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Using the literature to evaluate parasitoid host ranges: a case study of *Macrocentrus grandii* (Hymenoptera: Braconidae) introduced into North America to control *Ostrinia nubilalis* (Lepidoptera: Crambidae)

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Abstract

We propose a method for using the literature to evaluate host ranges of parasitoids that are candidates for biological control introductions. Data on the parasitoids that attack a given host species can be used as negative evidence concerning the candidate whose host range is being evaluated. By compiling studies for a variety of host species, one can delineate those taxa unlikely to be attacked by the candidate. Using a retrospective case study of a parasitoid introduced into North America, we describe (1) this approach to using the literature to evaluate host range and (2) how well predictions based on such an evaluation match actual host range. Based on the host range of *Macrocentrus grandii* in Eurasia as reported in the literature, we predicted that the species in the genus *Ostrinia* are the most likely hosts. Of native North American species, *Ostrinia obumbratalis* is the only non-target species likely to be attacked by *M. grandii*. The predicted host range for North America matched the actual host range found in the field. This suggests that a careful literature review could be used as an important source of data on host range of parasitoid species proposed for introduction into a new environment.
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1. Introduction

Historically, biological control has been considered an environmentally safe approach to pest control. However, because of potential impact on non-target species, biological control introductions have received increased scrutiny during the last 20 years, and the potential for non-target impacts has become controversial (Carruthers and Osanger, 1993; Cory and Myers, 2000; Funasaki et al., 1988; Hokkanen and Lynch, 1995; Howarth, 1983; Howarth and Ramsay, 1991; Lai, 1988; Lockwood, 1993; Louda et al., 1997; Samways, 1997; Simberloff and Stiling, 1996a,b, Strong and Pemberton, 2000; Thomas and Willis, 1998; Turner, 1985). In the last decade, several workshops were held on this subject (e.g., Wajnberg et al., 2000).

Increased trade, changes in agricultural practices, and greater efforts in environmental protection may lead to an increased demand for biological control introductions. As interest in biological control introductions grows, new practitioners are becoming involved who have little experience with the procedures for such introductions. Thus, there is a need for generally accepted

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protocols for introduction of exotic natural enemies to ensure the safety of biological control agents in their new environments (Waage, 1996). The Convention on Biodiversity and International Phytosanitary regulations require environmental risk assessments of exotic species to avoid introductions that threaten ecosystems, habitats or non-target species. For biological control agents, international, regional, and national initiatives have developed standards to ensure the safety of biological control projects. An example is the United Nations Food and Agriculture Organization (FAO) Code of Conduct for the Import and Release of Exotic Biological Control Agents, which was signed by FAO member countries in 1995 (FAO, 1996). Several countries have developed new legislation or revised existing regulations on the introduction of new organisms with a strong emphasis on minimizing environmental risks (AQIS, Australia, 1997; COSAVE, 1996; ERMA, New Zealand, 1997a,b). In come cases, these regulations have been based on the FAO code of conduct.

The primary method for assessing likelihood of non-target impacts of biological control introductions has been host range evaluation. Such evaluation can be based on data from the literature, field collections, and laboratory experiments, with each approach having different strengths and weaknesses. Host ranges reported in the literature are often flawed by misidentifications (Shaw, 1994). Furthermore, both data from the literature and the field collections upon which they are usually based suffer from an inherent asymmetry: sampling a host species over a sufficient spatial and temporal scale can reveal which herbivores or parasitoids attack that host, but not which hosts are used by a given herbivore or parasitoid species. The latter requires much more intensive sampling of the community of hosts over space and time (Memmott and Godfray, 1994). Host ranges tests in the laboratory measure behavioral and/or physiological capacity, but not ecological host range (Hopper, 2000). A complete evaluation of host range should include all three approaches.

Host range evaluation has been more formal with candidates for biocontrol of weeds than with candidates for biocontrol arthropods because of the potential for herbivore damage to crops. Protocols for experiments to measure the host ranges of herbivores have been developed and tested for many years, and such protocols are used in many countries (Andres et al., 1976; Harley and Forno, 1992; Harris, 1990; Harris and McEvoy, 1995; Wasphere, 1974). In recent years, introductions of arthropod parasitoids and predators have received increased scrutiny (McEvoy, 1996; Van Driesche and Hoddle, 1997). In Australia, New Zealand, South Africa, and the United States, formal host range evaluation has been required for introductions of insect natural enemies (Fuester et al., 2001; Goldson et al., 1992; Sands, 1998). However, protocols for experiments to test host ranges of entomophagous arthropods are not standardized. Furthermore, the cost of collecting, rearing, and testing non-target insect species makes protocols for entomophages particularly expensive. Initial evaluation of host range using data from the literature could greatly reduce the cost of experimental evaluations by focusing effort on candidates with relatively narrow host ranges and concentrating effort on non-target species most likely to be affected. Such cost savings are particularly important in less-developed countries that may lack funds for exhaustive evaluations.

Here, we propose a method for using the literature for initial host range evaluation that is more rigorous than current practice. We believe that our approach using the literature will provide a broader and more accurate preliminary evaluation of host range. Directly measuring the host range of a given parasitoid species is rather difficult, and publications on host ranges of parasitoid species are limited and often flawed. On the other hand, it is easier to determine which parasitoids attack a given host species by collecting and rearing various host stages, and the literature contains many studies of this sort. We propose here that data on the parasitoids which attack a given host species can be used as negative evidence concerning attack by the candidate whose host range one wants to evaluate. By compiling studies for a variety of host species, one can delineate those taxa unlikely to be attacked by the candidate. This will allow subsequent field and laboratory evaluations to concentrate on the most promising candidates and those non-target hosts most likely to be at risk. Using a retrospective case study of a parasitoid introduced into North America, we describe (1) this approach to using the literature to evaluate pre-introduction host range and predict post-introduction host range and (2) how well predictions based on such an evaluation match actual host range.

2. Materials and methods

2.1. Determining pre-introduction host range

For evaluation of host range of a candidate parasitoid prior to introduction, we propose using literature data on parasitism of species from regions where (1) known hosts of the candidate are endemic and (2) the candidate is known to occur, both where it is endemic and where it has been introduced. Positive evidence of attack on species in regions where the candidate has been introduced can help delimit host range, but negative evidence from such regions is not useful, because sufficient time may not have passed for population growth and spread of the candidate.

Data on parasitism should be obtained from potential hosts phylogenetically close to the target pest and from more distantly related species which resemble the target pest in behavior or ecology (e.g., feeding niche, habitat preference, and phenology). The idea is to use phylogenetic and ecological similarity to predict host range in the region of introduction. Source regions often have pest species phylogenetically and ecologically close to the target pest. Because they are pests, their parasitoids have been often been surveyed. Data from such surveys can be used to test whether non-target species were attacked by the candidate.

Because sampling effort varies among surveys, some assessment of effort is needed. We assess effort using the number and geographical range of sites, survey duration, and the number of the relevant host stage collected. From the last variable, one can calculate a crude estimate of the threshold of parasitism (p) below which the proportion of hosts parasitized must be to remain undetected. Let us assume that the probability that an host individual is parasitized follows a binomial distribution so that the probability of finding no parasitized hosts is given by $\Pr(0) = (1 - p)^n$, where p is the proportion of hosts actually parasitized and n is the number of host individuals examined. Letting $\Pr(0) = 0.05$ is equivalent to setting the upper confidence limit for estimating p at 95%, and rearrangement gives $p < 1\text{–}0.05^{(1/n)}$. Although this approach ignores heterogeneity in parasitism in space and time, it does provide a crude detection threshold based on the number of hosts sampled and found not to be parasitized.

2.2. Predicting post-introduction host range

The list of potential hosts in the target region depends on the phylogenetic and ecological affinities of species in the geographic range to which the candidate spreads. To predict this spread, one could use the geographic range of the target pest or the distribution of climates matching those in which the candidate occurs in the source region. Although the geographic range of the target pest is normally well known, climate matching for the candidate is often difficult because its distribution in the source region is usually poorly known. To err on the side of caution, we use a region larger than both the geographic range of the target pest and the predicted climatic range of the candidate.

2.3. Host–parasitoid system studied

As a test case, we used *Macrocentrus grandii* Goidanich (Hymenoptera: Braconidae), which was introduced into North America during 1930s for control of *Ostrinia nubilalis* Hubner (Lepidoptera: Crambidae), the European corn borer (Baker et al., 1949). Because *M. grandii* was introduced in North America more than 60 years ago, sufficient time has elapsed to assess parasitism on non-target species. *M. grandii* was introduced initially from two regions: from France collected from *Ostrinia nubilalis* on *Artemisia vulgaris* L. (Thompson and Parker, 1928) and from Korea collected from *Ostrinia furnacalis* on sorghum (Baker et al., 1949; Clark, 1934). However, only the Korean releases appear to have established (Baker et al., 1949). The parasitoid has spread throughout most of the range of *O. nubilalis* in North America (Andreadis, 1982; Baker et al., 1949; Clausen, 1978; Lewis, 1982; Losey et al., 1992; Manson et al., 1994; Siegel et al., 1987; Winnie and Chiang, 1982).

Female *M. grandii* oviposit in larvae of *O. nubilalis* and *O. furnacalis* on many host plant species, but only when the host larvae are accessible in a web or a hole because the females do not oviposit through plant tissue. Furthermore, female *M. grandii* have difficulty ovipositing in free-crawling larvae (Parker, 1931). Female *M. grandii* readily learn new combinations of odors from host and host plant complexes (Ding et al., 1989a) and attraction to such odors increases with experience (Ding et al., 1989b). Differential attraction of host plant odors may explain differences in parasitism among host plant species (Udayagiri and Jones, 1993). Several species names have been used for the material introduced into North America (*Macrocentrus abdominalis*, *Macrocentrus gifuensis*, *M. grandii*, and *M. cingulum*) and so host range information in the literature on this parasitoid may involve more than one parasitoid species.

Ostrinia nubilalis is found throughout Europe, North Africa, and temperate Asia (CAB International, 1997; Mutuura and Munroe, 1970). First discovered in the United States in 1917 in Massachusetts (Vinal, 1917), it has since spread to an area delimited by Minnesota and Missouri in the west and Virginia and Ontario in the east. *O. nubilalis* is a stem borer and a major pest in corn, but it also attacks a variety of other plant species with different chemistries: sweet pepper, potato, cotton, green beans, tomato, maize, wheat, and other grasses (Kennedy and Anderson, 1980). *O. furnacalis* is found in central, eastern, and southeastern Asia, Japan, Indonesia, Australia, and western Pacific islands (CAB International, 1997). It is also a stem borer in a variety of hosts plant species, including corn, sweet pepper, cotton, millet, maize, sorghum, and ginger (Ishikawa et al., 1999).

2.4. Sources of data on parasitism

Data on parasitism by *M. grandii* were obtained from two sources:(1) published literature on this species and on biological control of *O. nubilalis* and *O. furnacalis*, (2) published literature on species of Lepidoptera that might be hosts of *M. grandii* because of phylogenetic or ecological affinities with known hosts of this parasitoid. We searched three bibliographical databases: (1) Agricola, which covers from 1970 to present, especially in North America, (2) Commonwealth Agricultural Bureau International (CABI), which covers from 1972 to present, especially in Europe, and (3) AGRIS, which covers from 1980 to present, especially in developing countries. We also used catalogues of host–parasitoid associations. Finally, we used data from papers cited in papers found in all these sources.

3. Results

3.1. Pre-introduction host range

Although most records indicate that *M. grandii* appears to be restricted to species in the genus *Ostrinia* (Baker et al., 1949; Parker, 1931), there are reports of attack on other crambids, a noctuid, a lymantriid, and a nymphalid (Table 1). These reports appear to be based on rearing records for museum specimens of *M. grandii*, and given the problems with *M. grandii* taxonomy, these reports may be spurious. Indeed, van Achterberg and Haeselbarth (1983) suggest that parasitism of *Orgyia antiqua* should be checked because Brischke (1882) said this host is only recorded as being attacked by *Macrocentrus linearis*.

Table 1
Macrocentrus grandii reported host range in Eurasia (19th century) (van Achterberg and Haeselbarth, 1983)

Species	Family	Host plant
Ostrinia nubilialis	Pyralidae	*Artemisia* sp.
Ostrinia furnicalis	Pyralidae	*Zea mays*
Sitichroa verticalis	Pyralidae	*Urtica* sp.
Pleuroptya ruralis	Pyralidae	*Urtica* sp.
Orgya antiqua	Lymantriidae	—
Plusia sp.	Noctuidae	*Urtica* sp.
Vanessa sp.	Nymphalidae	*Urtica* sp.

For other species in the genus *Macrocentrus*, host range is variable. Some species have broad ranges (e.g., several families of Lepidoptera) and others that have narrow ranges (e.g., a single genus) (Eady and Clark, 1964). Thus, parasitoid phylogeny does not reveal much about host range of *M. grandii*. However, hosts of *Macrocentrus* spp. are usually concealed (Eady and Clark, 1964), but larvae of *Vanessa* spp. (Nymphalidae) and *Orgyia antiqua* (Lymantriidae) are not concealed. Furthermore, *M. grandii* is particularly poor at attacking free-crawling larvae so these records of attack on free-living species may be spurious.

To determine whether *M. grandii* attacks crambids other than *Ostrinia* spp., pyralids, noctuids, lymantriids, or nymphalids, we examined records of parasitism of species in these groups in Eurasia to see whether *M. grandii* was ever reported from them. None of 15 species of crambids and pyralids in eight countries were parasitized by *M. grandii* (Table 2). One to eight sites were sam-

Table 2
Eurasian (A) Crambidae and (B) Pyralidae from which *Macrocentrus grandii* was not reported

Species	Country	No. of sites	No. of years	No. of hosts	*p*	Sites × years	Citation
(A) Crambidae							
Cnaphalocrocis medinalis	India	5	2	235	1.27E−02	10	Talgeri and Dalaya (1971)
Cnaphalocrocis medinalis	India	1	2	400	7.46E−03	2	Manisegaran et al. (1997)
Cnaphalocrocis medinalis	Sri Lanka	1	2	1103	2.71E−03	2	Rajapakse (1990)
Cnaphalocrocis medinalis	China	1	1	1591	1.88E−03	1	Liu (1982)
Cnaphalocrocis spp.	China	3	1	1104	2.71E−03	3	Zhimo (1986)
Chilo suppressalis	Philippines	5	2	1734	1.73E−03	10	Kamran and Raros (1969)
Chilo suppressalis	China	1	4	318	9.38E−03	4	She and He (1988)
Chilo polychrysus	Philippines	5	1	247	1.21E−02	5	Kamran and Raros (1969)
Crocidolomia binotalis	Indonesia	4	3	4820	6.21E−04	12	Shepard and Barrion (1998)
Diaphania indica	India	1	1	7198	4.16E−04	1	Peter and David (1991)
Eutectona macchoeralis	India	1	2	180	1.65E−02	2	Patil and Thontadarya (1986)
Hellula undalis	Malaysia	5	2	799	3.74E−03	10	Sivapragasam and Chua (1997)
Hymenia recurvalis	India	1	1	87	3.38E−02	1	Narayanan et al. (1957)
Maruca vitrata	Indonesia	4	3	149	1.99E−02	12	Shepard and Barrion (1998)
Maruca vitrata	Philippines	5	1	500	5.97E−03	5	Sison et al. (1996)
Omiodes indicata	Indonesia	4	3	302	9.87E−03	12	Shepard and Barrion (1998)
Scirpophaga incertulas	India	3	2	2000	1.50E−03	6	Catling and Islam (1995)
Scirpophaga incertulas	India	1	2	960	3.12E−03	2	Chandramohan and Chelliah (1990)
Scirpophaga incertulas	Philippines	5	2	1029	2.91E−03	10	Kamran and Raros (1969)
(B) Pyralidae							
Dioryctria abietella	India	1	1	650	4.60E−03	1	Singh (1998)
Ectomyelois ceratoniae	Israel	8	4	2600	1.15E−03	32	Gothilf and Mazor (1987)
Ectomyelois ceratoniae	Israel	6	2	1873	1.60E−03	12	Gothilf (1969)
Ectomyelois ceratoniae	Iraq	5	3	1216	2.46E−03	15	Al-Maliky and Al-Izzi (1986)
Etiella spp.	Indonesia	4	3	1896	1.58E−03	12	Shepard and Barrion (1998)

pled for periods varying from 1 to 4 years, for a total of 182 site-years, and the number of larvae collected varied from 87 to 7198. With this effort, $p < 0.03\text{–}4 \times 10^{-4}$. For crambids and pyralids, all the data were from Asia and the Middle East. We did find parasitoid surveys in Europe, but they did not include information for an analysis of sampling effort. However, the only hosts of *M. grandii* reported in the 20th century literature from Eurasia were *O. nubilalis* and *O. furnacalis*. These data suggest that *M. grandii* does not parasitize other crambids or pyralids, or if it does, it is not a major parasitoid of species in these families in Eurasia.

None of six species of lymantriids in 13 countries in Eurasia were parasitized by *M. grandii* (Table 3). One to 50 sites were sampled for periods varying from 1 to 5 years, for a total of 724 site-years, and the number of larvae collected varied from 38 to 52,351. With this effort, $p < 0.08\text{–}6 \times 10^{-5}$. Furthermore, *Orgyia antiqua*, a putative host of *M. grandii*, was one of the species sampled, but in none of 4000 larvae were any *M. grandii* found. Unfortunately, all of the effort on *O. antiqua* was in Poland and Germany, where high densities of *M. grandii* have not been reported. Thus, this lack of parasitism could be from lack of exposure to high populations of *M. grandii*. Nonetheless, these data suggest that *M. grandii* does not parasitize lymantriids, or if it does, it is not a major parasitoid of species in this family in Eurasia.

None of 18 species of Noctuidae in 12 countries in Eurasia were parasitized by *M. grandii* (Table 4). One to 10 sites were sampled for periods varying from 1 to 5 years, for 262 site-years, and the number of larvae collected varied from 38 to 41,596. With this effort, $p < 0.08\text{–}7 \times 10^{-5}$. Again, the data suggest that *M. grandii* does not parasitize noctuids, or if it does, it is not a major parasitoid of species in this family in Eurasia.

None of five species of Nymphalidae in three countries from Eurasia plus Australia were parasitized (Table 5). One to five sites were sampled for periods varying from 1 to 4 years, for a total of 33 site-years, and the number of larvae collected varied from 136 to 3908. With this effort, $p < 0.02\text{–}8 \times 10^{-4}$. There are few surveys in the literature on parasitoids of Nymphalidae, perhaps because few Eurasian nymphalids are pests. The countries with published research on nymphalid natural enemies either lack *M. grandii* entirely or have low densities of *M. grandii*, and so lack of parasitism could be from lack of exposure. Thus, these data do not say much about the likelihood of *M. grandii* attack on nymphalids. However, *Macrocentrus* species usually attack concealed hosts and

Table 3
Eurasian Lymantriidae from which *Macrocentrus grandii* was not reported

Species	Country	No. of sites	No. of years	No. of hosts	p	Sites × years	Citation
Ivela auripes	Japan	3	1	469	6.37E−03	3	Togashi (1988)
Lymantria dispar	Austria	12	2	31,000	9.66E−05	24	Fuester et al. (1983)
Lymantria dispar	Austria	2	1	4789	6.25E−04	2	Eichhorn (1996)
Lymantria dispar	Germany	1	1	5000	5.99E−04	1	Fuester et al. (1983)
Lymantria dispar	Poland	8	1	5700	5.25E−04	8	Drea and Fuester (1979)
Lymantria dispar	Austria	12	4	26200	1.14E−04	48	Drea (1978)
Lymantria dispar	France	6	4	27836	1.08E−04	24	Drea (1978)
Lymantria dispar	France	35	5	50499	5.93E−05	175	Fuester et al. (1981)
Lymantria dispar	Iran	5	4	4035	7.42E−04	20	Drea (1978)
Lymantria dispar	Germany	1	4	4782	6.26E−04	4	Drea (1978)
Lymantria dispar	Spain	2	5	28000	1.07E−04	10	Reardon (1976)
Lymantria dispar	Iran	5	4	15,809	1.89E−04	20	Fuester et al. (1983)
Lymantria dispar	Poland	1	4	4558	6.57E−04	4	Fuester et al. (1983)
Lymantria dispar	Yugoslavia	14	3	5288	5.66E−04	42	Drea (1978)
Lymantria dispar	Korea	7	5	52,351	5.72E−05	35	Pemberton et al. (1993)
Lymantria dispar	China	12	1	2560	1.17E−03	12	Schaefer et al. (1984)
Lymantria dispar	Germany	2	2	2000	1.50E−03	4	Bogenschutz et al. (1989)
Lymantria dispar	Yugoslavia	6	1	8000	3.74E−04	6	Hackett (1971)
Lymantria dispar	Romania	7	3	9496	3.15E−04	21	Constantineanu and Constantineanu (1983)
Lymantria dispar	Korea	1	2	7886	3.80E−04	2	Lee et al. (1987)
Lymantria obfuscata	India	50	3	6500	4.61E−04	150	Rishi and Shah (1985)
Orgya antiqua	Poland	1	1	2,000	1.50E−03	1	Drea and Fuester (1979)
Orgya antiqua	Germany	2	2	2,000	1.50E−03	4	Skatulla (1974)
Porthesia similis	Poland	2	1	38	7.58E−02	2	Drea and Fuester (1979)
Stilpnotia salicis	Poland	2	1	421	7.09E−03	2	Drea and Fuester (1979)
Stilpnotia salicis	Bulgaria	7	4	2112	1.42E−03	28	Zaharieva-Pentcheva and Georgiev (1997)
Stilpnotia salicis	Austria	1	4	50,000	5.99E−05	4	Brown (1931)
Stilpnotia salicis	Hungary	17	4	1618	1.85E−03	68	Brown (1931)

Table 4
Eurasian Noctuidae from which *Macrocentrus grandii* was not reported

Species	Country	No. of sites	No. of years	No. of hosts	p	Sites × years	Citation
Agrotis exclamationis	Poland	1	3	40	7.22E−02	3	Napiorkoska-Kowalik and Machowicz-Stefaniak (1986)
Agrotis ipsilon	Egypt	3	3	700	4.27E−03	9	El-Heneidy and Hassanein (1987)
Agrotis ipsilon	Japan	1	1	38	7.58E−02	1	Goro et al. (1986)
Agrotis segetum	Poland	1	3	305	9.77E−03	3	Napiorkoska-Kowalik and Machowicz-Stefaniak (1986)
Autographa gamma	Poland	1	3	130	2.28E−02	3	Napiorkoska-Kowalik and Machowicz-Stefaniak (1986)
Chrysodeixis chalcites	Indonesia	4	3	2361	1.27E−03	12	Shepard and Barrion (1998)
Helicoverpa armigera	Indonesia	3	4	356	8.38E−03	12	Shepard and Barrion (1998)
Heliothis armigera	Philippines	1	2	650	4.60E−03	2	Divina and Irabagon (1976)
Hydraecia micacea	France, Switzerland, and W. Germany	5	1	589	5.07E−03	5	West et al. (1983)
Janseodes melanospila	India	1	1	500	5.97E−03	1	Peter and Balasubramanian (1984)
Mamestra brassicae	Poland	1	3	1688	1.77E−03	3	Napiorkoska-Kowalik and Machowicz-Stefaniak (1986)
Mythimna convecta	Australia	6	4	5336	5.61E−04	24	McDonald and Smith (1986)
Mythimna separata	India	1	2	1100	2.72E−03	2	Naganagoud and Kulkarni (1997)
Mythima separata	China	1	3	3679	8.14E−04	3	Liu (1982)
Persectania dyscrita	Australia	6	4	215	1.38E−02	24	McDonald and Smith (1986)
Persectania ewingii	Australia	6	4	1564	1.91E−03	24	McDonald and Smith (1986)
Sesamia inferens	Japan	3	4	1652	1.81E−03	12	Nagatomi (1972)
Sesamia inferens	India	7	1	14216	2.11E−04	7	Muttalib and Rahman (1981)
Sesamia Inferens	Philippines	5	2	685	4.36E−03	10	Kamran and Raros (1969)
Sesamia turpis	Japan	1	1	42	6.88E−02	1	Nagatomi (1972)
Spodoptera exigua	Indonesia	4	3	8403	3.56E−04	12	Shepard and Barrion (1998)
Spodoptera exigua	Israel	2	1	1547	1.93E−03	2	Schwartz et al. (1980)
Spodoptera littoralis	Egypt	8	2	4280	7.00E−04	16	Hegazi et al. (1977)
Spodoptera littoralis	Egypt	10	5	41,596	7.20E−05	50	Hafez et al. (1976)
Spodoptera littoralis	Israel	9	1	3250	9.21E−04	9	Gerling (1971)
Spodoptera litura	Indonesia	4	3	1493	2.00E−03	12	Shepard and Barrion (1998)

Table 5
Eurasian Nymphalidae from which *Macrocentrus grandii* was not reported

Species	Country	No. of sites	No. of years	No. of hosts	p	Sites × years	Citation
Aglais urticae	Finland	4	4	3908	7.66E−04	16	Pyornila (1976)
Danaus plexippus	Australia	4	2	229	1.30E−02	8	Zalucki (1981)
Euphydryas aurinia	England	1	3	370	8.06E−03	3	Porter (1984)
Euploea core corina	Australia	1	1	136	2.18E−02	1	Rahman and Zalucki (1986)
Melitaea cinxia	Finland	5	1	1691	1.77E−03	5	Lei et al. (1997)

nymphalid larvae are usually not concealed, so the likelihood that *M. grandii* parasitizes them is low.

3.2. Predicted post-introduction host range

Based on the host range of *M. grandii* in Eurasia as reported in the literature, we can predict the potential hosts of this parasitoid in North America. The species in the genus *Ostrinia* are the most likely hosts. There are three native species that are close relatives of *O. nubilalis* in North America: *Ostrinia penitalis* (Grote), *Ostrinia obumbratalis* (Lederer), and *Ostrinia marginalis* (Walker) (Mutuura and Munroe, 1970). According to Mutuura and Munroe (1970), *O. penitalis* and *O. obumbratalis* are more related to *O. nubilalis* than is *O. marginalis*. However, the larvae of *O. penitalis* are aquatic and are unlikely to be attacked by *M. grandii*. Thus, *O. obumbratalis* is the only non-target host species likely to be attacked by *M. grandii* in North America.

3.3. Testing the predicted host range in North America

To determine the actual host range of *M. grandii* in North America, we used the procedures described above for Eurasia. In 1932, *M. grandii* was recovered from *O. penitalis* (three larvae) and *O. obumbratalis*, but *M. grandii* was not recovered in subsequent collections of these hosts (Baker et al., 1949). In a survey of imported and native parasitoids of species in the genus *Ostrinia* (=*Pyrausta*) in Iowa, Blickenstaff (1948) recovered *M. grandii* from *O. nubilalis* but not from *O. obumbratalis* or *O. penitalis*. On the other hand, in a survey of parasitoids of lepidopterous larvae in corn fields in Iowa, Schaffner (1953) did not recover *M. grandii*, not even

Table 6
North American (A) Crambidae and (B) Pyralidae from which *Macrocentrus grandii* was not reported

Species	State	No. of sites	No. of years	No. of hosts	*p*	Sites × years	Citation
(A) Crambidae							
Desmia funeralis	Iowa	8	1	134	2.21E−02	8	Schaffner (1953)
Diaphania nitidalis	Florida	5	2	2,353	1.27E−03	10	Pena et al. (1987)
Diaphania hyalinata	Florida	5	2	5,405	5.54E−04	10	Pena et al. (1987)
Diatraea muellerella	Mexico	1	1	250	1.19E−02	1	Rodriguez del Bosque and Smith (1991)
Diatraea grandiosella	Texas	2	2	5329	5.62E−04	4	Knutson and Gilstrap (1989)
Diatraea lineolata	Texas	1	3	180	1.65E−02	3	Youm et al. (1990)
Diatraea saccharalis	Texas	480	13	2,057	1.46E−03	6240	Meagher et al. (1998)
Diatraea saccharalis	Texas	1	3	531	5.63E−03	3	Youm et al. (1990)
Eoreuma loftini	Texas	480	13	36,897	8.12E−05	6240	Meagher et al. (1998)
Eoreuma loftini	Texas	1	1	1750	1.71E−03	1	Pfannenstiel et al. (1990)
Eoreuma loftini	Texas	1	3	4136	7.24E−04	3	Youm et al. (1990)
Herpetogramma pertextalis	Maine, Massachusetts, New Hampshire, New Jersey, New York, Pennsylvannia	39	13	286	1.04E−02	507	Schaffner (1959)
Herpetogramma bipunctalis	Florida	2	2	390	7.65E−03	4	Tingle et al. (1978)
Ostrinia obumbratalis	Kansas	3	1	150	1.98E−02	3	Schopp (1931)
Ostrinia obumbratalis	Iowa	14	3	250	1.19E−02	42	Blickenstaff et al. (1953)
Ostrinia obumbratalis	Iowa	3	1	23	1.22E−01	3	Schaffner (1953)
Ostrinia penitalis	Iowa	1	2	600	4.98E−03	2	Schaffner (1953)
Ostrinia penitalis	Iowa	14	3	10	2.59E−01	42	Blickenstaff et al. (1953)
Phlyctaenia coronata	Maine, Massachusetts, and Rhode Island	9	4	417	7.16E−03	36	Schaffner (1959)
Saucrobotys futilalis	Maine, New Hampshire, Massachusetts, Vermont, New Jersey, Connecticut	36	13	3520	8.51E−04	468	Schaffner (1959)
Saucrobotys futilalis	Iowa	6	1	110	2.69E−02	6	Schaffner (1953)
(B) Pyralidae							
Acrobasis betulella	Maine, New Hampshire, Massachusetts	31	12	509	5.87E−03	372	Schaffner (1959)
Acrobasis caryivorella	Massachusetts, Connecticut	6	5	101	2.92E−02	30	Schaffner (1959)
Acrobasis comptoniella	Maine, New Hampshire, Massachusetts	16	10	531	5.63E−03	160	Schaffner (1959)
Acrobasis nuxvorella	Texas	5	2	3019	9.92E−04	10	Gunasena and Harris (1988)
Arobasis vaccinii	Michigan	1	1	278	1.07E−02	1	Murray et al. (1996)
Dioryctria auranticella	Nebrasca	3	4	1900	1.58E−03	12	Pasek and Dix (1989)
Dioryctria disclusa	Nebrasca	3	4	100	2.95E−02	12	Pasek and Dix (1989)
Dioryctria ponderosae	Nebrasca	1	10	193	1.54E−02	10	Harrell et al. (1996)
Dioryctria tumicolella	Nebrasca	1	10	310	9.62E−03	10	Harrell et al. (1996)
Elasmopalpus lignosellus	Texas	1	1	23	1.22E−01	1	Youm et al. (1990)
Elasmopalpus lignosellus	Texas	1	3	4118	7.27E−04	3	Johnson and Smith (1981)
Elasmopalpus lignosellus	Texas	1	3	433,173	6.92E−06	3	Smith and Johnson (1989)
Elasmopalpus lignosellus	Georgia	2	10	600	4.98E−03	20	Leuck and Dupree (1965)
Elasmopalpus lignosellus	Oklahoma	5	3	5344	5.60E−04	15	Wall and Berberet (1975)
Etiella zinckenella	Maryland	1	2	100	2.95E−02	2	Segarra-Carmona and Barbosa (1990)
Homoeosoma electellum	Texas, North Dakota, Arizona, Colorado	17	2	1350	2.22E−03	34	Beregovoy (1985)
Macala thyrsisalis	Florida	4	1	125	2.37E−02	4	Howard and Solis (1989)
Nephopterix subfuscella	Maine, Massachusetts	4	4	475	6.29E−03	16	Schaffner (1959)

from *O. nubilalis*, although *M. grandii* was released in Iowa from 1944 to 1950 and *M. grandii* is now the predominant parasitoid of *O. nubilalis* in Iowa (Lewis, 1982). Because *O. obumbratalis* and *O. penitalis* are very close relatives of *O. nubilalis* and have similar life cycles and morphologies (Heinrich, 1919; Mutuura and Munroe, 1970), some confusion among them may have occurred. Other than *O. nubilalis* and its congeners, none of 27 species of crambids and pyralids were parasitized by *M. grandii* in North America (Table 6). One to 480 sites were sampled for periods varying from 1 to 13 years, for a total of 14,351 site-years, and the number of larvae collected varied from 10 to 433,173. With this effort, $p < 0.3–7 \times 10^{-6}$.

None of three species of Lymantriidae in North America were parasitized (Table 7). One to 39 sites were sampled for periods varying from 1 to 24 years for a total of 445 site-years. The sampling effort measured by the number of larvae collected varied from 259 to 240,000. With this effort, $p < 2 \times 10^{-4}–2 \times 10^{-7}$. The data suggest that, if *M. grandii* does parasitize lymantriids, it is not a major parasitoid of the species in this family.

None of 24 species of Noctuidae in North America were parasitized (Table 8). One to 150 sites were sampled for periods varying from 1 to 4 years for a total of 1972 site-years, and the number of larvae collected varied from 12 to 44,000. With this effort, $p < 0.1–7 \times 10^{-5}$. The data suggest that, if *M. grandii* does parasitize noctuids, it is not a major parasitoid of the species in this family.

None of 12 species of Nymphalidae in North America were parasitized (Table 9). One to 323 sites were sampled for periods varying from 1 to 15 years for a total 11,862 of site-years, and the number of larvae collected varied from 24 to 21,529. With this effort, $p < 0.2–10^{-4}$. Very little work with natural enemies of nymphalids is available in the literature. The majority of the data come from surveys done in early 1930s, when *M. grandii* was just beginning to be released into North America. Thus, the evidence for lack of attack by *M. grandii* on nymphalids is not conclusive.

In addition to the above analyses, we also examined the literature for other species in the Pyralidae and Crambidae with special economic, ecological, or societal value, i.e., biological control agents, pollinators, and endangered species, which might be exposed to parasitism by *M. grandii*.

Few data are available about native North American species that provide biological control of actual or potential weeds. However, we examined the literature for species that were exported from North America for biological control because this might indicate they provide unrecognized biological control in North America. We also considered species introduced into North America for biological control of weeds. Data on biological control species were obtained mainly from monographs on such introductions (Clausen, 1978; Julien and Griffiths, 1999; Sarazin, 1990, 1992) and additional information from citations in the bibliographic databases described above.

We found five species of Pyralidae/Crambidae that were exported from North America for biological control of weeds and five species that were imported or introduced accidentally into North America, and may provide biological control of weeds (Table 10). For most of the species listed, we were not able to find parasitoid surveys. However, they differ from the target pest, *O. nubilalis* in host plant, feeding habit, phenol-

Table 7
North American Lymantriidae from which *Macrocentrus grandii* was not reported

Species	State	No. of sites	No. of years	No. of hosts	p	Sites × years	Citation
Lymantria dispar	Massachusetts	2	1	3921	7.64E−04	2	Barbosa et al. (1975)
Lymantria dispar	Massachusetts, New York, New Jersey	6	2	165,810	1.81E−05	12	Reardon (1976)
Lymantria dispar	Connnnecticut	2	1	500	5.97E−03	2	Weseloh (1972)
Lymantria dispar	Connnnecticut	2	1	3000	9.98E−04	2	Weseloh (1973)
Lymantria dispar	New York	5	2	3257	9.19E−04	10	Kamran (1977)
Lymantria dispar	New York	3	1	8773	3.41E−04	3	Tigner (1974)
Lymantria dispar	New York	39	1	240,000	1.25E−05	39	Tigner (1974)
Lymantria dispar	Canada	3	2	6000	4.99E−04	6	Madrid and Stewart (1980)
Lymantria dispar	Canada	2	3	598	5.00E−03	6	Quednau (1983)
Lymantria dispar	Pennsylvania	5	2	45,000	6.66E−05	10	Ticehurst (1984)
Lymantria dispar	Pennsylvania	3	3	2700	1.11E−03	9	Hedlund and Angalet (1979)
Lymamtria dispar	Pennsylvania	4	4	50,000	5.99E−05	16	Ticehurst et al. (1978)
Lymantria dispar	Connecticut	2	1	1000	2.99E−03	2	Dunbar et al. (1973)
Orgya pseudotsugata	California	4	3	2000	1.50E−03	12	Dahlsten et al. (1977)
Orgya pseudotsugata	Idaho	1	1	1000	2.99E−03	1	Gast and Gibson (1987)
Stilpnotia salicis	Canada	13	24	14,500	2.07E−04	312	Reeks and Smith (1956)
Stilpnotia salicis	Canada	1	1	259	1.15E−02	1	McLeod (1954)

Table 8
North American Noctuidae from which *Macrocentrus grandii* was not reported

Species	State	No. of sites	No. of years	No. of hosts	*p*	Sites × years	Citation
Anticarsia gemmatalis	Oklahoma	5	3	567	5.27E−03	15	Wall and Berberet (1975)
Artogeia rapae	Virginia	1	2	2110	1.42E−03	2	Chamberlin and Kok (1986)
Autographa californica	California	1	2	500	5.97E−03	2	Henneberry et al. (1991)
Autographa californica	California	5	2	792	3.78E−03	10	Clancy (1969)
Autoplusia egena	California	5	2	62	4.72E−02	10	Clancy (1969)
Euxoa auxiliaris	Oklahoma	150	3	3500	8.56E−04	450	Soteres et al. (1984)
Feltia subterranea	Oklahoma	5	3	393	7.59E−03	15	Wall and Berberet (1975)
Helicoverpa zea	Arizona	1	2	74	3.97E−02	2	Rathman and Watson (1985)
Helicoverpa zea	Mississippi	10	3	3449	8.68E−04	30	Lewis and Brazzel (1968)
Helicoverpa zea	Mississippi	7	2	2248	1.33E−03	14	Lewis and Brazzel (1966)
Helicoverpa zea	New Mexico	8	2	40	7.22E−02	16	Gordon et al. (1987)
Helicoverpa zea	Oklahoma	4	2	1538	1.95E−03	8	Bottrell et al. (1968)
Helicoverpa zea	Oklahoma	20	1	44000	6.81E−05	20	Young and Price (1975)
Helicoverpa zea	South Carolina	26	2	617	4.84E−03	52	Roach (1975)
Helicoverpa zea	Tennessee	2	2	501	5.96E−03	4	Bidlack et al. (1991)
Helicoverpa zea	Virginia	11	2	2820	1.06E−03	22	Zehnder et al. (1990)
Heliothis armigera	Texas	11	1	850	3.52E−03	11	Bibby and Smithville (1942)
Heliothis armigera	Iowa	3	1	72	4.08E−02	3	Schaffner (1953)
Heliothis phloxiphaga	Arizona	1	2	612	4.88E−03	2	Rathman and Watson (1985)
Heliothis spp	Oklahoma	10	2	1538	1.95E−03	20	Bottrell (1968)
Heliothis spp	Oklahoma	4	2	1185	2.52E−03	8	Bottrell et al. (1968)
Heliothis spp	Texas	1	2	1719	1.74E−03	2	Shepard and Sterling (1972)
Heliothis spp	Texas	8	2	5658	5.29E−04	16	Puterka et al. (1985)
Heliothis virescens	Arizona	1	2	555	5.38E−03	2	Rathman and Watson (1985)
Heliothis virescens	California	1	2	500	5.97E−03	2	Henneberry et al. (1991)
Heliothis virescens	Mississippi	8	2	1503	1.99E−03	16	Lewis and Brazzel (1966)
Heliothis virescens	Mississippi	10	3	1894	1.58E−03	30	Lewis and Brazzel (1968)
Heliothis virescens	Oklahoma	4	2	69	4.25E−02	8	Bottrell et al. (1968)
Heliothis virescens	South Carolina	26	2	1495	2.00E−03	52	Roach (1975)
Heliothis virescens	South Carolina	11	2	2415	1.24E−03	22	Johnson and Manley (1982)
Heliothis virescens	Tennessee	2	2	2945	1.02E−03	4	Bidlack et al. (1991)
Heliothis virescens	Virginia	3	1	848	3.53E−03	3	Grayson (1944)
Heliothis virescens	Virginia	11	1	690	4.33E−03	11	Wene (1943)
Homoeosoma electellum	Missouri, Illinois, Louisianna	3	1	1500	2.00E−03	3	Satterthwait and Swain (1946)
Hydraecia micacea	Ontario, Canada	2	3	1869	1.60E−03	6	West et al. (1983)
Papaipema nebris	Iowa	10	1	2025	1.48E−03	10	Schaffner (1953)
Peridroma saucia	Oklahoma	150	3	2500	1.20E−03	450	Soteres et al. (1984)
Peridroma saucia	Oregon	15	2	2158	1.39E−03	30	Coop and Berry (1986)
Plathypena scabra	Delaware	20	1	1400	2.14E−03	20	Whiteside et al. (1967)
Plathypena scabra	Ohio	2	3	959	3.12E−03	6	Hammond (1983)
Plathypena scabra	South Carolina	8	2	2852	1.05E−03	16	McCutcheon and Turnipseed (1981)
Platynota nigrocervina	Oklahoma	5	3	69	4.25E−02	15	Wall and Berberet (1975)
Prodenia orithogalli	Oklahoma	4	1	614	4.87E−03	4	Bottrell (1968)
Pseudaletia unipuncta	Ontario, Canada	4	4	1000	2.99E−03	16	Guppy (1967)
Pseudoplusia includens	Georgia	6	3	4917	6.09E−04	18	Beach and Todd (1985)
Pseudoplusia includens	Louisianna	3	2	3624	8.26E−04	6	Burleigh (1972)
Pseudoplusia includens	Louisianna	3	2	5330	5.62E−04	6	Burleigh (1971)
Pseudoplusia includens	South Carolina	3	2	1502	1.99E−03	6	McCutcheon and Turnipseed (1981)
Pseudoplusia includens	Texas	29	4	1152	2.60E−03	116	Harding (1976)
Spodoptera eridana	Florida	5	2	390	7.65E−03	10	Tingle et al. (1978)
Spodoptera exigua	Florida	5	2	662	4.52E−03	10	Tingle et al. (1978)
Spodoptera exigua	New Mexico	8	2	34	8.43E−02	16	Gordon et al. (1987)

Table 8 (*continued*)

Species	State	No. of sites	No. of years	No. of hosts	*p*	Sites × years	Citation
Spodoptera exigua	Oklahoma	5	3	33	8.68E−02	15	Wall and Berberet (1975)
Spodoptera frugiperda	Alabama	8	2	3450	8.68E−04	16	Rohlfs and Mack (1985)
Spodoptera frugiperda	Florida	3	1	1648	1.82E−03	3	Ashley et al. (1983)
Spodoptera frugiperda	Florida	5	1	8994	3.33E−04	5	Ashley et al. (1982)
Spodoptera frugiperda	Florida	3	1	399	7.48E−03	3	Ashley et al. (1980)
Spodoptera frugiperda	Florida, Georgia, Alabama, South Carolina, Louisianna, Mississippi, Texas, Mexico	20	3	10838	2.76E−04	60	Pair et al. (1986)
Spodoptera frugiperda	Georgia	2	2	5000	5.99E−04	4	Riggin et al. (1992)
Spodoptera frugiperda	Mississippi	14	1	638	4.68E−03	14	Smith (1982)
Spodoptera frugiperda	Oklahoma	5	3	1864	1.61E−03	15	Wall and Berberet (1975)
Spodoptera frugiperda	Oklahoma	5	3	167	1.78E−02	15	Wall and Berberet (1975)
Spodoptera frugiperda	South Carolina	1	1	1403	2.13E−03	1	McCutcheon (1991)
Stegasta bosqueella	Oklahoma	5	3	2739	1.09E−03	15	Wall and Berberet (1975)
Trichoplusia ni	California	5	2	2728	1.10E−03	10	Clancy (1969)
Trichoplusia ni	Oklahoma	5	3	127	2.33E−02	15	Wall and Berberet (1975)
Trichoplusia ni	Texas	29	4	2852	1.05E−03	116	Harding (1976)
Trichoplusia ni	Virginia	1	2	2000	1.50E−03	2	Chamberlin and Kok (1986)

Table 9
North American Nymphalidae from which *Macrocentrus grandii* was not reported

Species	State	No. of sites	No. of years	No. of hosts	*p*	Sites × years	Citation
Basilarchia archippus	Iowa	3	1	16	1.71E−01	3	Schaffner (1953)
Basilarchia archippus	New England, New York, New Jersey	191	15	1039	2.88E−03	2865	Schaffner and Griswold (1934)
Basilarchia arthemis	Vermont, Massachusets, New Jersey	19	8	24	1.17E−01	152	Schaffner and Griswold (1934)
Cynthia virginiensis	Maine, New Hampshire, Massachusetts, New York, New Jersey, Pennsylvania	29	9	201	1.48E−02	261	Schaffner and Griswold (1934)
Euphydryas phaeton	Virginia	1	2	1040	2.88E−03	2	Stamp (1981)
Euphydryas phaeton	Maine, Mass., New York, New Jersey	31	10	1171	2.55E−03	310	Schaffner and Griswold (1934)
Hamadryas J-Album	New Hampshire, Massachusetts	16	5	176	1.69E−02	80	Schaffner and Griswold (1934)
Hamadryas antiopa	New England, New York, New Jersey, Pennsylvania	323	15	21,529	1.39E−04	4845	Schaffner and Griswold (1934)
Hamadryas milberti	New England, New Jersey	56	9	5,100	5.87E−04	504	Schaffner and Griswold (1934)
Leomonias harrisii	Maine, New Hampshire, Vermont, Massachusetts, New Jersey	25	10	714	4.19E−03	250	Schaffner and Griswold (1934)
Polygonia interrogationis	Maine, New Hampshire, Massachusetts, Rhode Island, Connecticut, New York, New Jersey, Pennsylvania	94	12	977	3.06E−03	1128	Schaffner and Griswold (1934)
Polygonia comma	Maine, Massachusetts, New York, New Jersey, Vermont	8	5	118	2.51E−02	40	Schaffner and Griswold (1934)
Vanessa atalanta	Maine, New Hampshire, Massachusetts, New York, New Jersey, Pennsylvania	99	*13*	2730	1.10E−03	1287	Schaffner and Griswold (1934)
Vanessa cardui	New England, New York, New Jersey	32	4	846	3.53E−03	128	Schaffner and Griswold (1934)
Vanessa cardui	Iowa	7	1	72	4.08E−02	7	Schaffner (1953)

ogy, habitat preference, and abundance. Thus, it is unlikely that *M. grandii* will attack these weed biocontrol agents in North America.

Publications on North American Pyralidae as pollinators are very rare. The only species we found was *Anageshna primordialis* (Dyar) (Pyralidae: Pyraustinae),

Table 10
Crambidae/Pyralidae introduced into North America or exported from North America which may provide biological control

Herbivore	Weed	Source country	Target Country	Fate
Acentria ephemerella	*Myriophyllum spicatum*	Europe	USA	Established?
Arcola malloi	*Alternanthera philoxeroides*	Argentina	USA	Established
Cactoblastis cactorum	*Opuntia* spp.	South America	Florida, USA	accidentally established
Loxomorpha flavidissima	*Opuntia stricta*	Texas, USA	Australia	Not established
Melitara dendata	*Opuntia ficus-indica*	Texas, USA	Australia; Hawaii, USA	Not established
Melitara prodeniales	*Opuntia* spp.	Florida, Texas, USA	Australia; Hawaii, USA	Not established
Niphograpta albigutalis	*Eichhornia crassipes*	Argentina	Florida, USA	Established
Olycella junctolinella	*Opuntia stricta*	Texas, USA	Australia	Established
Salbia haemorrhoidalis	*Lantana camara*	Florida, USA	Australia; Fiji; Hawaii, USA; South Africa	Established
Salbia haemorrhoidalis	*Lantana camara*	Florida, USA	Guam; Kenya; Palau	Not established
Samea multiplicalis	*Salvinia minima*	South America	USA	Established?

which pollinates *Habenaria obtusata* (Pursh) (Voss and Riefner, 1983), and we found no information on its parasitoids.

Neither the US Fish and Wildlife Service nor the Canadian Committee on the Status of Endangered Wildlife list any pyralids/crambids as endangered. One pyralid, *Psammobotys fordi*, Ford's Sand Dune moth, is proposed for endangered status by the State of California, but we found no information on its parasitoids. Given that it occurs in California, where neither *O. nubilalis* nor *M. grandii* are found, it is unlikely to be at risk from parasitism by *M. grandii*.

4. Discussion

Retrospective studies with previously introduced arthropod parasitoids and predators can be useful in assessing how well our attempts at predicting host ranges are actually working (Van Driesche and Hoddle, 1997). Such studies are needed to identify cases of significant non-target impacts and determine the mechanisms involved where such impacts are found (Hopper, 2000). Based on literature data on parasitism of species closely related taxonomically to *O. nubilalis*, as well as more distantly related species similar in behavior or ecology, our investigation suggests that *M. grandii* parasitizes only *Ostrinia* spp., and not all the species in this genus. The predicted host range for North America matched the actual host range found in the field. This suggests that a careful literature review could be used as the main initial source of data on host range of parasitoid species proposed for introduction into a new environment. Some species cited in the 19th century literature as hosts of *M. grandii* in Eurasia were subsequently not found to be attacked in the field. Thus, careful use of data from the literature is key to predicting host range. More case studies with a variety of parasitoids and predators are needed to determine whether the approach proposed here is sound.

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