Interspecific Competition Between Idiobiont Larval Parasitoids of Emerald Ash Borer

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Abstract New associations between parasitoid species is common in biological control with interactions ranging from coexistence to competitive exclusion. *Spathius agrili* and *Spathius galinae*, native to North East Asia, are two host-specific idiobiont larval parasitoids of the invasive emerald ash borer *Agrilus planipennis* that do not overlap in their native ranges but have been recently introduced to the United States for biocontrol of *A. planipennis*. We conducted laboratory experiments to determine the results of competition between these two species. Competition between parasitoid larvae on a single host (intrinsic competition) and competition between adult parasitoids for oviposition sites (extrinsic competition) were evaluated. Successful multiparasitism did not occur in any intrinsic trials. Extrinsic competition favored *S. agrili*, but *S. galinae* was not excluded. Competition lowered parasitism rates for both species, but overall parasitism was not lowered.

Keywords Novel interactions · Biological control · Competition · Parasitoids · Interspecific interactions · Braconidae

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Introduction

Ecological theory suggests that strong interspecific competition is a likely outcome when two or more species of highly host-specific parasitoids from the same feeding guild (e.g., attacking the same host stage) are introduced to an area against the same target pest (Godfray 1994; Mills 2006). This interspecific competition can occur intrinsically between immature parasitoids on a host or extrinsically between adults searching for similar host resources (Godfray 1994; Mills 2006; Wang et al. 2008). Multiple species of parasitoids are often introduced in a classical biological control program for an invasive pest (Smith 1929; Myers et al. 1989; Hajek 2004). These parasitoids are selected for a high degree of host specificity with the invasive pest and a narrow host range (Debach and Rosen 1991). These selection criteria may lead to strong interspecific competition when novel interactions occur (Hajek 2004). Outcomes of interspecific competition can range from competitive exclusion to coexistence, due to successful niche partitioning, thus having serious consequences in biological control of the targeted pest (DeBach 1966; Collier and Hunter 2001; Hajek 2004).

Emerald ash borer (EAB) *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae) is an invasive beetle accidentally introduced to Michigan in the 1990's from Asia where it feeds on ash trees (*Fraxinus* spp.) (Cappaert et al. 2005; Bray et al. 2011; Siegert et al. 2014). Since its introduction EAB has spread to over

35 US states and five Canadian provinces, and caused widespread mortality across North America (Emerald Ash Borer Information 2019). Chemical control options exist for residential or high value trees, but are not suitable for forest settings or ecosystem level control (Mercader et al. 2015). Four hymenopteran biological control agents of the emerald ash borer have been approved for release and introduced to North America (Canadian Food Inspection Agency 2020a; Federal Register 2007): two larval idiobiont ectoparasitoids, *Spathius agrili* Yang (Hymenoptera: Braconidae) and *Spathius galinae* Belokobylskij and Strazanac (Hymenoptera: Braconidae), one larval koinobiont endoparasitoid, *Tetrastichus planipennisi* Yang (Hymenoptera: Eulophidae), and one solitary egg parasitoid, *Oobius agrili* Zhang (Hymenoptera: Encyrtidae). The two congener species, *S. agrili* and *S. galinae*, share many life history traits that could lead to competitive interference between species. Both species are idiobiont larval parasitoids, paralyzing their host upon attack, and attack the same late stages (3rd–4th instar) of EAB larvae (Yang et al. 2006, 2010; Belokobylskij et al. 2012; Duan et al. 2014; Watt and Duan 2014).

Since initial approval by regulatory agencies these parasitoids have been released in over 28 US states and three Canadian provinces (Duan et al. 2018; MapBiocontrol 2019; Canadian Food Inspection Agency 2020b). Currently *T. planipennisi* and *O. agrili* have established self-sustaining populations in areas of the Midwest, mid-Atlantic, and northeastern US (Duan et al. 2013; Davidson and Rieske 2016; Jennings et al. 2016). No published study has reported establishment of *S. agrili* at any release site (MapBiocontrol 2019). *Spathius galinae* has established abundant self-sustaining populations at several sites in the northeastern US 2 years post-release, but it is too early to evaluate its establishment and impact in other recently released regions (Duan et al. 2019).

Prior studies have addressed competition for larval resources between *T. planipennisi* and *S. agrili* or *S. galinae*, which indicated that competition would likely be a minimal factor towards establishment in either case (Yang et al. 2012, 2013). Consumptive competition leading to exclusion may occur between parasitoid species utilizing the same host resources (Schoener 1983). However, emerald ash borer larvae which have already been parasitized by *S. agrili* or

S. galinae are still susceptible to multiparasitism by *T. planipennisi* for 48 h after the initial parasitization by *Spathius* (Yang et al. 2012, 2013; Wang et al. 2015). Competition between *S. agrili* and *S. galinae* adults had been observed anecdotally at the USDA ARS Beneficial Insect Introduction Unit (BIIRU) in Newark, DE, which indicated a strong response favoring *S. agrili* (JJD unpublished data).

In the present study, we evaluate the potential competition between *S. agrili* and *S. galinae* for host resources via interactions on the same parasitized host (consumptive and intrinsic competition), or via the same host larva by adult parasitoids (extrinsic competition). Specifically, in sequential trials we aim to determine if either species of *Spathius* can distinguish between a healthy host or a parasitized host, if consumptive competition excludes either species, or if multiparasitism can occur. In simultaneous trials we aim to determine the result of competition between adult parasitoids for the same host larva for oviposition.

Materials and methods

Host larvae and substrate

All EAB larvae used in the competition experiments were 4th instar reared by the USDA ARS BIIRU in Newark, DE. Larvae were reared from eggs in tropical ash, *Fraxinus uhdei* Wenz., bolts (1–2 cm diam, 20–25 cm length) using the methods described in Duan et al (2012). In order to standardize larval density, and ensure an exact parasitoid to host ratio, the 4th instar EAB were reared in tropical ash bolts, dissected out live, then individually inserted into new bolts cut from green ash trees, *Fraxinus pennsylvanica*, Marshal. Bolts of green ash (1–2 cm diam, 15 cm length) were cut from naturally grown trees at the USDA BIIRU. A flap of outer bark (3–4 cm long) was peeled from each bolt, and an artificial EAB gallery was carved into the phloem tissue using a gouge chisel (Palm Block Size #11, ChippingAway). A single larva was then inserted into each artificial gallery and covered with the bark flap, which was secured with two thin Parafilm strips. The bottom 1 cm of each bolt was wrapped in tightly wound paper towel and secured in a small 113 ml sample cup (4 oz Medline Polypropylene Specimen Container, Medline) filled with rock

wool (Rockwool) saturated with tap water, and then capped with Parafilm to prevent desiccation. Inserted larvae were left to feed for 24 h and then checked for feeding activity prior to use in the experiments. Larvae that did not show any feeding activities 24 h after insertion were discarded. All competition trials were conducted in a clear butyrate tube (63 mm diam, 20–40 cm height, Thermoplastic Processes), which was friction-fit over the plastic sample cup containing the artificially infested bolt. A single green ash bolt containing one inserted 4th instar EAB larva was then used in each replicate of exposure to adult parasitoids and thus represents an independent experimental unit in different experiments.

Adult parasitoids

Both species of parasitoids used in this experiment have a pre-oviposition period, *S. agrili* of 11–20 days (Gould et al. 2011), and *S. galinae* of 5 days (Watt and Duan 2016). Additionally, the fecundity of *S. galinae* peaks 2–3 weeks post-eclosion (Duan et al. 2014). Therefore, all adult parasitoids used

in this experiment were naïve gravid females 2–3 weeks post-emergence in order to maximize chances of parasitism. *Spathius galinae* were reared by the BIIRU in Newark DE according to procedures described in Duan et al. (2014), whereas *S. agrili* were reared by the USDA APHIS PPQ Biological Control Production Facility in Brighton, MI according to methods described in Gould et al. (2011). *Spathius agrili* adults were shipped overnight in an insulated cooler and acclimated to experimental conditions for at least 48 h prior to use.

Sequential exposures

We used sequential exposures to evaluate intrinsic and consumptive competition between *S. agrili* and *S. galinae*. For each experiment five groups were established based on four staggered time-between-exposures to the *S. galinae* with a non-parasitized control group (Fig. 1). To ensure a high likelihood of parasitism in a short exposure time a 10:1 parasitoid:host ratio was used for parasitism by *S. agrili*, based on the rearing methods outlined in Gould et al. (2011)

Fig. 1 Sequential exposure trial for intrinsic competition. All experimental treatment groups were exposed to 10 gravid females (of either *S. agrili* or *S. galinae*) for 24 h to create a high likelihood of parasitism. After a delay of 0, 1, 3 or 5 days,

likely parasitized EAB larvae were exposed to 2 gravid females of the opposite species for 7 days. The control group was not exposed to the first species

and Duan et al. (2014). Each bolt of green ash with a single EAB larvae inserted were first exposed to 10 gravid female *S. agrili* for 24 h. These parasitized larvae were divided into four treatment groups based on staggered exposure to two *S. galinae* adults: (1) immediate exposure to *S. galinae*, (2) a 1-day delay, (3) a 3-day delay, and (4) a 5-day delay. At the corresponding time, a control group of non-parasitized EAB were exposed to *S. galinae*. Exposure to adults of *S. galinae* lasted for seven days for each of the staggered treatments. Each of the staggered exposure treatments with *S. galinae* was repeated 20 times.

A second round of this experiment was performed with the order of exposure reversed, exposing each green ash bolt with a single EAB larva inserted to 10 *S. galinae* for 24 h, followed with exposure to two *S. agrili* at staggered times for one week. These staggered-exposure trials with *S. agrili* were repeated 12 times for each treatment. The reduced number of replicates was due to a lack of available EAB larvae. Emergence of adult wasps from all treatments was observed for 8 weeks.

Once eight weeks had passed, bolts from all replicates were dissected using a sharp utility knife to peel the outer bark. Larval remains were dissected under a dissecting microscope for evidence of multiparasitism (parasitoid larvae). Each EAB larva was scored as alive (escaped parasitism), dead (unknown causes), successfully parasitized by *S. agrili*, successfully parasitized by *S. galinae*, or parasitized by both. Species were identified by morphologically distinct wing patterning. Unemerged larvae were to be identified using molecular methods, but none were present in non-control trials.

Simultaneous exposures

We used simultaneous exposures to evaluate extrinsic (adult) competition between *S. agrili* and *S. galinae*. Three treatment groups of parasitoid exposures were created: (1) A control group of two *S. agrili*, (2) a control group of two *S. galinae*, and (3) the competition group containing one *S. agrili* and one *S. galinae*. Each group of adult parasitoids was provided with one inserted EAB larvae in a green ash bolt for 7 days. At the end of 7 days the adult parasitoids were removed. The emergence of the parasitoid progeny in each test arena was observed

three times per week for 8 weeks. Once 8 weeks had passed, bolts were dissected and each EAB larva was scored using the methods described above. The three groups of parasitoids exposure treatments were replicated 31 times each.

Statistical analysis

No multiparasitism events were detected during bolt dissections in either sequential or simultaneous trials. Larvae which were scored “dead (unknown causes)” were excluded from all data analysis due to concerns that the reinsertion process can cause delayed mortality. Larvae which escaped parasitism (scored “alive”) were excluded because no competition event occurred.

Consumptive competition results from the sequential exposure were analyzed using a generalized linear model (GLM) with a binomial distribution (parasitism by test species/pre-exposure species). Successful parasitism by the test species (second species exposed) was analyzed using the same GLM procedure to determine if there was any effect of delay in pre-exposure time (0, 1, 3, or 5 days) on parasitism by the test species. If no difference was detected, all sequential exposures to the second species were grouped and parasitism success was then analyzed against the control (no second species exposure) group using the same GLM model with binomial distribution.

EAB fate during the extrinsic competition was analyzed in four parts, all using logistic regression analyses: (1) Comparisons between the competition group and both control groups to determine differences in species-specific parasitism success, (2) comparisons between the competition group and the *S. agrili* control group to determine differences in *S. agrili* parasitism success, (3) comparisons between the competition group and the *S. galinae* control group to determine differences in *S. galinae* parasitism success, and (4) comparisons between the competition group and both control groups to determine parasitism success regardless of species. Data were analyzed using SAS JMP Pro 14.0.0 (SAS Institute 2019).

Results

Consumptive competition

In both staggered exposure tests there were significant differences in the probability of successful parasitism by the test (second) species between pre-exposed larvae and control (healthy) larvae. In the test with pre-exposure to *S. agrili* followed by *S. galinae*, exposure to *S. agrili* almost completely excluded *S. galinae* regardless of the sequential exposure delay (Table 1). Number of days after exposure to *S. agrili* had no effect on the probability of parasitism by *S. galinae* (likelihood ratio $\chi^2=0.219$; $df=1$; $P=0.6401$). Any pre-exposure to *S. agrili* significantly decreased the probability of parasitism by *S. galinae* (likelihood ratio $\chi^2=31.204$; $df=1$; $P<0.0001$).

Pre-exposure to *S. galinae* followed by *S. agrili* decreased probability of parasitism by *S. agrili*; however, *S. agrili* was still able to parasitize larvae in all trials (Table 1). Number of days after exposure to *S. galinae* had no effect on the probability of parasitism by *S. agrili* (likelihood ratio $\chi^2=0.527$; $df=1$; $P=0.4679$). Any pre-exposure to *S. galinae* significantly decreased the probability of parasitism

by *S. agrili* (likelihood ratio $\chi^2=18.386$; $df=1$; $P<0.0001$).

Intrinsic competition

Multiparasitism was not observed in any bolt or larval dissection. Parasitoid larvae were only observed in one control bolt which had only been exposed to *S. galinae*.

Extrinsic competition

Species-specific parasitism success (a parasitoid developing to the adult stage from a larval host) was impacted by competition between *S. agrili* and *S. galinae* adults (likelihood ratio $\chi^2=38.80$; $df=6$, $P<0.0001$). Competition lowered the probability of parasitism success by *S. agrili* compared to *S. agrili*-only control (likelihood ratio $\chi^2=8.636$; $df=3$, $P=0.0345$) (Table 2). Competition also lowered the probability of parasitism success by *S. galinae* compared to *S. galinae*-only control (likelihood ratio $\chi^2=16.62$; $df=3$, $P=0.0008$) (Table 2). Competition did not affect the overall probability of parasitism of EAB larvae (likelihood ratio $\chi^2=0.102$; $df=2$, $P=0.9501$) (Table 2).

Table 1 Parasitism of EAB larvae by *S. agrili* and *S. galinae* when exposed to a single pre-exposed (likely parasitized by the opposite species) larvae at staggered time intervals

Treatment	Pre-exposure by <i>S. agrili</i>		Pre-exposure by <i>S. galinae</i>	
	# of replicates	% Parasitism (<i>S. galinae</i>)	# of replicates	% Parasitism (<i>S. agrili</i>)
No delay	12	0	10	18.2
One-day delay	11	0	10	10.0
Three-day delay	17	5.9	10	20.0
Five-day delay	8	0	10	18.2
Unparasitized control	14	42.9*	11	80*

Asterisk indicates significant difference from other groups within column (Generalized Linear Model, $P<0.05$)

Table 2 Parasitism of EAB larvae to *S. agrili* and *S. galinae* when under extrinsic competition, exposed to a single EAB larvae simultaneously

	# of replicates	<i>S. agrili</i> % parasitism	<i>S. galinae</i> % parasitism	Overall % parasitism
Competition	28	33.3*	16.67*	54.17
<i>S. agrili</i> control	28	58.33	–	58.33
<i>S. galinae</i> control	28	–	54.55	54.55

Asterisks indicate groups which differed from control within column (Logistic Regression, $P<0.05$)

Discussion

Our experiments determined extrinsic competition occurred between *S. agrili* and *S. galinae*, thus lowering species-specific parasitism of EAB larvae by both species. There was no significant difference in parasitism success of either species and neither completely excluded the other. Intrinsic competition did not occur because pre-exposure to a parasitoid prevented any parasitism by a subsequent species. In previous studies of competition between either *S. agrili* or *S. galinae* and *T. planipennisi*, an endoparasitoid of EAB, multiparasitism occurred rarely in a brief window after initial attack (Yang et al. 2012, 2013). Multiparasitism between these species was possible due to *T. planipennisi* not paralyzing larvae after oviposition and *Spathius* relying on feeding vibrations to locate hosts (Ulyshen et al. 2011; Yang et al. 2012, 2013). Because both species of *Spathius* paralyze their host larva upon oviposition, multiparasitism was unlikely to occur and never occurred in our experiments. Based on this, competition between *S. agrili* and *S. galinae* larvae in field settings is extremely unlikely to occur.

Consumptive competition in the sequential exposure experiments revealed differences in the two *Spathius* species. A 24-h exposure to *S. agrili* nearly excluded *S. galinae* from successfully parasitizing a host (Table 1). With the order reversed, *S. galinae* reduced the successful parasitism of *S. agrili*, to a lesser extent, with 10–18% of EAB larvae still being available for parasitism by *S. agrili* after exposure to *S. galinae*. From our results we cannot determine if this is due to: (1) *S. agrili* larvae fully consuming the larvae of *S. galinae* prior to dissection, (2) if *S. galinae* did not detect the EAB larvae, or (3) chose not to attack the EAB larvae.

When extrinsically competing for a single EAB larva, both species together were less successful than when they were alone. Both species were equally successful, neither outcompeting the other. Overall parasitism of EAB larvae was not negatively affected by competition. A nominally higher ratio of *S. agrili* succeeded, although this difference was not statistically significant. This is a positive result for EAB biological control and indicates that these two species can coexist in regions where they overlap.

Competition between congener parasitoids could result in competitive exclusion from a number of

advantages, assuming the species do not partition their host resources. The outcome of competition could be determined by the early-acting-superiority (Wang et al. 2003), life history strategies (Wang and Messing 2004), or host-feeding on parasitized hosts (Collier and Hunter 2001). In the case of *S. agrili* and *S. galinae*, it appears that the competitive advantage of the faster acting species dictated the winner of the competition. In other wood boring beetle systems, niche partitioning by host life stage or habitat (i.e. bark thickness) mitigated negative competitive effects (Hanks et al. 2001). Unfortunately, in the case of *S. agrili* and *S. galinae*, they both occupy the same niche of parasitizing 3rd to 4th instar EAB larvae (Yang et al. 2006, 2010; Belokobylskij et al. 2012; Duan et al. 2014; Watt and Duan 2014). Additionally, bark thickness did not restrict either species (Gould et al. 2011; Murphy et al. 2017), despite *S. galinae* having a longer ovipositor than *S. agrili* (Yang et al. 2006; Belokobylskij et al. 2012).

Even though competitive interference reduced the individual success of both *S. agrili* and *S. galinae* in this experiment, the ecological implications of this interaction may be limited. In field settings EAB larval density can be as high as 46 EAB larvae per m² at peak infestation (Duan et al. 2015). With such high host density in areas where EAB has established, competition for limited larval resources is mostly irrelevant to parasitoid establishment. In new and emerging areas of infestation, competition may play a larger role in successful establishment. With no instances of successful multiparasitism under this extremely host-limited scenario, there will be no measurable intrinsic competition effects in the field. Future research will observe these trends in field conditions to determine if competition affects success and establishment, and if niche partitioning occurs through novel means.

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Declarations

Conflict of interest None.

Data availability Available upon request.

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