Biological Control 130 (2019) 44–50

Contents lists available at ScienceDirect

Biological Control

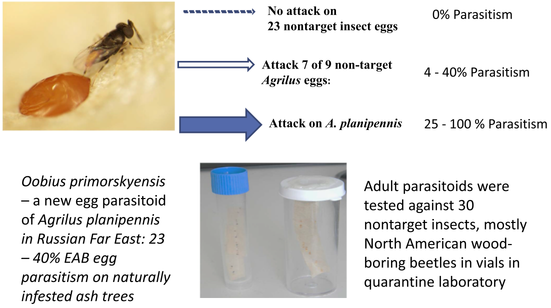
journal homepage: www.elsevier.com/locate/ybcon

Field parasitism and host specificity of *Oobius primorskyensis* (Hymenoptera: Encyrtidae), an egg parasitoid of the emerald ash borer (Coleoptera: Buprestidae) in the Russian Far East

Jian J. Duan[a,*], Jonathan M. Schmude[a], Kristi M. Larson[a], Roger W. Fuester[a], Juli R. Gould[b], Michael D. Ulyshen[c]

[a] *USDA ARS, Beneficial Insects Introduction Research Unit, Newark, DE 19713, United States*
[b] *USDA APHIS PPQ CPHST, Buzzards Bay, MA 02542, United States*
[c] *USDA Forest Service, Southern Research Station, Athens, GA 30602, United States*

GRAPHICAL ABSTRACT



ARTICLE INFO

Keywords:
Biological control
Host range
Risk assessment
Wood borers
Agrilus planipennis

ABSTRACT

Oobius primorskyensis Yao and Duan (Hymenoptera: Encyrtidae) is a recently described egg parasitoid of the emerald ash borer (EAB), *Agrilus planipennis* Fairmaire, from the Russian Far East. To support the potential introduction of this new parasitoid for biocontrol of EAB in North America, we surveyed EAB eggs on infested green ash (*Fraxinus pennsylvanica* Marsh) trees in the Russian Far East and documented the rate of EAB egg parasitism by *O. primorskyensis*. After establishing quarantine colonies of *O. primorskyensis* in the United States, we tested the parasitoid against eggs of 30 taxa of insects, mostly native North American wood-boring beetles in the families Buprestidae and Cerambycidae plus one unidentified weevil, one predatory coccinellid, one pentatomid and one moth. Field observations showed that EAB egg parasitism rate ranged from 23 to 44% in the Russian Far East and *O. primorskyensis* was the only egg parasitoid recovered from the parasitized eggs collected there. Quarantine testing showed that *O. primorskyensis* attacked seven out of nine *Agrilus* species, but not any of the other non-target species tested. Percentage parasitism of *A. anxius* (40%) and *A. cephalicus* (30%) was comparable to parasitism of their corresponding EAB (positive) control (29–30%). However, percentage parasitism of the other five attacked species (*A. bilineatus*, *A. egenus*, *A. fallax*, *A. macer*, and *A. oblongus*) were significantly less (4–17%) than for the EAB control (60–90%). These results indicate that the host specificity of *O. primorskyensis* may be limited to species phylogenetically closely related to EAB, such as those in the genus *Agrilus*. Additional testing is needed to determine whether the eggs of other buprestid genera are utilized by the species as well.

---

[*] Corresponding author.
E-mail address: jian.duan@ars.usda.gov (J.J. Duan).

https://doi.org/10.1016/j.biocontrol.2018.12.005
Received 13 July 2018; Received in revised form 27 November 2018; Accepted 19 December 2018

1. Introduction

Invasion by non-native insects, often associated with the rapidly expanding global economy, poses one of the greatest threats to the ecological sustainability of agriculture and forest ecosystems throughout the world (Pimentel, 1986; Aukema et al., 2010; Boyd et al., 2013). Classical biological control, involving the introduction and establishment of co-evolved natural enemies (predators, parasitoids, or pathogens) from the invasive pest's native range, has long been used for sustainable management of invasive insect pests in both agriculture and forest ecosystems (e.g., in van den Bosch et al., 1982; van Driesche et al., 2010). Successful development of a classical biocontrol program against the invasive pest requires information on host specificity as well as the target-impact of the potential agents (or associated natural enemies) in the pest's native range (Follett and Duan, 2000; van Lenteren and Loomans, 2006; van Driesche and Hoddle, 2017).

The emerald ash borer (EAB), *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae), accidentally introduced from northeastern Asia during the 1990s, has become a serious invasive forest pest since it was first discovered as the cause of ash (*Fraxinus* spp.) tree mortality in southeast Michigan, USA and nearby Ontario, Canada in 2002 (Haack et al., 2002; Herms and McCullough, 2014). This invasive phloem-feeding beetle has now spread to 35 states in the USA and three provinces in Canada, continuing to degrade and damage ash-dominant forest ecosystems of North America (Jennings et al., 2017; Emerald Ash Borer Information, 2018; CFIA, 2018). Shortly after the detection of EAB in North America, a classical biological control program was initiated by the U.S. Department of Agriculture against this invasive wood-boring beetle (Bauer et al., 2008). This program led to the introduction of three species of hymenopteran parasitoids from northeast China in 2007 and one additional species from the Russian Far East in 2015 (Federal Register, 2007, 2015). The three biocontrol agents from China included the egg parasitoid *Oobius agrili* Zhang and Huang (Encyrtidae) and two larval parasitoids *Tetrastichus planipennisi* Yang (Eulophidae) and *Spathius agrili* Yang (Braconidae). The introduced agent from the Russian Far East is *Spathius galinae* Belokobylskij & Strazanac (Hymenoptera: Braconidae).

In many regions of the United States, the three Chinese biocontrol agents are recovered from EAB larvae or eggs one year after release, indicating successful reproduction and overwintering in the target host (see reviews in Bauer et al., 2015; Duan et al., 2018). However, only *O. agrili* and *T. planipennisi* are consistently recovered two or more years after the last release, and these two species are now considered established and spreading naturally beyond their initial release sites (Jennings et al., 2016; Mapbiocontrol, 2018; Duan et al., 2018). Releases of *S. galinae* began in 2015, and it is too soon to confirm its establishment. Recent field studies have shown that the larval parasitoid *T. planipennisi* plays a significant role in protecting ash saplings and smaller trees (DBH < 12 cm) in aftermath forests in Michigan (Duan et al., 2015a, 2017). However, the ability of *T. planipennisi* to attack EAB larvae in large ash trees (DBH > 15 cm) is limited by its short ovipositor (Abell et al., 2014). Larval parasitoids with longer ovipositors such as *S. galinae* or egg parasitoids such as *O. agrili* are needed to protect growing and surviving large ash trees from EAB. Unfortunately, parasitism rates by the egg parasitoid *O. agrili* are variable among different released areas (1–32%) and its role in reducing EAB population growth requires further evaluation (Abell et al., 2014; Davidson and Rieske, 2016; Duan et al., 2018).

The encyrtid wasp *Oobius primorskyensis* Yao and Duan (Hymenoptera: Encyrtidae), is a recently described egg parasitoid of *A. planipennis* that is known from the Russian Far East as well as South Korea (Yao et al., 2016, 2018). In Russia, *O. primorskyensis* exhibits obligatory diapause behavior in response to a shortage of host eggs and in order to overwinter (Yao et al., 2016). This diapause behavior is apparently different from that of its congener *O. agrili,* which is primarily induced by short-day photoperiod (Hoban et al., 2016; Larson and Duan, 2016). If successfully introduced to North America, *O. primorskyensis* may have the potential to complement the current EAB biocontrol program because it has a geographic distribution and diapause behavior different than *O. agrili*.

Prior to this research we had little information on *O. primorskyensis'* potential impact on EAB populations in its native range, and the only information available to predict the species' impact and host range came from the limited data on field parasitism and host records of the congener *O. agrili* (as reported in USDA APHIS, 2007; Liu et al., 2007). However, predicting a parasitoid's impact and host range based on parasitism rate and host records of related congeners has been notoriously unreliable and is not considered an acceptable approach for both target and non-target impact assessments (Follett and Duan, 2000; Desneux et al., 2009).

To support both target and nontarget impact assessments for potential introduction of *O. primorskyensis* against EAB in North America, we surveyed EAB eggs on infested green ash (*Fraxinus pennsylvanica* Marsh) trees in the Russian Far East and documented the rate of EAB egg parasitism by *O. primorskyensis*. After having established quarantine colonies of *O. primorskyensis* in the U.S., we tested the parasitoid against eggs of 30 species of insects, mostly native North American wood-boring beetles in the families Buprestidae and Cerambycidae.

2. Materials and methods

2.1. Field survey of EAB egg parasitism in the Russian Far East

Surveys of EAB eggs and associated parasitoids were conducted on infested green ash trees (*F. pennsylvanica* Marsh.) at two different sites in the Primorsky Kray of the Russian Federation in the fall (September) of both 2010 and of 2012, respectively. The first site was a natural forest in the Vladivostok area (43°05 N; 131°57 E) while the second site was also a natural forest in the Vozdvizhenka area (43.°56 N, 131°55 E). At both sites, three to five green ash trees (diameters at breast height = 8–21 cm) with apparent symptoms of EAB infestations (crown declining, bark-splits, and D-shaped exit holes) were felled and the main trunk of each felled-tree was cut into meter-long logs prior to searching for EAB eggs.

To search for EAB eggs, flakes of bark on the meter-long logs from the trunks of the trees were gently removed with a utility knife and exposed EAB eggs were collected with a small brush and placed into 1.5 ml Eppendorf® snap-cap tubes. Depending upon the size (diameter) of the log and bark textures, an observer spent 15–60 min on each log searching for EAB eggs. All collected EAB eggs were later examined in the laboratory for parasitism under a stereomicroscope (2 – 3X magnification). EAB eggs with a yellowish or golden appearance and containing frass from hatched-neonate larvae were classified as unparasitized eggs, while parasitized EAB eggs with a darkened appearance were easily recognized. Parasitized EAB eggs were further classified into two categories: old parasitized eggs, each with a small adult parasitoid exit hole on the top of the egg, and viable (overwintering) parasitized eggs with no parasitoid exit holes, each containing a diapausing parasitoid larva.

The viable parasitized EAB eggs (with no parasitoid exit holes) collected in both 2010 and 2012 were hand-carried to the quarantine laboratory at the Beneficial Insects Introduction Research Unit (BIIRU) of the U.S. Department of Agriculture (USDA), Agricultural Research Service (Newark, Delaware) within seven days by JJD via commercial flights under the USDA APHIS PPQ permit (#P526P-10-01043). Upon arrival at the BIIRU quarantine laboratory, all the parasitized eggs were placed inside ventilated 1.5 ml micro-centrifuge tubes and stored in a 1.7 °C refrigerator for approximately 6 months (to break diapause) before they were incubated for adult emergence in a growth chamber under normal rearing conditions (25 ± 1.5 °C, 65 + 10% RH and 16:8h L:D photoperiod). EAB egg parasitism rates were calculated as the proportion of parasitized eggs (including both old and viable ones) relative to the total number of eggs collected from all the ash logs at each location. Adult parasitoids recovered from rearing in the laboratory were later described as the new species *O. primorskyensis* (Yao et al., 2016). Holotype specimens of *O. primorskyensis* were deposited at the Smithsonian National Museum of Natural History (Washington DC, USA) (Yao et al., 2016). The remaining paratype specimens were deposited at the USDA ARS BIIRU (Newark, Delaware, USA).

2.2. Quarantine host specificity testing

2.2.1. Parasitoid colony

Adults of *O. primorskyensis* used for host specificity testing at the USDA ARS BIIRU were the $F_{3–12}$ progeny of a founder colony collected in 2010 in the Russian Far East region near Vladivostok, which started with several F_0 individuals and had since been reared with EAB eggs (Larson and Duan, 2016). Before testing, naïve adult parasitoids were contained in 250 ml screw-cap jars (5–20 parasitoids per jar; Tri-State Plastics, Latonia, KY, USA) and maintained in environmental chambers (Percival Scientific, Perry, Iowa) at 25 (± 1) °C, with 65 ± 10% RH and 16:8 (L:D) hr. photoperiod. To provide the wasps with a source of food and water, thin streaks of non-diluted clover honey were applied to the inside wall of each jar with an insect pin.

2.2.2. Nontarget insects

To select non-target insects for host specificity testing with *O. primorskyensis,* we first considered phylogenetic affinities of the non-target species to EAB starting with the closely related taxa (e.g., *Agrilus* spp. in the family Buprestidae) to distantly related ones (e.g., wood-boring species in the family Cerambycidae and Curculionidae) within the order Coleoptera (Arnett, 1985; Evans et al., 2015). Secondly, we also considered similarities in oviposition behaviors between non-target insects and EAB so that *O. primorskyensis* was presented with a range of non-target insect eggs irrespective of relatedness to EAB. However, we point out that the centrifugal phylogenetic approach commonly used for selection of plants for testing host specificity of herbivorous insects (Wapshere, 1974) could not be strictly followed in our study due to the difficulty in finding adults and/or eggs of many insect species. A total of 30 non-target taxa belonging to three orders and six families were selected for testing. Two taxa outside the order Coleoptera, *Halyomorpha halys* Stål (Hemiptera: Pentatomidae) and *Heliothis virescens* (Fabricius) (Lepidoptera: Noctuidae) were included as negative controls in addition to a predatory ladybird beetle, *Coleomegilla maculata* (Coleoptera: Coccinellidae). All three of these species lay eggs on the surfaces of plant substrates. The remaining 27 species were species of wood-boring beetles (Coleoptera) belonging to the families Buprestidae, Cerambycidae, and Curculionidae. All of these species lay eggs under the bark or bark crevices (typically a few millimeters in depth) of their host plants. Of the wood-boring beetles, nine species were in the genus *Agrilus* (not including the target pest), and were thus closely related to the EAB. In addition, an unidentified species of weevil (Curculionidae) collected from honey locust was tested. Detailed information on the host plants, collection localities, and oviposition habitats for these non-target wood borers are presented in Table 1.

Eggs of all the wood-boring beetles in the family Buprestidae, Cerambycidae, and Curculionidae (except *Agrilus macer*) were freshly laid (< 7 days old) by field-collected adult beetles under laboratory conditions (20–25 °C, viable humidity and a photoperiod of 16:8h L:D). Eggs from most of these nontarget beetles were laid either on their host plant logs (15–22 cm long, 1.5–3.5 cm in diameter) wrapped with curling ribbon (0.5 cm width × 15–25 cm long) or on coffee filter papers according to methods described in Duan et al. (2011, 2013a) and Gould et al. (2018). However, some longhorned beetles such as *Anoplophora glabripennis* lay their eggs in pits in the stems of host plants, so host plant logs were not wrapped with curling ribbon for their oviposition. Egg masses of *A. macer* (unknown age) (laid on the bark surface) were collected in mid-June of 2017 by cutting off pieces of bark (1.5 cm width × 3 cm long) with a utility knife directly from the main trunk of hackberry trees (*Celtis laevigata* Willd.) and tested at USDA ARS BIIRU

Table 1
Non-target taxa, their host plants and location of collections for testing with *Oobius primorskyensis.*

Test species	Order/Family	Host Plant	Location of Collections	Oviposition Habitat
Agrilus anxius	Coleoptera: Buprestidae	Birch	Newark, DE	Bark crevice
Agrilus bilineatus	Coleoptera: Buprestidae	Red Oak	Newark, DE	Bark crevice
Agrilus cephalicus	Coleoptera: Buprestidae	Dogwood	Wilmington, DE	Bark crevice
Agrilus egenus	Coleoptera: Buprestidae	Freesia	Newark, DE	Bark crevice
Agrilus difficilis	Coleoptera: Buprestidae	Honey Locust	Newark, DE	Bark crevice
Agrilus fallax	Coleoptera: Buprestidae	Honey Locust	Newark, DE	Bark crevice
Agrilus macer	Coleoptera: Buprestidae	Hackberry	South Carolina	Exposed
Agrilus oblongus	Coleoptera: Buprestidae	Hackberry	Newark, DE	Bark crevice
Agrilus celti	Coleoptera: Buprestidae	Hackberry	Newark, DE	Bark crevice
Agrilus planipennis	Coleoptera: Buprestidae	Ash	ARS-BIIRU	Bark crevice
Aegomorphus modestus	Coleoptera: Cerambycidae	Birch/maple	southeastern MA	Pits in Bark
Analeptura lineola	Coleoptera: Cerambycidae	Birch	southeastern MA	Under ribbon
Anoplophora glabripennis	Coleoptera: Cerambycidae	Maple	ARS-BIIRU	Under bark
Anelaphus villosus	Coleoptera: Cerambycidae	Maple	southeastern MA	Under ribbon/on twig
Cyrtophorous verrucosus	Coleoptera: Cerambycidae	Red Oak	southeastern MA	under ribbon, coffee filter
Elaphidion mucronatum	Coleoptera: Cerambycidae	Maple	Newark, DE	under ribbon, coffee filter
Gaurotes cyanipennis	Coleoptera: Cerambycidae	Sumac/dogwood	southeastern MA	under ribbon
Judolia cordifera	Coleoptera: Cerambycidae	Unknown	southeastern MA	coffee filter
Megacyllene robiniae	Coleoptera: Cerambycidae	Black Locust	Newark, DE	Under bark
Monochamus scuttelatus	Coleoptera: Cerambycidae	White Pine	southeastern MA	Pits in Bark
Neoclytus acuminatus	Coleoptera: Cerambycidae	Ash	Newark, DE	Under bark
Neoclytus scutellaris	Coleoptera: Cerambycidae	Hickory/hackberry	Newark, DE	Under bark
Phymatodes aureus	Coleoptera: Cerambycidae	Dead oak	southeastern MA	coffee filter
Phymatodes testaceus	Coleoptera: Cerambycidae	Oak bark	southeastern MA	coffee filter
Tilloclytus geminatus	Coleoptera: Cerambycidae	Oak	Newark, DE	Under bark
Graphisurus fasciatus	Coleoptera: Cerambycidae	Maple	Newark, DE	Under bark
Xylotrechus colonus	Coleoptera: Cerambycidae	Oak	Newark, DE	Under bark
Unidentified weevil	Coleoptera: Curculionidae	Ash	Newark, DE	Bark crevice
Coleomegilla maculata	Coleoptera: Coccinellidae	N/A	ARS-Beltsville	Exposed
Halyomorpha halys	Hemiptera: Pentatomidae	Produce	ARS-BIIRU	Exposed
Heliothis virescens	Lepidoptera: Noctuidae	Tobacco	ARS-BIIRU	Exposed

Table 2
Taxa of non-target wood boring insects used in host specificity tests, number of replications and test eggs, and parasitism rate by the potential biological control agent *Oobius primorskyensis.* The target pest, *Agrilus planipennis*, was used in each paired test as a positive control (see text for explanation).

Test ID	Test Taxa	No. trials or replicates	No. test parasitoids	No. test eggs exposed to parasitoids	% Trials producing parasitism[a]	% Egg parasitism (Mean ± SE)[b]	Likelihood-Ratio X^{2}[c]	P-value[c]
1	*Agrilus anxius*	20	31	21	40.0	40.0 ± 11.2	0.441	0.5068
	Agrilus planipennis	20	31	21	30.0	30.0 ± 10.5		
2	*Agrilus bilineatus*	20	36	25	5.00	5.00 ± 5.00	13.403	0.0003
	Agrilus planipennis	20	36	25	55.0	55.0 ± 11.4		
3	*Agrilus cephalicus*	20	37	24	30.0	28.8 ± 10.1	0.205	0.6504
	Agrilus planipennis	20	32	24	36.8	36.8 ± 11.4		
4	*Agrilus egenus*	20	20	20	10.0	10.0 ± 6.90	22.44	< 0.0001
	Agrilus planipennis	20	20	20	85.0	85.0 ± 8.20		
5	*Agrilus difficilis*	16	16	16	0.00	0.00 ± 0.00	7.863	0.005
	Agrilus planipennis	16	16	16	31.3	31.3 ± 12.0		
6	*Agrilus fallax*	17	17	42	11.8	7.80 ± 6.10	15.793	0.0004
	Agrilus planipennis	17	17	39	76.5	70.1 ± 10.6		
7	*Agrilus macer*	12	21	177	25.0	16.8 ± 9.20	18.259	< 0.0001
	Agrilus planipennis	12	24	196	100	90.0 ± 2.10		
8	*Agrilus oblongus*	20	20	27	15.0	15.0 ± 8.20	9.069	0.0026
	Agrilus planipennis	20	20	34	60.0	54.0 ± 10.5		
9	*Agrilus celti*	6	6	6	0.00	0.00 ± 0.00	5.439	0.0197
	Agrilus planipennis	11	11	11	45.5	45.5 + 15.7		
10	*Aegomorphus modestus*	10	10	10	0.00	0.00 ± 0.00	8.63	0.0033
	Agrilus planipennis	10	10	10	50.0	50.0 ± 16.7		
11	*Analeptura lineola*	28	36	36	0.00	0.00 ± 0.00	21.779	< 0.0001
	Agrilus planipennis	14	14	16	57.1	57.1 ± 13.7		
12	*Anoplophora glabripennis*	20	20	20	0.00	0.00 ± 0.00	29.92	< 0.0001
	Agrilus planipennis	15	15	15	80.00	80.0 + 10.7		
13	*Anelaphus villosus*	20	20	20	0.00	0.00 + 0.00	7.648	0.0057
	Agrilus planipennis	20	20	20	25.0	25.0 + 9.90		
14	*Cyrtophorous verrucosus*	18	18	18	0.00	0.00 + 0.00	7.863	0.005
	Agrilus planipennis	16	16	16	31.25	31.3 + 12.0		
15	*Elaphidion mucronatum*	20	20	20	0.00	0.00 + 0.00	9.382	0.0022
	Agrilus planipennis	20	20	20	30.0	30.0 + 10.5		
16	*Gaurotes cyanipennis*	5	5	5	0.00	0.00 + 0.00	5.487	0.0192
	Agrilus planipennis	5	5	5	60.0	60.0 + 24.5		
17	*Judolia cordifera*	20	20	20	0.00	0.00 + 0.00	13.112	0.0003
	Agrilus planipennis	20	20	20	40.0	40.0 + 11.2		
18	*Megacyllene robiniae*	20	20	20	0.00	0.0 + 0.0	33.825	< 0.0001
	Agrilus planipennis	20	20	20	80.0	80.0 + 9.20		
19	*Monochamus scuttelatus*	5	9	5	0.00	0.00 + 0.00	6.733	0.0095
	Agrilus planipennis	5	10	5	60.0	60.0 + 16.3		
20	*Neoclytus acuminatus*	29	29	29	0.00	0.00 + 0.00	41.117	< 0.0001
	Agrilus planipennis	29	29	29	82.61	82.6 + 8.1		
21	*Neoclytus scuttelaris*	20	20	20	0.00	0.00 + 0.00	21.497	< 0.0001
	Agrilus planipennis	20	20	20	60.0	60.0 + 11.2		
22	*Phymatodes aureus*	6	6	6	0.00	0.00 + 0.00	12.636	< 0.0001
	Agrilus planipennis	6	6	6	100	100 + 0.00		
23	*Phymatodes testaceus*	20	20	20	0.00	0.00 + 0.00	9.382	0.0022
	Agrilus planipennis	20	20	20	30.0	30.0 + 10.5		
24	*Tilloclytus geminatus*	10	17	10	0.00	0.00 + 0.00	4.691	0.0303
	Agrilus planipennis	10	15	10	30.0	30.0 + 15.3		
25	*Graphisurus fasciatus*	5	10	5	0.00	0.00 + 0.00	5.487	0.0192
	Agrilus planipennis	5	10	5	60.0	60.0 + 24.5		
26	*Xylotrechus colonus*	30	33	31	0.00	0.00 + 0.00	25.891	< 0.0001
	Agrilus planipennis	30	33	32	50.0	50.0 + 9.30		
27	Unidentifed sp.	23	23	119	0.00	0.00 + 0.00	24.669	< 0.0001
	Agrilus planipennis	24	24	121	58.3	54.8 + 9.8		
28	*Coleomegilla maculata*	20	20	22	0.00	0.00 + 0.00	24.549	< 0.0001
	Agrilus planipennis	20	20	29	65.0	65.0 + 10.9		
29	*Halyomorpha halys*	20	20	20	0.00	0.0 0 + 0.00	15.128	0.0001
	Agrilus planipennis	20	20	24	45.0	45.0 + 11.4		
30	*Heliothis virescens*	20	20	20	0.00	0.00 + 0.00	21.949	< 0.0001
	Agrilus planipennis	29	20	20	60.0	60.0 + 11.2		

---

[a] Proportion of replicated trials producing parasitism in each test taxon was compared with that in positive (EAB) control with likelihood ratio Chi-square (Y^2) tests.

[b] For each test taxon, percentage parasitism rate was calculated for each trail and then used for calculation of the mean percentage parasitism and standard error (SE) across the replicated trials.

[c] X^2 values and type I error rates from likelihood ratio Chi-square (X^2) tests on the proportion of replicated trials producing parasitism in each test taxon against that in positive (EAB) control.

quarantine laboratory within 3 days of field collection.

2.2.3. Testing procedures

All trials were conducted under standard laboratory rearing conditions [25 ± 1.5 °C; photoperiod of 16:8h L:D] for *O. primorskyensis* as described in Larson and Duan (2016). Trials with different groups or taxa of non-target insects had to be conducted with different generations of *O. primorskyensis* at different times over a five and half year period (2013–2017) due to the logistical challenges of obtaining non-target species for testing. To control variation among trials with different taxa conducted at different times, the target host EAB eggs were included (or paired) as a positive control for each replicated trial of the test with a non-target taxon. Trials with the same non-target taxon and its positive EAB controls were conducted at the same time and normally completed in the same year.

Each test arena consisted of a clear screwcap vial (12 cm long × 1 cm in diameter, Tri-State Plastics, Latonia, KY, USA). Four or five thin streaks of non-diluted clover honey were applied to the inside of the vial wall with an insect pin as a food and water source for test parasitoids. For the non-target species laying individual eggs that were easily separated from each other, one or two test eggs (on pieces of their host tree bark, ~5 mm long × 5 mm width × < 1 mm thick) were presented to the same number of gravid naïve female parasitoids in each test arena (or replicate). In tests with *A. macer*, which lays eggs in tightly compacted masses, the entire egg mass (consisting of 12–17 eggs) on the surface of host tree bark (≈10 mm long × 5 mm width × 1 mm thick) was exposed to two gravid naïve female parasitoids. Throughout the study, the number of EAB eggs used as the positive control for each test were comparable to that of the tested nontarget species. The parasitoid exposure time was five days for all tests; the parasitoid-to-host ratio was approximately 1:1 for tests with the non-target species laying individual eggs and approximately 1:9 for tests with *A. macer* egg masses. Following the 5-day exposure to parasitoids, eggs of both EAB and non-target insects were reared for approximately six weeks under standard rearing laboratory conditions described earlier. By then, *O. primorskyensis* would have emerged as adults or diapaused as mature larvae in parasitized host eggs (Larson and Duan, 2016). Test eggs that died without yielding parasitoids were dissected to see if aborted parasitism had occurred (e.g., presence of parasitoid larval cadavers).

2.3. Data analysis

Throughout the study, a few test eggs of both EAB and non-target insects (< 5% of the exposed eggs) did not hatch, but showed no evidence of parasitism (i.e., containing no parasitoid cadavers). Those "unhatched" eggs were excluded from data analysis because their viability could not be confirmed. For tests with each taxon of nontarget insects, likelihood Chi-square tests were used to compare the proportion of replicated trials producing parasitism in the non-target taxon against that in positive (EAB) control (SAS Institute Inc., 2012). We did not statistically compare levels of parasitism between EAB and the non-target taxon mainly because some trials consisted of more than one test eggs and would violate the "independence" assumption of Chi-square tests. However, percentage parasitism rate was calculated for each trail and then used for calculation of the mean percentage parasitism and standard error (SE) across the replicated trials for each test taxon.

3. Results

3.1. Field EAB egg parasitism in the Russian Far East

A total of 131 and 50 EAB eggs were collected from infested ash trees in the Vladivostok area in 2010 and in the Vozdvizhenka area in 2012, respectively. Of the collected EAB eggs in the Vladivostok area, approximately 23% showed evidence of parasitism (dark in color); among the parasitized eggs, 66.7% had small adult wasp exit holes on the top or outward egg shell (n = 20) and 33.3% contained mature parasitoid larvae (n = 10). In contrast, approximately 44% of EAB eggs in the Vozdvizhenka area were parasitized; among the parasitized eggs, 22.7% (n = 5) had adult parasitoid exit holes and 77.3% (n = 17) contained mature parasitoid larvae. In both regions, *O. primorskyensis* was the only egg parasitoid reared from the parasitized EAB eggs in the Russian Far East.

3.2. Quarantine testing with non-target insects

Among all the non-target taxa tested, *O. primorskyensis* attacked seven out of nine *Agrilus* species (Table 2). The proportion of the trials producing parasitism by *O. primorskyensis* in two of the attacked species, *A. anxius* (40%) and *A. cephalicus* (30%) were comparable to that of their corresponding EAB (positive) control (29–37%) (Likelihood Chi-square tests, P = 0.5068 and 0.6504, respectively). However, the proportions of trials producing parasitism in the other five attacked *Agrilus* species (*A. bilineatus*, *A. egenus*, *A. fallax*, *A. macer*, and *A. oblongus*) were significantly less (4–17%) than those of trials with their respective EAB control (60–90%). Finally, no parasitism of *A. celti, A. difficilis* or any of the non-buprestid taxa was observed in these trials compared to 25–100% of EAB positive controls being parasitized (likelihood Chi-square tests, P < 0.05 for all tests with negative responses).

4. Discussion

Our field survey at two different sites in the Primorsky Krai region of Russian Federation revealed 23–44% of EAB egg parasitism rate with *O. primorskyensis* being the only parasitoid recovered from parasitized EAB eggs in the region. However, the difference in parasitism rate between the two locations (Vladivostok vs Vozdvizhenka area) could have resulted from different years of sampling, geographic range (~85 km apart) variation or both. Expanded field surveys to include more locations in the same year and the same locations in multiple years are needed to quantify both temporal and spatial variations in EAB egg parasitism by *O. primorskyensis* in this part of EAB's native range.

Previous field studies in Northeast China showed that EAB egg parasitism rates by the congener egg parasitoid *O. agrili* varied significantly among different years and locations from 12 to 62% (Liu et al., 2007; Wang et al., 2016). In fact, *O. agrili* is the only EAB egg parasitoid collected consistently in Jilin and Liaoning provinces of Northeast China. It is currently not known if the distribution of both *O. agrili* and *O. primorskyensis* overlap in Northeast Asia. However, recent laboratory studies reveal that *O. primorskyensis* diapause is obligatory or "pre-programed" in response to seasonal shortage of host eggs in the late summer, fall and winter. In contrast, *O. agrili* has evolved a facultative diapause, which is primarily induced by short-day photoperiod (Hoban et al., 2016). The difference in diapause behaviors between these two egg parasitoid species may in fact result in different phenology to synchronize with EAB oviposition in both their native or newly introduced regions. In addition, findings from our limited field surveys suggest that *O. primorskyensis* has the potential to inflict levels of EAB egg mortality comparable to that by *O. agrili*. Together, we suggest that the current EAB biocontrol programs may potentially benefit from the introduction of *O. primorskyensis* for protection of ash resources in North America.

Our quarantine testing with 30 taxa of nontarget insects, mostly native North American wood-boring insects in the family Buprestidae or Cerambycidae, showed that only *Agrilius* (seven out of nine) species are attacked by *O. primorskyensis,* with five of them being attacked significantly less than and two at the level of parasitism comparable to EAB. It is possible that *O. primorskyensis* may be restricted to the non-target species in the family Buprestidae, but further testing with eggs from other buprestid genera is needed to more fully understand the host specificity of *O. primorskyensis*. However, the fact that *O. primorskyensis* rejected all non-buprestid eggs in this study suggests that future host-range testing need not include additional taxa outside this family. Furthermore, we point out that laboratory host range testing can only be conducted at very limited spatial and temporal scales and often lacks the real ecological context. Therefore, there are always uncertainties associated with laboratory host range studies even if every single relevant non-target species is tested with the concerned biocontrol agent. Sound non-target risk assessment protocols need to factor in these uncertainties associated with the laboratory host range results.

Throughout the study, we noted a wide range of variation in EAB egg parasitism rates (25–100%) across tests with different non-target species, which were conducted over a period of five years (2013–2017) due to logistical challenges associated with collecting and rearing many non-target species. Currently, we do not know what has caused the large variation in EAB egg parasitism rates across tests with different non-target species. We speculate that variations in the quality of EAB eggs and/or parasitoids reared across the five-year study period for different tests may have contributed to the variation in EAB parasitism rates. As we used the "pair-wise" design of having separate EAB treatment alongside each test taxon for each trial, variations across different trials should have been accounted for and not greatly reduced our statistical power to detect the difference in parasitism rates between EAB and the tested non-target taxon.

Host-specificity testing with the EAB egg parasitoid *O. agrili*, as well as the larval parasitoids *S. galinae*, *S. agrili,* and *T. planipennisi*, suggests that the host ranges of these introduced Asiatic EAB parasitoids are limited to species closely related to EAB (Yang et al., 2008; Duan et al., 2015b; Federal Register, 2007, 2015). For example, *T. planipennisi*, a koinobiont endoparasitoid of EAB larvae, did not attack any of the 14 species of tested non-target insects including five species of *Agrilus* (Bauer et al., 2015), while the other three introduced idobionts, – *O. agrili, S. agrili, and S. galinae* – did attack some Asian and North American species of *Agrilus,* but not any other non-*Agrilus* beetles (Bauer et al., 2015; Duan et al., 2018). In addition, none of these three introduced EAB parasitoids attacked non-buprestid beetles in previous studies (Yang et al., 2008; Bauer et al., 2015; Duan et al., 2018). The predicted non-target impact from introduction of these Asiatic parasitoids including *O. primorskyensis* for EAB biocontrol would be limited to the potential use of some non-target *Agrilus* species as alternative hosts in North America.

There are approximately 3000 species of *Agrilus* worldwide, with about 175 species in the United States (Bellamy, 2008; Nelson et al., 2008). Based on the results of our host range testing, it is possible that *O. primorskyensis*, like the previously introduced *O. agrili* (as well as *S. agrili* and *S. galinae*), may use some non-target *Agrilus* species as alternative hosts in North America under conditions that mostly favor parasitism – e.g. the low presence of EAB hosts in the aftermath of an EAB outbreak. A recent analysis of the non-target impacts of introduced arthropod biocontrol agents showed that the potential to use the non-target species as alternative hosts under field conditions does not lead to the population level impact on the nontarget species in a majority of cases and causes no significant harm to the susceptible nontarget species (van Driesche and Hoddle, 2017). To date, field surveys of non-target insects associated with ash trees following field releases of introduced EAB parasitoids in Michigan and Maryland have found no evidence of attack on ash-associated non-target insects from any of these previously introduced parasitoids (Duan et al., 2013b; Jennings et al., 2016, 2017; Duan et al., 2017). So far, however, no surveys of non-target insects associated with non-ash tree species have been conducted.

In addition, the possibility of risk from the introduction of *O. primorskyensis* to the non-target *Agrilus* species in North America needs to be balanced against the potential benefit that could result from successful biological control of the emerald ash borer. EAB is decimating ash forests throughout eastern North America and continues to expand into new areas. Successful control of EAB in North America is clearly urgent and there is a tremendous potential for both economic and ecological benefits (Kovacs et al., 2010; Duan et al., 2018). Classical biological control via successful introduction and establishment of EAB parasitoids from Northeast Asia, the pest's native range, is one of the most sustainable and promising EAB management options that needs to be seriously considered. Unlike small larval parasitoids, which can only provide protection to small thin-barked trees (Abell et al., 2012)., egg parasitoids such as *O. primorskyensis*, as well as *O. agrili*, can effectively reduce the pest load regardless of tree size. An informative risk assessment and/or cost-benefit analysis based on the present study on the host range of *O. primorskyensis* and the potential benefit of the EAB biocontrol program is needed prior to potential introduction of this egg parasitoid for biological control of EAB in North America.

CRediT authorship contribution statement

Jian J. Duan: Conceptualization, Project administration, Supervision, Methodology, Resources, Formal analysis, Writing - original draft, Writing - review & editing. **Jonathan M. Schmude:** Data curation, Formal analysis, Methodology, Writing - review & editing. **Kristi M. Larson:** Data curation, Methodology, Writing - review & editing. **Roger W. Fuester:** Conceptualization, Writing - review & editing. **Juli R. Gould:** Methodology, Writing - review & editing. **Michael D. Ulyshen:** Methodology, Writing - review & editing.

Acknowledgments

We thank Galina Yurchenko (The Far East Forest Research Institute, Forest Management Agency of the Russian Federation, Khabarovsk, Post Code 680020, Russia) for assistance with our work in the Russian Far East. We are grateful to Deborah Miller (USDA Forest Service), Jason Hansen, Tim Watt and Ian Lane (Michigan State University, Dept. Entomology), Tony Capizzo, Cherie Keenan, Joseph Short, Jane Slater, Philip B. Taylor and Mike Vella (USDA Agricultural Research Service) for assistance in laboratory work and collection of non-target species. Kim Hoelmer (USDA Agricultural Research Service) for helpful comments on an early version of this manuscript. Finally, we acknowledge the cooperation, assistance and advice of Rob Line and Chris Bennett, DNREC Division of Parks and Recreation; Kenneth Reynolds and Bill McAvoy, DNREC Delaware Division of Fish & Wildlife; Jim Dobson and Marcia Fox, Blackbird State Forest; Dwight Anttila, Brandywine Creek State Park; Mike Moyer, Lums Pond State Park; Nick McFadden, White Clay Creek State Park; Andy Roy, Alapocas Run State Park; and Frank Graves, New Castle County. This project is supported by USDA ARS appropriated funds (CRIS Project # 8010-2200-028-00D).

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocontrol.2018.12.005.

References

Arnett, R.H., 1985. American Insects: A Handbook of the Insects of America North of Mexico. Van Nostrand Reinhold Company, New York.

Abell, K.J., Duan, J.J., Bauer, L.S., Lelito, J.P., Van Driesche, R.G., 2012. The effect of bark thickness on host partitioning between *Tetrastichus planipennisi* (Hymen: Eulophidae) and *Atanycolus* spp. (Hymen: Braconidae), two parasitoids of emerald ash borer (Coleop: Buprestidae). Biol. Control 63, 320–325.

Abell, K.J., Bauer, L.S., Duan, J.J., Van Driesche, R.G., 2014. Long-term monitoring of the introduced emerald ash borer (Coleoptera: Buprestidae) egg parasitoid, *Oobius agrili* (Hymenoptera: Encyrtidae), in Michigan, USA and evaluation of a newly developed monitoring technique. Biol. Control 79, 36–42.

Aukema, J.E., McCullough, D.G., Von Holle, B., Liebhold, A.M., Britton, K., Frankel, S.J., 2010. Historical accumulation of non-indigenous forest pests in the continental United States. Bioscience 60, 886–897.

Boyd, I.L., Freer-Smith, P.H., Gilligan, C.A., Godfray, H.C., 2013. The consequence of tree pests and diseases for ecosystem services. Science 342, 823.

Bellamy, C.L., 2008. A World Catalogue and Bibliography of the Jewel Beetles (Coleoptera: Buprestoidea), Pensoft Series Faunistica, vol. 76–79, vol. 1–4. Pensoft Publishers, Sofia-Moscow, Russia.

Bauer, L.S., Liu, H.P., Miller, D.L., Gould, J., 2008. Developing a biological control program for emerald ash borer (*Agrilus planipennis*), an invasive ash pest in North America. Michigan Entomol. Soc. Newslett. 53, 38–39.

Bauer, L.S., Duan, J.J., Gould, J.R., Van Driesche, R.G., 2015. Progress in the classical biological control of *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae) in North America. Can. Entomol. 147, 300–317.

CFIA. Canadian Food Inspection Agency, 2018. Emerald Ash Borer. < http://www.inspection.gc.ca/plants/plant-pests-invasive-species/insects/emerald-ash-borer/eng/1337273882117/1337273975030 > (accessed 29.01.18).

Desneux, N., Barta, R.J., Hoelmer, K.A., Hopper, K.R., Heimpel, G.E., 2009. Multifaceted determinants of host specificity in an aphid parasitoid. Oecologia 160, 387–398.

Davidson, W., Rieske, L.K., 2016. Establishment of classical biological control targeting emerald ash borer is facilitated by use of insecticides, with little effect on native arthropod communities. Biol. Control 101, 78–86.

Duan, J.J., Watt, T., Oppel, C.B., 2011. An alternative host plant-based method for laboratory rearing of emerald ash borer to produce larval parasitoids for biological control. In: Parra, G., Lance, D., Mastro, V., Reardon, R., Benedict, C. (Eds.), Proceedings of Emerald Ash Borer Research and Technology Meeting, October 10–23, 2011, Wooster Ohio. USDA Forest Service/APHIS/FHTET-2011-06, pp. 3.

Duan, J.J., Watt, T., Larson, K., Taylor, P., Lelito, J.P., 2013a. Effects of ambient temperature on egg and larval development of the invasive emerald ash borer (Coleoptera: Buprestidae): implications for laboratory rearing. J. Econ. Entomol. 106, 2101–2108.

Duan, J.J., Bauer, L.S., Abell, K.J., Lelito, J.P., Van Driesche, R.G., 2013b. Establishment and abundance of *Tetrastichus planipennisi* (Hymenoptera: Eulophidae) in Michigan: potential for success in classical biocontrol of the invasive emerald ash borer (Coleoptera: Buprestidae). J. Econ. Entomol. 106, 1145–1154.

Duan, J.J., Bauer, L.S., Abell, K.J., Ulyshen, M.D., Van Driesche, R.G., 2015a. Population dynamics of an invasive forest insect and associated natural enemies in the aftermath of invasion: implications for biological control. J. Appl. Ecol. 52, 1246–1254.

Duan, J.J., Gould, J.R., Fuester, R.W., 2015b. Evaluation of the host specificity of *Spathius galinae* (Hymenoptera: Braconidae), a larval parasitoid of the emerald ash borer (Coleoptera: Buprestidae) in Northeast Asia. Biol. Control 89, 91–97.

Duan, J.J., Bauer, L.S., Van Driesche, R.G., 2017. Emerald ash borer biocontrol in ash saplings: The potential for early stage recovery of North American ash trees. For. Ecol. Manage. 394, 64–72.

Duan, J.J., Bauer, L.S., Van Driesche, R.G., 2018. Progress and challenges of protecting North American ash trees from the emerald ash borer using biological control. Forests 9 (142), 1–17. https://doi.org/10.3390/f9030142.

Emerald Ash Borer Information, Emerald ash borer information network, 2018. < http://www.emeraldashborer.info/ > (accessed 18.03.18).

Evans, A.M., Mckenna, D.D., Bellamy, C.L., Farrell, C.L., 2015. Large-scale molecular phylogeny of metallic wood-boring beetles (Coleoptera: Buprestoidea) provides new insights into relationships and reveals multiple evolutionary origins of the larval leaf-mining habit. System. Entomol. 40, 385–400.

Follett, P.A., Duan, J.J., 2000. Nontarget Effects of Biological Control. Kluwer Academic Publisher, Boston/Dordrecht/London, USA, pp. 316.

Federal Register Availability of an environmental assessment for the proposed release of three parasitoids for the biological control of the emerald ash borer (Agrilus planipennis) in the continental United States Federal Register 72: 28947–28948 [Docket No. 2007 APHIS-2007-006].

Federal Register, 2015. Availability of an environmental assessment for field release of the parasitoid Spathius galinae for the biological control of the emerald ash borer (Agrilus planipennis) in the contiguous United States. Fed. Regist. 80: 7827–7828, [docket number APHIS–2014–0094] < https://www.regulations.gov/docket?D=APHIS-2014-0094 > (accessed 18.12.17).

Gould, J.R., Aflague, B., Murphy, T.C., McCartin, L., Elkinton, J.D., Rim, K., Duan, J.J., 2018. Collecting non-target wood-boring insects for host-specificity testing of natural enemies of cerambycids: a case study with Dastarcus helophoroides (Coleoptera: Bothrideridae), a parasitoid of the Asian longhorned beetle (Coleoptera: Cerambycidae). Environ. Entomol. 47, 1440–1450.

Haack, R.A., Jendek, E., Liu, H.P., Marchant, K.R., Petrice, T.R., Poland, T.M., Ye, H., 2002. The emerald ash borer: a new exotic pest in North America. Newslett. Michigan Entomol. Soc. 47, 1–5.

Hoban, J., Duan, J.J., Hough-Goldstein, J., 2016. Effects of temperature and photoperiod on the reproductive biology and diapause of *Oobius agrili* (Hymenoptera: Encyrtidae), an egg parasitoid of emerald ash borer (Coleoptera: Buprestidae). Environ. Entomol. 45, 726–731. https://doi.org/10.1093/ee/nvw034.

Herms, D.A., McCullough, D.G., 2014. Emerald ash borer invasion of North America: history, biology, ecology, impact and management. Ann. Rev. Entomol. 59, 13–30.

Jennings, D.E., Duan, J.J., Bean, D., Gould, J.R., Kimberly, A.R., Shrewsbury, P.M., 2016. Monitoring the establishment and abundance of introduced parasitoids of emerald ash borer larvae in Maryland, U.S.A. Biol. Control 101, 138–144.

Jennings, D.E., Duan, J.J., Bean, D., Kimberly, A.R., Williams, G.L., Bells, S.K., Shurtleff, A.S., Shrewsbury, P.M., 2017. Effects of the emerald ash borer invasion on the community composition of arthropods associated with ash tree boles in Maryland, U.S.A. Agric. For. Entomol. 19, 122–129. https://doi.org/10.1111/afe.12186.

Kovacs, K.F., Haight, R.G., McCullough, D.G., Mercader, R.J., Siegert, N.W., Liebhold, A.M., 2010. Cost of potential emerald ash borer damage in US communities, 2009–2019. Ecol. Econ. 69, 569–578.

Larson, K.M., Duan, J.J., 2016. Differences in the reproductive biology and diapause of two congeneric species of egg parasitoids (Hymenoptera: Encyrtidae) from northeast Asia: Implications for biological control of the invasive emerald ash borer (Coleoptera: Buprestidae). Biol. Control 101, 39–115.

Liu, H.P., Bauer, L.S., Miller, D.L., Zhao, T.H., Gao, R.T., Song, L., Luan, Q., Jin, R., Gao, C., 2007. Seasonal abundance of *Agrilus planipennis* (Coleoptera: Buprestidae) and its natural enemies *Oobius agrili* (Hymenoptera: Encyrtidae) and *Tetrastichus planipennisi* (Hymenoptera: Eulophidae) in China. Biol. Control 42, 61–71.

Mapbiocontrol, 2018. Agent release tracking and data management for federal, state, and researchers releasing three biocontrol agents released against emerald ash borer. http://www.mapbiocontrol.org/.

Nelson, G.H., Walters, G.C., Haines, D.R., Bellamy, C.L., 2008. A catalog and bibliography of the Buprestoidea of America North of Mexico. Coleopterists Society Special Publication No. 4., The Coleopterists Society, Nevada City, California, USA.

Pimentel, D., 1986. Biological invasions of plants and animals in agriculture and forestry. In: Mooney, H.A., Drake, J.A. (Eds.), Ecology of Biological Invasions of North America and Hawaii, Ecological Studies 58. Springer-Verlag, New York, pp. 149–162.

SAS Institute Inc., 2012. JMP Pro 10.0.1 Introductory Guide. SAS Institute Inc, SAS Campus Drive, Cary NC 27513, USA.

USDA APHIS, 2007. Proposed release of three parasitoids for the biological control of the emerald ash borer (Agrilus planipennis) in the continental United States: environmental assessment (document ID" APHIS-2007-0060-044). http://www.regulations.gov/#!docketDetail;D=APHIS-2007-0060-0044.pdf.

van den Bosch, R., Messenger, P.S., Gutierrez, A.P., 1982. An Introduction to Biological Control. Plenum Press, New York.

van Lenteren, J.C., Loomans, A.J.M., 2006. Environmental risk assessment: methods for comprehensive evaluation and quick scan. In: Bigler, E., Babemdreoer, D., Kuhlmann, U. (Eds.), Environmental Impact of Invertebrates for Biological Control of Arthropods: Methods and Risk Assessment. CABI Publishing, CAB Internonal Wallingford, Oxon, UK, pp. 254–272.

Van Driesche, R.G., Carruthers, R.I., Centers, T., Hoddle, M.S., Hough-Goldstein, J., Morin, L., 2010. Classical biological control for the protection of natural ecosystems. Biol. Control 45, 52–533.

Van Driesche, R.G., Hoddle, M., 2017. A review of nontarget effects of insect biological control agents: concepts and examples. In: United States Department of Agriculture, Forest Service, Forest Health Technology Enterprise Team, FHTET-2016-02. Morgantown, West Virginia, P. 127.

Wapshere, A.J., 1974. A strategy for evaluating the safety of organisms for biological control. Ann. of Appl. Biol. 77, 201–211.

Wang, X.Y., Cao, L.M., Yang, Z.Q., Duan, J.J., Gould, J.R., Bauer, L.S., 2016. Natural enemies of emerald ash borer (Coleoptera: Buprestidae) in northeast China, with notes on two species of parasitic Coleoptera. Can. Entomol. 148, 329–342.

Yang, Z.-Q., Wang, X.-Y., Gould, J.R., Wu, H., 2008. Host specificity of *Spathius agrili* Yang (Hymenoptera: Braconidae), an important parasitoid of the emerald ash borer. Biol. Control 47, 216–221.

Yao, Y.X., Duan, J.J., Hopper, K.R., Mottern, J.L., Gates, M.W., 2016. A new species of *Oobius* Trjapitzin (Hymenoptera: Encyrtidae) from the Russian Far East that parasitizes eggs of emerald ash borer (Coleoptera: Buprestidae). Ann. Entomol. Soc. Am. 106, 629–638.

Yao, Y.X., Duan, J.J., Mottern, K.R., Wang, J.L., Yang, X.-Y., Bauer, Z.Q., Gates, L.S., 2018. Two new species of Oobius (Hymenoptera: Encyrtidae) and their phylogenetic relationship with other congeners from northeastern Asia. Can. Entomol. 150, 303–316.