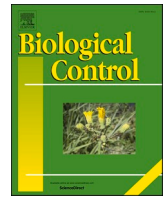




Comparative responses of two congeneric larval parasitoids of emerald ash borer to ambient temperatures: Implications for biocontrol introduction

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Perspective

Comparative responses of two congeneric larval parasitoids of emerald ash borer to ambient temperatures: Implications for biocontrol introduction

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HIGHLIGHTS

- *Spathius agrili* (SA) and *S. galinae* (SG) are larval parasitoids of invasive emerald ash borer (EAB).
- SA attacked higher proportion of hosts (90.0 and 25.67%) than SG (46.43 and 0%) at 28.9 and 32.8 °C.
- SA also developed faster and emerged around 9 days earlier than SG at 21.1 – 28.9 °C.
- Low temperature (17.2 °C) exposure effectively induced larval diapause of both *Spathius* species.
- SA is expected to perform better in warmer climate conditions than SG for biocontrol of EAB.

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ABSTRACT

Understanding how climate influences the establishment of introduced species is critical to classical biological control programs against insect pests. Even closely related species with similar life histories may establish and perform differently in new environments due to different responses to ambient temperature. Here we compared the host attack rate and immature development of two congeneric larval parasitoids of emerald ash borer (EAB) *Agrilus planipennis* Fairmaire, *Spathius agrili* Yang and *S. galinae* Belokobylskij and Strazenac, under a range of temperatures from 17.2 to 32.8 °C. We found significant differences between the two parasitoids in host attack rates and progeny development. *Spathius agrili* could parasitize EAB larvae across the temperature range of 17.2 °C to 32.8 °C and caused the highest parasitism rate (~90.0 %) at 28.9 °C. In contrast, *S. galinae* did not attack any host larvae at 32.8 °C and caused the highest parasitism rate (~92 %) at 25 °C. From 21.1 °C to 28.9 °C, *S. agrili* emerged on average nine days earlier than *S. galinae* and had a higher low-temperature threshold for development. Both species arrested their development as mature (5th) instars inside their cocoons at 17.2 °C, suggesting facultative diapause that may be induced by exposure to cool temperatures. These findings suggest that *S. agrili* may perform better in warmer climates than *S. galinae* and could be an effective biocontrol agent in the southern U.S., whereas *S. galinae* is better suited to be released in the northern U.S.

1. Introduction

An important consideration in classical biological control is ensuring that natural enemies are introduced into areas with favorable environmental conditions similar to their place of origin (Van Driesche and Reardon, 2014; Kenis et al., 2017). Nonetheless, differences in local factors, such as host resource availability, presence of natural enemies, human activities, and climate may all influence the effectiveness of

introduced natural enemies in suppressing target pest populations (Zalucki and van Klinken, 2006; Kenis et al., 2017; Fischbein et al., 2019). Climatic conditions, such as temperature, may affect the development, distribution, and spread of introduced natural enemies (Chandler et al., 2020; Gould et al., 2020; Scherr et al., 2023). Even closely related parasitoid species that share habitat requirements may demonstrate differing cold and heat tolerance and developmental responses (Le Lann et al., 2011). This variability in climate response can

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impact their survival and effectiveness in establishing populations in different regions, thereby influencing the success of biological control (Wang et al., 2013; Furlong and Zalucki, 2017; Ragozzino et al., 2020). Understanding the behavioral and developmental responses of introduced natural enemies to climate conditions are therefore important to the development of successful classical biological control programs (Nechols et al., 1989).

Spathius agrili Yang and *S. galinae* Belokobylskij and Strazenac (Hymenoptera: Braconidae) are larval parasitoids of the emerald ash borer (EAB) *Agilus planipennis* Fairmaire (Coleoptera: Buprestidae) in their native range (northeast Asia) (Yang et al., 2005; Belokobylskij et al., 2012). Both species are gregarious, idobiont ectoparasitoids attacking late instars of EAB and were introduced from different locations and at different times to the United States for classical biological control of EAB. *Spathius agrili* from Tianjin, China (39°N) was introduced to the U. S. in 2007, whereas *S. galinae* from the Russian Far East (43°N) was introduced in 2015 (Duan et al., 2023).

Both species appear to have similar thermal requirements for completion of larval development, taking 3 or 4 weeks to complete development from eggs to adults at the normal rearing temperature (~25 °C) (Tian, 2009; Watt et al., 2016). Despite this similarity in thermal requirements for larval development, these two *Spathius* species have exhibited different patterns in survival and establishment in North America forest ecosystems following their field releases. *Spathius galinae* has successfully established abundant, self-sustaining populations in northern and mid-Atlantic regions of the U.S. (above 39°N) and contributed significantly to EAB population suppression there (Aker et al., 2022; Butler et al., 2022; Quinn et al., 2022; Duan et al., 2023). *Spathius agrili* has not successfully established in those regions, despite being released over a longer period and greater areas than *S. galinae* in some states at ~39°N, such as Maryland and Delaware (Duan et al., 2018; Aker et al., 2022; JJD unpublished).

Hypotheses regarding the differential patterns of *S. agrili* and *S. galinae* establishment following their field releases across the U.S. have primarily focused on differing synchrony of their larval development with suitable host larval stages and climate suitability of different release regions. Several recent studies have investigated the developmental synchrony of these two parasitoids with suitable host larval stages in the field, inside open-air insectaries, or in growth chambers programmed with various climatic conditions (e.g., Jennings et al., 2016; Brennan et al., 2017; Palmer, 2018; Jones et al., 2020; Ragozzino et al., 2020; Butler et al., 2022; Quinn et al., 2022). These studies revealed that both *S. galinae* and *S. agrili* could overwinter in the northeastern U.S. but *S. galinae* adult emergence appeared to be synchronized with presence of susceptible stages of EAB larvae (3rd and 4th instars), whereas *S. agrili* did not appear to be synchronized with the availability of suitable stages of EAB larvae in northern U.S. Jones et al. (2020) showed that adults of *S. agrili* emerged later in early summer when there were fewer suitable stages of EAB larvae in the northeastern U.S. and even though a subsequent generation of *S. agrili* emerged later in fall, colder temperatures might have limited their survival. Although *S. galinae* has not been released in southern U.S., it still is conceivable that *S. galinae* would encounter similar problems to synchronize with suitable stages of EAB larvae in southern U.S. where a majority EAB larvae overwinter as J-larvae (not suitable to parasitism) inside the pupation chamber (Gould et al. 2020). Additionally, it is suggested that both species overwinter as mature 5th instars, but *S. agrili* is less cold-tolerant than *S. galinae* due to its more southern origin (Chandler et al., 2020; Jones et al., 2020). Although these findings offer some insights into the divergent establishment of these two parasitoids, none of the studies have directly compared the behavioral and developmental responses of the two congeners to the same range of temperatures from early to late growing seasons.

In the present study, adults of both *S. agrili* and *S. galinae* were exposed to 3rd or 4th instar EAB larvae across a range of five distinct constant temperatures from 17.2 °C to 32.8 °C. Following the parasitoid

exposure, we then determined the host larval attack (parasitism) rate and monitored immature parasitoid development to adult stages under each exposure temperature regime. We chose these temperatures since EAB larvae are found during the spring, summer, and fall months (Poland et al., 2015), in areas where average daily temperatures range between -5.1 °C and 34.3 °C (Palecki et al., 2021). Additionally, Watt et al. (2016) noted that *S. galinae* failed to emerge at 15 °C and its eggs did not hatch at 35 °C, which constrained our upper and lower bounds.

2. Materials and Methods

2.1. Parasitoids

Spathius agrili used in this study originated from a founder colony collected from Tianjin, China in 2003 (Gould et al., 2011), whereas *S. galinae* adults were from a founder colony collected near Vladivostok, Russia 2010 (Duan et al., 2012). Both *S. agrili* and *S. galinae* adults used in this study were reared on EAB larvae infesting green (*Fraxinus pennsylvanica* Marsh.) or tropical [*F. uhdei* (Wenzig) Lingelsh] ash bolts, following the procedures detailed in Gould et al. (2011) and Duan et al. (2014) at the USDA APHIS PPQ Biological Control Production Facility (Brighton, MI) and the USDA, ARS Beneficial Insects Introduction Research Unit (BIIRU) (Newark, DE), respectively. Prior to use in the experiment, newly emerged (< 1 week old) female and male adult parasitoids for each species were housed in ventilated acrylic cylinders (25 cm height × 12 cm diameter) within a walk-in environmental chamber (CTH-1215, Percival Scientific, Perry, IA) set at 25 °C (±1.5), 65 (±10)% relative humidity (RH), and a 16: 8 h (L: D) photoperiod for mating. A water source was provided inside each rearing cylinder with a 10-dram clear plastic vial fitted with a braided cotton dental wick and pure honey were streaked on the ventilating screen of the cylinder as food resources.

2.2. Host larvae

All 3rd or 4th instar larvae of EAB used in the experiment were reared with freshly cut, green or tropical ash bolts at the USDA, ARS BIIRU in Newark, DE, according to procedures described in Duan et al. (2013). Briefly, each freshly cut ash bolt (1.5 – 2.5 cm diameter and 20 – 22 cm length) was infested with 5 – 7 fertilized EAB eggs (~7 days old) and then incubated in an environmental chamber at 27 °C (±1), 65 (±10)% RH, and a photoperiod of 16:8 (L:D) h for ~4 weeks prior to use in the experiment. By then, EAB larvae had reached 3rd to 4th instars and were suitable to parasitism by both *S. agrili* and *S. galinae* (Duan et al., 2013, 2014).

2.3. Exposure temperature regimes

We selected five constant temperatures: 17.2, 21.1, 25, 28.9, and 32.8 °C for parasitoid exposures and development that correspond with the range where EAB larvae can develop during the growing season (spring, summer, and fall). We programmed these constant temperatures in five environmental chambers, each maintaining a relative humidity (RH) of 65 (±10)% and a photoperiod of 16: 8 h (L: D). A HOBO data logger was used to monitor temperature and RH in each chamber (Watt et al., 2016). Within each chamber, groups (4 – 8) of ash bolts containing approximately five 3rd or 4th instar EAB larvae were exposed to 10 naïve gravid females and 5 males of either *S. agrili* or *S. galinae* adults in a rearing container (3.5 L) for 7 days to ensure high rates of parasitism. After the 7-day parasitoid exposure period, we removed all adult parasitoids and left the ash bolts inside the same container under the same chamber (temperature regime) until complete emergence of their progeny (12–16 weeks after parasitoid exposure). Previous studies (Tian, 2009; Watt et al., 2016) as well as our laboratory colony rearing experience indicated that both *Spathius* species normally completed their development to adult (emergence) from exposure (laying eggs) to

host larvae within a three to four weeks under the normal rearing temperature (25 °C). Based on these data, we estimate that both species should complete their normal development to adults following their exposure to host larvae even at the lowest test temperature (17.2°) within 12 – 16 weeks. We set up five containers (replicates) for each parasitoid species within each temperature regime.

2.4. Effect of temperature on host attack rate by exposed adult parasitoids

Following the 1-week parasitoid exposure and 12 – 16 weeks of incubation under each temperature regime, we dissected all ash bolts from each replicate. Upon dissection of exposed ash bolts of each replicate, we recorded the stage and fate of each host larva (alive, parasitized, or dead for unknown reasons). Parasitism of host larvae were easily recognized by the presence of parasitoid cocoons (with or without adult exit holes) in the host larval galleries. The rate of host attack (or parasitism) by adult parasitoids for each replicate was calculated as the proportion of parasitized EAB larvae relative to the total number of EAB larvae in the replicate. The total number of EAB larvae in each replicate was the sum of parasitized EAB larvae plus dead or live unparasitized 3rd – 4th instars (including J-shaped mature larvae).

2.5. Effect of temperature on parasitoid development

We monitored the immature parasitoid development to adult stages (emergence) three days a week (Monday, Wednesday, Friday) following the initial 1-week parasitoid exposure. Observations of adult parasitoid emergence for each replicate were stopped four weeks after the last adult parasitoid emergence was observed in the replicate. The mean development time of immature parasitoids to adults for each replicate of temperature regimes was then calculated as the number of days from the median time (day) of the initial 1-week exposure to the time (day) when 50 % adult parasitoids emerged throughout the entire observation period (12 – 16 weeks). The developmental rate for both *S. agrili* and *S. galinae* under different temperature regimes was further calculated as the reciprocal of the mean development time (1/d). We estimated the low-temperature thresholds and growing degree days for each parasitoid species using least squares regression analysis, following the methodology described by Whitfield (1984).

2.6. Effect of temperature on diapause

Upon dissection of exposed ash bolts at ~ 16 weeks after the initial 1-week parasitoid exposure, we found that all the parasitoid larvae from 17.2 °C and some from 21.1 °C were alive as cocooned mature (5th) instars for both *S. agrili* and *S. galinae*. We then moved these cocooned parasitoid larvae to the normal rearing conditions (25 °C, 16:8h L:D photoperiod) and monitored their development to adults for additional 16 weeks. Those mature parasitoid larvae took additional three to 16 weeks to emerge as adults under the normal rearing conditions, strongly indicating that they must have been induced to a diapausing stage (with development arrestment) by the low temperature regimes used in this study, as suggested in previous studies (Yang et al., 2010; Hanson et al., 2013; Watt et al., 2016). The diapause rate of the parasitoid larvae for each species under each temperature was then calculated as the proportion of cocooned live parasitoid larvae relative to the total number of parasitoid progeny including all emerging adults, dead adults (not emerged), and dead or live pupae and larvae 16 weeks after the initial 1-week parasitoid exposure.

2.7. Statistical analysis

We analyzed the host attack rate in relation to temperature and parasitoid species using a generalized regression platform with the binomial distribution model. The model included the effects of temperature, parasitoid species, and their interactions, which were then

tested for significance with Wald Chi-square (χ^2) statistics at type I error rate of 0.05. We then analyzed the mean development time or rate in relation to temperature and parasitoid species as well as their interactions with ANOVA based on linear regression models. All mean values were reported as averages \pm standard error (SE) (Stacconi et al., 2017), and all analyses were conducted using JMP Pro 17 (SAS, 2023).

3. Results

3.1. Effects of temperature on host attack rates by exposed adult parasitoids

Host attack rates by adult parasitoids increased from 36 (± 9.7)% at 17.2 °C to 90 (± 10)% at 28.9 °C for *S. agrili* and from 47 (± 16.8)% at 17.2 °C to 92 (± 4.9)% at 25.0 °C for *S. galinae* (Fig. 1). Host attack rates decreased with increasing temperature above 28.9 °C for *S. agrili* and 25.0 °C for *S. galinae* (Fig. 1). At the highest temperature (32.8 °C), host attack rates decreased to 26 (± 10.7)% for *S. agrili* and zero for *S. galinae* (Fig. 1). Logistic regression analysis detected significant effects of test temperature regimes ($\chi^2 = 9.1939$, $df = 1$, $P = 0.0024$), parasitoid species ($\chi^2 = 5.1304$, $df = 1$, $P = 0.0235$), but non-significant interactions ($\chi^2 = 2.8015$, $df = 1$, $P = 0.0942$). These results indicate that there are significant differences in the optimal temperature range for host attacks between the two parasitoid species – with higher host attack rates by *S. agrili* at higher temperatures (28.9 – 32.8 °C) than *S. galinae*.

3.2. Effects of temperature on parasitoid development

Larvae of both *S. agrili* and *S. galinae* arrested development as mature (5th) instars inside their cocoons at 17.2 °C and no adult parasitoids emerged from this lowest test temperature before being moved to the normal rearing temperature 25 °C for additional observation. At the highest test temperature (32.8 °C), adults of *S. agrili* emerged, whereas no adults of *S. galinae* emerged because no hosts were attacked at this temperature. For the temperature range that allowed adult parasitoid emergence (Fig. 2A), there were significant differences in parasitoid developmental time to adults between *S. agrili* and *S. galinae* ($F = 75.3379$, $df = 1$, 31, $P < 0.0001$) as well as among these temperature treatments ($F = 64.5556$, $df = 1$, 31, $P < 0.0001$). There was no significant interaction between parasitoid species and temperature treatments ($F = 2.2743$, $df = 1$, 31, $P = 0.1427$). The mean development time to adults for *S. agrili* was significantly shorter than that for *S. galinae*, with *S. agrili* emerging approximately 9 days earlier than *S. galinae* at temperature treatments of 21.1 – 28.9 °C (Fig. 2A).

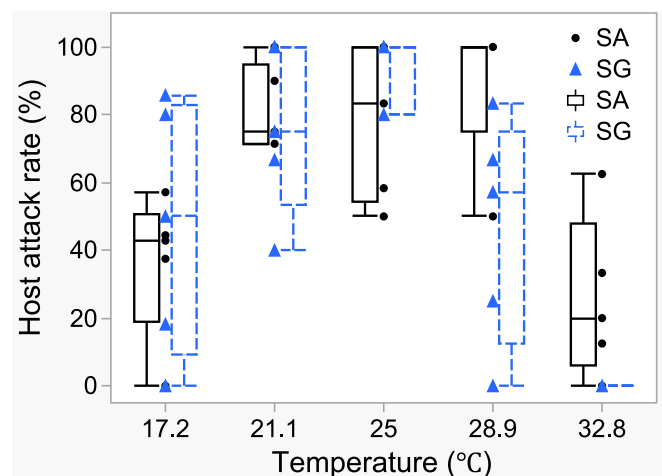


Fig. 1. Host attack rate for *S. agrili* (SA) and *S. galinae* (SG) under different temperatures. Black dots and solid boxplots are for *S. agrili* and blue triangles and dashed boxplots are for *S. galinae*.

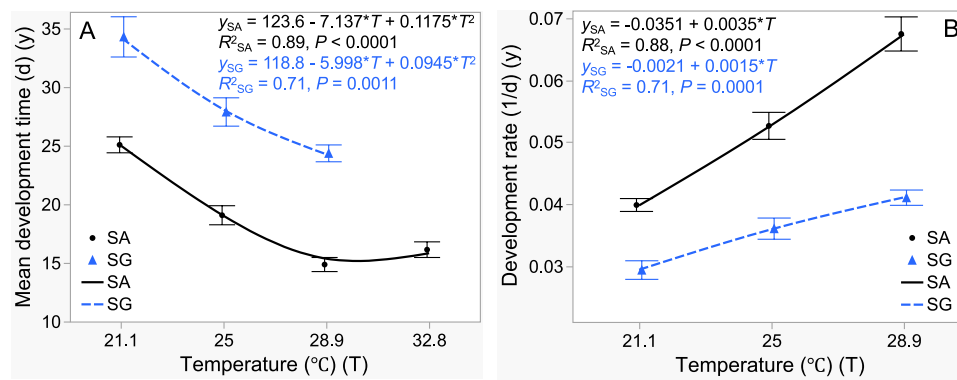


Fig. 2. Mean development time (A) and development rate (B) of *S. agrili* (SA) and *S. galinae* (SG) under different temperatures. Black dots, solid lines, and equations are for *S. agrili* and blue triangles, dashed lines, and equations are for *S. galinae*. All data are presented as averages \pm standard error (SE).

The development rate from 21.1 °C to 28.9 °C exhibited a positive linear relationship with temperature for both species (*S. agrili*: $R^2 = 0.8751$; *S. galinae*: $R^2 = 0.7126$) (Fig. 2B). Linear regression of the mean rate of development and temperature indicated that the estimated low-temperature threshold for *S. agrili* (10.0 °C) was around 6.1 times higher than that for *S. galinae* (1.4 °C), while the growing degree days for *S. agrili* (285.7 degree-days, base 10.0 °C) were approximately 1.3 times lower than that for *S. galinae* (666.7 degree-days, base 1.4 °C).

3.3. Diapause rates of *S. agrili* and *S. galinae*

All surviving larvae of both *S. agrili* and *S. galinae* from 17.2 °C and some from 21.1 °C arrested their development (i.e., were in diapause) as mature (5th) instars inside their cocoons, whereas no larvae of both species were in diapause within the temperature range of 25 °C to 32.8 °C (Fig. 3). These results indicate that both *S. agrili* and *S. galinae* have a facultative diapause that depends on the exposure of immature stages or parental adults to appropriate low temperature regime (e.g., 17.2 °C). Although there were significant differences in diapause rates for both parasitoid species between 17.2 °C and the other temperature treatments ($F = 47.2597$, $df = 1, 40$, $P < 0.0001$), there was no significant difference in diapause rates between *S. agrili* and *S. galinae* ($F = 1.2137$, $df = 1, 40$, $P = 0.2777$), nor was there any significant interaction between temperature and parasitoid species on the diapause rate ($F = 1.4624$, $df = 1, 40$, $P = 0.2342$).

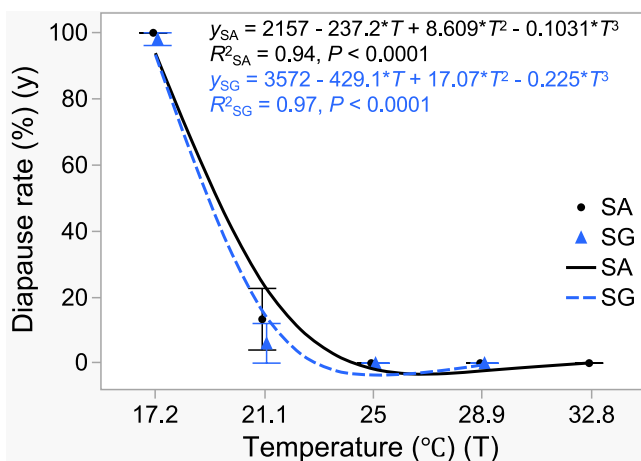


Fig. 3. Diapause rate for *S. agrili* (SA) and *S. galinae* (SG) under different temperatures. Black dots, solid line, and equation are for *S. agrili* and blue triangles, dashed line, and equation are for *S. galinae*. All data are presented as averages \pm standard error (SE).

4. Discussion

The present study demonstrates differences in host attack rates and progeny development between two emerald ash borer larval parasitoids, *S. agrili* and *S. galinae*, when reared under the same range of constant temperatures from 17.2 °C to 32.8 °C. *Spathius agrili* could parasitize EAB larvae within the temperature range of 17.2 °C to 32.8 °C and caused the highest parasitism rate at 28.9 °C. In contrast, *S. galinae* could not attack any host larvae at 32.8 °C and caused the highest parasitism rate at 25 °C. Within the temperature range from 21.1 °C to 28.9 °C, *S. agrili* consistently emerged ~ 9 days earlier. However, *S. galinae* has a lower low-temperature threshold for development, which suggests that they can start development earlier in the spring and are thus better suited to colder climates. *Spathius agrili*, with its higher development threshold, faster development above that threshold, and ability to continue to parasitize larvae at high temperatures, suggest that this species is more likely to thrive in the warmer climate conditions in the southern U.S.

Two separate studies have also determined the effects of ambient temperature on the development of *S. agrili* (Tian, 2009) and *S. galinae* (Watt et al., 2016) under laboratory conditions, but each with a different range of constant temperatures. Tian (2009) determined the development time from oviposition to adult emergence of *S. agrili* across a temperature range (22 – 32 °C) and found that the development time decreased with increasing temperatures in the range. Watt et al. (2016) found that *S. galinae* could complete larval development to adults within the temperature range of 20 – 30 °C, but not 15 °C or 35 °C. Results from those two published studies support our findings of the temperature-dependent variations in developmental time of both parasitoid species. However, none of the previous studies explicitly described the diapausing behavior of *S. agrili* and *S. galinae* in their low temperature regimes (15 °C to 22 °C), as observed in our study at temperatures from 17.2 °C to 21.1 °C.

Several previous studies suggested that low temperature and short-day photoperiod mimicking the fall climate conditions might induce larval diapause of both *S. agrili* and *S. galinae* (Wang et al., 2010; Gould et al., 2011; Hanson et al., 2013; Duan et al., 2014; Watt et al., 2016). To date, no studies have determined both extraneous and endogenous factors affecting the diapause development (including induction and termination) of these two congeneric parasitoids. Both *S. agrili* and *S. galinae* effectively arrested their development at the mature (5th) instars inside their cocoons at 17.2 °C, even though they were exposed to a long-day photoperiod (16:8h L:D) throughout the experiment. This finding suggests that exposure to an appropriate low temperature regime at certain sensitive immature stages (e.g., eggs or early instars of larvae) may be critical factors inducing diapause of *S. agrili* and *S. galinae*, regardless of the photoperiod. Such facultative diapause behavior in *S. agrili* and *S. galinae* allows these two parasitoids to overcome unfavorable conditions such as seasonal food or host shortages and

extreme low winter temperature. Future studies should determine the impact of both extraneous (e.g., low temperature regimes) and endogenous factors (e.g., parasitoid age or stages) on diapause induction and termination of both *Spathius* parasitoids, which may have significant implications to parasitoid rearing and field establishment for biological control of the emerald ash borer across different geographic regions.

Developmental synchrony with host insects and climate plays a crucial role in the establishment and long-term effectiveness of parasitoids in biological control (Ruberson et al., 1989). Temperature-dependent variations in development can impact the synchronization between parasitoids and their host populations, thus affecting the efficacy of biological control in the field. For instance, differences in the optimal temperature range for three parasitoids of *Drosophila suzukii* may lead to varying time windows for host attack or parasitism, thereby influencing the efficacy or outcomes of biological control (Stacconi et al., 2017). Findings from our study showed that *S. agrili* performed better than *S. galinae* at higher temperature ranges (28.9 – 32.2 °C), suggesting that *S. agrili* may establish better and be more effective for biological control of emerald ash borer than *S. galinae* in the southern U.S. However, this does not explain why *S. agrili* has not established well in the northern U.S. Other factors such as diapause-regulated synchronization with the availability of host larvae in early spring or late fall may likely limit *S. agrili* establishment in the northern U.S. (Jones et al., 2020). Nevertheless, our results do support the guidelines proposed by USDA-APHIS/ARS/FS (2020), which are based on climate-matching of the parasitoid's native and introduced ranges and suggest releasing *S. galinae* in the northern U.S. (above 40°N).

Our study underscores the profound differences in temperature effects on the host attack capacity and immature development of two closely related parasitoid species introduced for biological control of the invasive emerald ash borer. While our study focused on comparing the responses of two parasitoids to constant temperatures, it is essential to recognize that their ability to withstand temperature fluctuations, especially in the context of climate change, can also influence their long-term persistence and effectiveness in biological control programs. Therefore, further research investigating the comparative developmental responses of these parasitoids to fluctuating temperatures, particularly in field settings, is warranted.

CRedit authorship contribution statement

Yingqiao Dang: Writing – original draft, Methodology, Formal analysis, Data curation, Conceptualization. **Mitchell A. Green:** Writing – review & editing, Methodology, Formal analysis, Data curation. **Xiaoyi Wang:** Writing – review & editing, Supervision, Methodology. **Jian J. Duan:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. . Supplementary data

Supplementary data to this article can be found through the Ag Data Commons (National Agricultural Library, USDA Agricultural Research Service) once the manuscript is published.

Data availability

Data will be made available on request.

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