because of the parasitoid's refractory behavior. Sequential choice tests, with flies presented first to nontarget species and then shortly thereafter to the target pest could have been used to provide an appropriate control, but were not. Because we used long exposure times (48 hours), we thought our choice tests would provide the parasitoids ample opportunity to attack the non-target species offered. In the case of *O. leucostigma*, the only other acceptable North American host besides gypsy moth, we saw a female of *A. samarensis* attempt oviposition within a minute of introduction to the test arena. Extended direct observation of fly behavior in choice tests might have shown whether attention paid to the higher ranked host was preempting discovery and assessment of the nontarget host.

As of December 2003, *A. samarensis* has not been recovered from gypsy moth at release sites in Canada or the United States, so field studies have not been run to detect its presence in non-target species. If *A. samarensis* is recovered, such studies will be implemented.

RECOMMENDATIONS FOR FUTURE WORKERS

Because entomophagous insects can behave abnormally in the laboratory, attacking hosts that are not normally attacked in nature (Simmonds, 1944), we agree with Greathead (1995) that field studies in the country of origin to determine an agent's natural host range are useful in assessing the risk that a candidate species for introduction might present to non-target organisms in the new environment. One of the problems in such an approach, of course, is the reality of community structure. Figure 1 shows the frequency distribution of the caterpillars of macrolepidoptera we recovered at our study sites in Europe. There are a large number of species (in fact, most) that are represented by only a few specimens – too few to allow for quantitative estimates of incidence of parasitism. Nevertheless, we feel that the information acquired was useful for three reasons. First, it was realistic: all hosts were collected in the field, where they had been naturally exposed to foraging females of the parasitoid. Second, all of the hosts collected were indigenous, suggesting that the host range of *A. samarensis* was stable and had not expanded to include invasive species. Third, it demonstrated that *A. samarensis* was not widely polyphagous: otherwise, we should have made numerous recoveries scattered over the various taxa collected. Our approach might be rendered more useful by making exposures of other hosts to augment sample sizes for host species of special interest, especially those related to the target pest or favoring the same host plants. In any case, we feel that this ap-

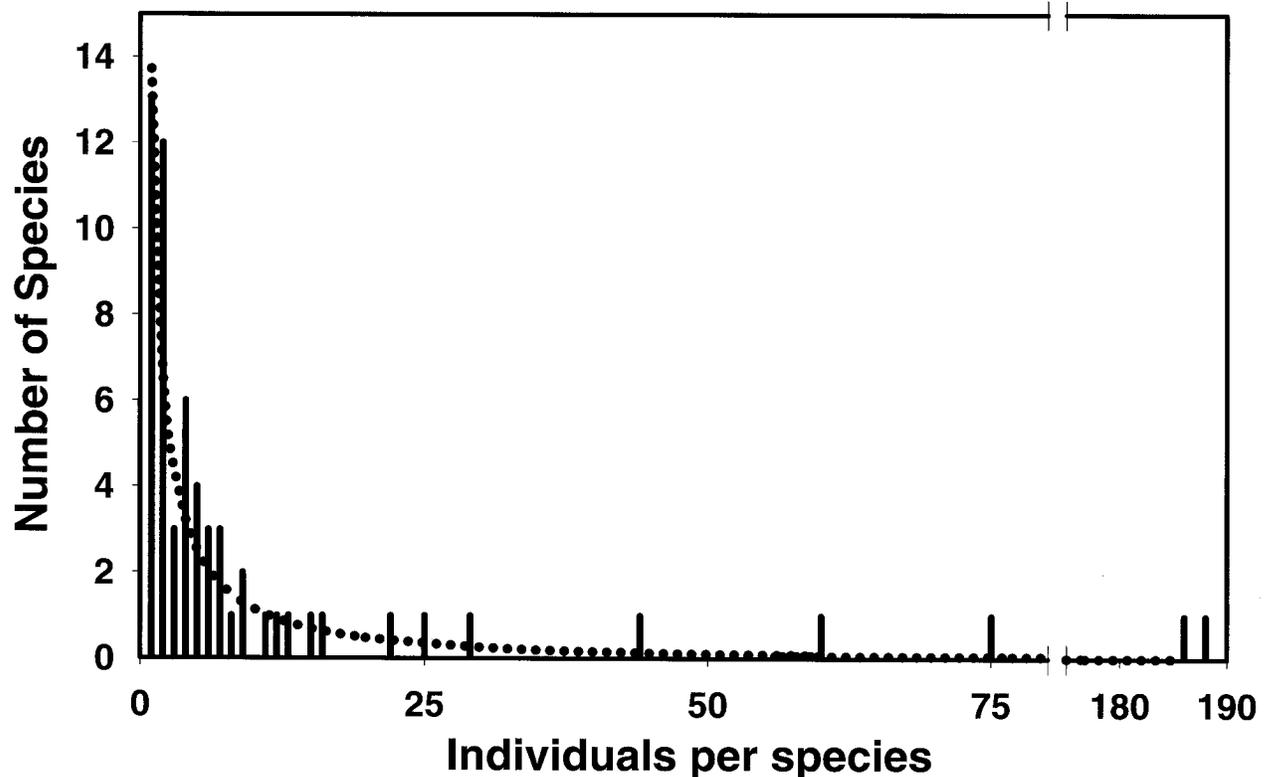


Figure 1. Frequency distribution of species of Macrolepidoptera, with different numbers of individuals, recovered at *A. samarensis* study sites in France and Switzerland, 1993-1999.

proach merits greater emphasis and that agencies involved in foreign exploration for natural enemies could commit more resources to it.

Another problem was the difficulty of obtaining and rearing potential non-target hosts for the laboratory screening tests. Most of the species selected for testing were not of economic interest, so laboratory colonies did not exist. We were successful in capturing and rearing some, but not all, of the species we sought. In addition, many forest Lepidoptera only have one generation a year, and we frequently had caterpillars available when the parasitoids were not or vice versa. A more flexible approach to developing a list of non-target species for testing might be to designate genera instead of species, at least in those cases where there is no specific concern for a particular species. The enlistment of amateur entomologists to aid in the search for test species might also prove useful.

Many of the females of *A. samarensis*, even though incubated long enough after mating to be gravid, didn't lay eggs. Consequently, many of our test caterpillars were wasted, which was a significant problem with the non-target species, which were usually in short supply. The failure of flies to lay eggs might have been mitigated by using more flies per trial, increasing the likelihood that at least one would attack the control host.

Another way to solve this problem might have been to use sequential no-choice tests instead of choice tests. This involves alternately offering a female of parasitoid, first, a given nontarget test species, then the target pest, then the same nontarget test species again. Dissection of the first series of target pest caterpillars would provide data to determine whether a particular parasitoid was able to oviposit in a known host (the pest). This approach has the advantage (over regular choice tests) that the target pest (presumably a preferred species) is not present with the nontarget test species and thus cannot divert the parasitoid from attacking it, should it prove to be a less desirable but acceptable host. Making the first exposures to the nontarget species (rather than the target pest) avoids conditioning the parasitoid to a preferred host. Similarly, this design has an advantage over no choice tests, because the ability of each individual parasitoid to oviposit is determined during the test.

We probably could have made greater use of the artificial inoculation approach in assessing the risk to non-target species, but it would have involved much more rearing of the latter. It might have been used profitably to get more information on the suitability of Saturniidae, a group of special conservation interest; several species are available commercially because they are showy and popular with collectors. This approach is not practical for most endoparasitoids because inoculation requires the use of hypodermic needles or some other procedure that would be traumatic to the host. With this particular system, it seemed to work well because the neonate parasite larva could enter the host on its own.

Our biggest problem in this research was the difficulty in rearing and handling the parasitoid. The rearing, performed by the late Dr. Kingsley, is very labor intensive. However, difficulty in rearing or otherwise handling a natural enemy, while important in mass rearing, should not be a prime consideration in classical biological control.

REFERENCES

- Andreadis, T. G. and R. M. Weseloh. 1990. Discovery of *Entomophaga maimaiga* in North American gypsy moth. *Proceedings of the National Academy of Sciences of the United States of America*. 87: 2461-2465.
- Baker, W. L. 1972. *Eastern Forest Insects*. Miscellaneous Publication No. 1175. United States Department of Agriculture, Washington, D.C.
- Blossey, B., M. Schwarzländer, P. Häfliger, R. Casagrande, and L. Tewksbury. 2002. Common Reed, pp. 131-138. In Van Driesche, R. G., S. Lyon, B. Blossey, M. Hoddle, and R. Reardon (eds.). *Biological Control of Invasive Plants in the Eastern United States*. Publication FHTET-2002-04. USDA Forest Service, Morgantown, West Virginia, USA.
- Blumenthal, E. M. and R. G. Wilt. 1998. Gypsy moth parasites vs. *Entomophaga maimaiga* in Pennsylvania, pp. 6-10. In Fosbroke, S. L. and K. W. Gottschalk (eds.). *Proceedings, USDA Interagency Gypsy Moth Research Forum, 1998; January 20-23, 1998, Annapolis, Maryland*. General Technical Report NE-248. U.S. Department of Agriculture, Forest Service, Northeast Forest Experiment Station, Radnor, Pennsylvania, USA.
- Boettner, G. H., J. S. Elkinton, and C. J. Boettner. 2000. Effects of a biological control introduction on three non-target species of saturniid moths. *Conservation Biology* 14: 1798-1806.
- Burgess, A. F., and S. S. Crossman. 1929. Imported insect enemies of the gypsy moth and the brown-tail moth. Technical Bulletin No. 86. U.S. Department of Agriculture, Washington, D.C.
- Clausen, C. P. (ed.). 1978. *Introduced Parasites and Predators of Arthropod Pests and Weeds: a World Review*. Handbook No. 480. U.S. Department of Agriculture, Washington, D.C.
- Delfosse, E. S., J. S. Elkinton, R. W. Fuester, W. C. Kauffman, and T. M. Odell. 1994. New directions in biological control of gypsy moth, pp. 1-6. In *Proceedings of the 1994 Annual Gypsy Moth Review*. Oregon Department of Agriculture, Salem, Oregon, USA.
- Drea, J. J. and R. W. Fuester. 1979. Larval and pupal parasites of *Lymantria dispar* and notes on parasites of other Lymantriidae (Lep.) in Poland. *Entomophaga* 24: 319-327.
- Drooz, A. T. 1985. *Insects of Eastern Forests*. USDA Forest Service. Miscellaneous Publication No. 1426.
- Drooz, A. T., T. F. Smith, and C. A. Doggett. 1986. Outbreak of a rare lymantriid, *Orgyia detrita*, in coastal North Carolina. Forest Research Note SE-340. USDA, Southeastern Forest Experiment Station, Asheville, North Carolina, USA.
- Fahringer, J. 1941. Zur Kenntnis der Parasiten der Nonne (*Lymantria monacha* L.). *Zeitschrift für Angewandte Entomologie* 28: 359-365.
- Faubert, H. and R. A. Casagrande. 2002. Cypress spurge, pp. 195-207. In Van Driesche, R. G., S. Lyon, B. Blossey, M. Hoddle, and R. Reardon (eds.). *Biological Control of Invasive Plants in the Eastern United States*. Publication FHTET-2002-04. USDA Forest Service Morgantown, West Virginia, USA.
- Ferguson, D. C. 1978. *The Moths of America North of Mexico, Fasc. 22.2 Noctuoidea, Lymantriidae*. E. W. Classey, Ltd. and The Wedge Entomological Research Foundation, London.
- Forbush, E. H. and C. H. Fernald. 1896. *The Gypsy Moth*. Wright and Potter, Boston, Massachusetts, USA.
- Fuester, R. W., J. J. Drea, F. Gruber, H. Hoyer, and G. Mercadier. 1983. Larval parasites and other natural enemies of *Lymantria dispar* (Lepidoptera: Lymantriidae) in Burgenland, Austria, and Würzburg, Germany. *Environmental Entomology* 12: 724-737.

- Fuester, R. W., M. Kenis, K. S. Swan, P. C. Kingsley, C. Lopez-Vaamonde, and F. Herard. 2001. Host range of *Aphantorhaphopsis samarensis* (Diptera: Tachinidae), a larval parasite of the gypsy moth (Lepidoptera: Lymantriidae). *Environmental Entomology* 30: 605-611.
- Glaser, R. W. and J. W. Chapman. 1913. The wilt disease of gypsy moth caterpillars. *Journal of Economic Entomology* 6: 479-488.
- Greathead, D. J. 1995. Benefits and risks of classical biological control, pp. 53-63. In Hokkanen, H.M.T. and J. M. Lynch (eds.). *Biological Control: Benefits and Risks*. Cambridge University Press, Cambridge, United Kingdom.
- Hajek, A. E., R. A. Humber, and J. S. Elkinton. 1995. Mysterious origin of *Entomophaga maimaiga* in North America. *American Entomologist* 41: 31-42.
- Hajek, A. E., L. Butler, J. K. Lieberr, and M. M. Wheeler. 2000. Risk of infection by the fungal pathogen *Entomophaga maimaiga* among Lepidoptera on the forest floor. *Environmental Entomology* 29: 645-650.
- Herting, B. 1960. Biologie der westpalaarktischen Raupenfliegen, Dipt. Tachinidae. *Monografieren Angewandte Entomologie* 16: 1-188.
- Herting, B. 1976. *A Catalogue of Parasites and Predators of Terrestrial Arthropods. Section A Vol. 7, Lepidoptera, Part 2: Macrolepidoptera*. Commonwealth Agricultural Bureaux. Farnham Royal, United Kingdom.
- Herting, B. 1984. *Catalogue to Palearctic Tachinidae (Diptera)*. Series A 369. Beiträge Naturkunde, Stuttgart, Germany.
- Howard, L. O. 1930. A history of applied entomology. Smithsonian Miscellaneous Collections No. 84, Washington, D.C.
- Howard, L. O. and W. F. Fiske. 1911. The importation into the United States of the parasites of the gypsy moth and browntail moth. Bureau of Entomology Bulletin No. 91. U.S. Department of Agriculture, Washington, D.C.
- Hoy, M. A. 1976. Establishment of gypsy moth parasitoids in North America: an evaluation of possible reasons for establishment or non-establishment, pp. 215-232. In Anderson, J. F. and H. H. Kaya (eds.). *Perspectives in Forest Entomology*. Academic Press, New York.
- Johnson, W. T. and H. H. Lyon. 1988. *Insects that Feed on Trees and Shrubs*. Cornell University Press, Ithaca, New York, USA.
- Kenis, M. and C. Lopez-Vaamonde. 1998. Classical biological control of the gypsy moth, *Lymantria dispar* (L.), in North America: Prospects and new strategies, pp. 213-221. In McManus, M. L. and A. M. Liebhold (eds.). *Proceedings: Population Dynamics, Impact and Integrated Management of Forest Defoliating Insects*. General Technical Report NE-247. USDA Forest Service, Radnor, Pennsylvania, USA.
- Komarek, J. 1937. Kritische Worte über die Bedeutung der Insektparasiten der Nonne. *Zeitschrift für Angewandte Entomologie* 24: 95-117.
- Leggett, W. E. 1949. *The Story of Silk*. Lifetime Editions, New York.
- Liebhold, A., V. Mastro, and P. Schaefer. 1989. Learning from the legacy of Léopold Trouvelot. *Bulletin of the Entomological Society of America* 35 (2): 20-22.
- Loan, C. C. and D. C. Holdaway. 1961. *Microctonus aethiops* (Nees) auctt. and *Perilitus rutilus* (Nees) (Hymenoptera: Braconidae), European parasites of the *Sitona* weevil (Coleoptera: Curculionidae). *The Canadian Entomologist* 93: 1057-1079.
- Maier, K. 1990. Contribution to the biology of primary and secondary parasitoids of *Lymantria dispar* L. (Lepidoptera, Lymantriidae). *Journal of Applied Entomology* 110: 167-182.

- McCullough, D. G., N. W. Siegert, A. E. Hajek, M. Wheeler, R. C. Venette, and W. C. Kauffman. 2001. Factors affecting the success of the gypsy moth biological control *Entomophaga maimaiga* in Michigan, pp. 91-92. In Fosbroke, S. and K. Gottschalk (eds.). *Proceedings of the U.S. Department of Agriculture Interagency Research Forum on Gypsy Moth and other Invasive Species 2001*. General Technical Report NE-285. USDA Forest Service, Northeast Forest Experiment Station, Newtown Square, Pennsylvania, USA.
- McManus, M. L. and T. McIntyre. 1981. Introduction, pp. 1-7. In Doane, C. C. and M. L. McManus (eds.). *The Gypsy Moth: Research toward Integrated Pest Management*. Agriculture Technical Bulletin No. 1584. U.S. Department of Agriculture, Washington, D.C.
- Mihalyi, F. 1986. *Diptera II. Furkzlegyek - Aszkalegyek Tachinidae - Rhinophoridae. Fauna Hungariae 161*, Vol. XV, Pt. 14-15, 425 pp.
- Mills, N. J. and V. G. Nealis. 1992. European field collections and Canadian releases of *Ceranthia samarensis* (Dipt.: Tachinidae), a parasitoid of the gypsy moth, *Lymantria dispar* (L.). *Entomophaga* 37: 181-191.
- Mills, N. J. and F. Schoenberg. 1985. Possibilities for the biological control of the Douglas-fir tussock moth, *Orgyia pseudotsugata* (Lymantriidae), in Canada using natural enemies from Europe. *Biocontrol News and Information* 6: 7-18.
- Nealis, V. G. and F. W. Quednau. 1996. Canadian field releases and overwinter survival of *Ceranthia samarensis* (Villeneuve) (Diptera: Tachinidae) for biological control of the gypsy moth, *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae). *Proceedings of the Entomological Society of Ontario* 127: 11-20.
- Nealis, V. G., N. Carter, M. Kenis, F. W. Quednau, and K. van Frankenhuyzen. 2002. *Lymantria dispar* (L.), Gypsy moth (Lepidoptera: Lymantriidae), pp. 159-169. In Mason, P. and J. Huber (eds.). *Biological Control Programs against Insects and Mites, Weeds, and Pathogens in Canada 1981-2000*. CABI, Wallingford, United Kingdom.
- Nowierski, R. M., and R. W. Pemberton. 2002. Leafy spurge, pp. 181-194. In Van Driesche, R. G., S. Lyon, B. Blossey, M. Hoddle, and R. Reardon (eds.). *Biological Control of Invasive Plants in the Eastern United States*. Publication FHTET-2002-04. USDA Forest Service Morgantown, West Virginia, USA.
- Pawlowicz, J. 1936. Beobachtungen über einige in *Porthetria dispar* L., *Malacosoma neustria* L. und *Stilpnotia salicis* L. (Lep.) Schmarotzende Hymenopteren und Dipteren. *Zoologica Polonia* 1: 98-118.
- Pisica, C., M. Lacatusu, C. Tudor, I. Teodorescu, and I. Nastase. 1978. [The natural enemies of the defoliator *Stilpnotia salicis* L. (Lepidoptera: Lymantriidae) in Europe and Romania]. *Travaux du Musee d'Histoire Naturelle "Grigore Antipa"* 19: 297-301.
- Quednau, F. W. 1993. Reproductive biology and laboratory rearing of *Ceranthia samarensis* (Villeneuve) (Diptera: Tachinidae), a parasitoid of the gypsy moth, *Lymantria dispar* (L.). *The Canadian Entomologist* 125: 749-759.
- Quednau, F. W. and K. Lamontagne. 1998. Principles of mass culture of the gypsy moth parasitoid *Ceranthia samarensis* (Villeneuve). Information Report LAU-X-121. Natural Resources Canada, Canadian Forest Service, Laurentian Forestry Centre, Sainte-Foy, Quebec, Canada.
- Reardon, R. C. 1981. Parasites, pp. 299-442. In Doane, C. C. and M. L. McManus (eds.). *The Gypsy Moth: Research toward Integrated Pest Management*. Technical Bulletin No. 1584. U.S. Department of Agriculture, Washington, D. C.
- Sabrosky, C. W. and R. C. Reardon. 1976. Tachinid parasites of the gypsy moth, *Lymantria dispar*, with keys to adults and puparia. *Miscellaneous Publications of the Entomological Society of America* 10 (2): 1-126.

- Schaefer, P. W., R. W. Fuester, R. J. Chianese, L. D. Rhoads, and R. B. Tichenor. 1989. Introduction and North American establishment of *Coccygomimus disparis* (Hymenoptera: Ichneumonidae), a polyphagous pupal parasite of Lepidoptera, including gypsy moth. *Environmental Entomology* 18: 1117-1125.
- Simmonds, F. J. 1944. The propagation of insect parasites on unnatural hosts. *Bulletin of Entomological Research* 35: 219-226.
- Sisojević, P., A. Serafimovski, M. Kusevska, and J. Cepelak. 1976. Tahine (Dipt., Tachinidae) - paraziti zutotrbe (*Euproctis chrysorrhoea* L.) u Makedoniji, 1972-1974. *Zastita Bilja* 27: 167-179.
- Story, J. 2002. Spotted knapweed, pp. 169-180. In R. Van Driesche, S. Lyon, B. Blossey, M. Hoddle, and R. Reardon (eds.). *Biological Control of Invasive Plants in the Eastern United States*. Publication FHTET-2002-04. USDA Forest Service, Morgantown, West Virginia, USA.
- Sukovata, L. 2000. The role of parasitoids in suppression of the gypsy moth (*Lymantria dispar* L.) populations in the Biebrza National park. PhD dissertation. Forest Research Institute, Warsaw (Poland): 95 pp. (in English).
- Thompson, W. R. 1944-1950. *A Catalogue of Parasites and Predators of Insect Pests*. Section 1, parts 5-10. (6 vols.). Commonwealth Institute of Biological Control. Ottawa, Ontario, Canada
- Thompson, W. R. and F. J. Simmonds. 1964-1965. *A Catalogue of the Parasites and Predators of Insect Pests*. Commonwealth Agricultural Bureaux, Burks, United Kingdom.
- Van Driesche, R. G., S. Healy, and R. C. Reardon. 1996. *Biological Control of Arthropod Pests of the Northeastern and North Central Forests in the United States: A Review and Recommendations*. FHTET-96-19, USDA, Forest Service. Morgantown, West Virginia, USA.
- Wallner, W. E. 1989. An overview of lymantriid pests in North America, pp. 65-79. In Wallner, W. E. and K. A. McManus (tech. coords.). *Proceedings, Lymantriidae: a Comparison of Features of New and Old World Tussock Moths*. June 26-July 1, 1988. New Haven, Connecticut, USA. General Technical Report NE-123. USDA Forest Service, Northeast Forest Experiment Station, Broomall, Pennsylvania, USA.
- Webb, R. E., G. B. White, K. W. Thorpe, and S. E. Talley. 1999. Quantitative analysis of a pathogen-induced premature collapse of a 'leading edge' gypsy moth (Lepidoptera: Lymantriidae) population in Virginia. *Journal of Entomological Science* 34: 84-100.
- Wellenstein, G. 1978. *Dasychira pudibunda* L., pp. 318-325. In Schwenke, W. (ed.). [*The Forest Pests of Europe*]. Parey, Hamburg, Germany.
- Wellenstein, G. and K. Fabritius. 1973. Beobachtungen am Schlehenspinner (*Orgyia antiqua*) und seinen Parasiten. *Anzeiger für Schädlingskunde, Pflanzenschutz, Umweltschutz* 46: 24-30.