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### ► To cite this version:

Yong-Ming Chen, Xing-Ran Qu, Tian-Hao Li, Asim Iqbal, Xingeng Wang, et al.. Performances of six eupelmid egg parasitoids from China on Japanese giant silkworm *Caligula japonica* with different host age regimes. *Journal of Pest Science*, 2021, 94 (2), pp.309-319. 10.1007/s10340-020-01271-1 . hal-03279613

HAL Id: hal-03279613

<https://hal.inrae.fr/hal-03279613v1>

Submitted on 6 Jul 2021

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# Performances of six eupelmid egg parasitoids from China on Japanese giant silkworm *Caligula japonica* with different host age regimes

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Received: 18 April 2020 / Revised: 7 August 2020 / Accepted: 10 August 2020 / Published online: 17 August 2020  
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## Abstract

The Japanese giant silkworm *Caligula japonica* Moore is an emerging defoliator pest of forest and fruit trees, causing severe economic losses in East Asia. To identify biological control agents for this pest, we comparatively evaluated six indigenous eupelmid egg parasitoids (*Anastatus fulloi*, *A. gansuensis*, *A. japonicus*, *A. meilingensis*, *Mesocomys albitarsis* and *M. trabalae*) from China, in terms of their performances (number of parasitized eggs, developmental time, offspring emergence and sex ratio) on *C. japonica* eggs of four different ages (0, 10, 20 and 30-d old). Results showed that all six parasitoids readily parasitized *C. japonica* eggs of all tested ages, but *A. japonicus* was the most efficient species based on the number of parasitized eggs, followed by *M. albitarsis* and *M. trabalae*, and the other three parasitoid species. All four *Anastatus* species parasitized more old than young eggs, while *M. albitarsis* did not show a strong host age preference and *M. trabalae* parasitized the oldest less than young eggs. For all host ages, developmental time was longest in *A. gansuensis* and shortest in *M. albitarsis*, offspring emergence was high (>90%), and progeny was strongly female biased (>70%) among all parasitoids except for *A. gansuensis* which produced all female progeny. Portions of *A. japonicus* offspring (<13.1%) entered diapause as pre-pupae. Accordingly, *A. japonicus*, *M. albitarsis* and *M. trabalae* were identified as the most suitable agents against *C. japonica*. This information may also help improve rearing and field-release protocols, in terms of host age-related effects on these parasitoids.

**Keywords** *Anastatus* · *Mesocomys* · Host age preference · Host suitability · Biological control

## Key message

- *Caligula japonica* is an emerging forest and fruit tree pest in East Asia
- Six indigenous eupelmid egg parasitoids in China were evaluated for their performances on *C. japonica* eggs of different ages
- All six parasitoids readily parasitized *C. japonica* eggs of different ages
- *Anastatus japonicus*, *Mesocomys albitarsis* and *M. trabalae* were identified as the most suitable agents against *C. japonica* eggs based on their overall performances

Communicated by M. Traugott.

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## Introduction

The Japanese giant silkworm (JGS) *Caligula japonica* Moore (Lepidoptera: Saturniidae) is a defoliator pest of forest and fruit trees in East Asia (Qiao et al. 2014; Abarenkov 2019; Nashiki 2019). In China, 38 plant species belonging to 30 genera in 20 families have been reported as hosts of this pest, including various important fruit trees such as walnut (*Juglans regia* L.), chestnut (*Castanea mollissima* Blume), ginkgo (*Ginkgo biloba* L.), plums (*Prunus* spp.), pears (*Pyrus* spp.), apple (*Malus pumila* Mill.) and sumac [*Toxicodendron vernicifluum* (Stokes)] (Yang et al. 2008a; Qiao et al. 2014). Since it was first reported in 2006 in Kangxian, Gansu Province (northwestern China), JGS has rapidly spread and emerged as a major pest of walnut trees. About 27,330 hectares of walnut trees were infested by JGS in 2011 in Kangxian alone, causing an estimated economic loss of \$20 million (Qiao et al. 2014). There is a high possibility of further outbreaks of this pest (Yang et al. 2008b; Qiao et al. 2014). In other regions in East Asia, JGS was also reported as a serious pest of deciduous forest and shade trees such as plums, chestnuts, camphor (*Cinnamomum* sp.) and birch (*Betula maximowicziana* Regel.) in Japan (Clausen 1927; Kawasaki and Sato 1985; Ohno et al. 2008).

Currently, control strategies against JGS rely on the application of broad-spectrum insecticides in China (Dong 2013). Unfortunately, insecticides are often not applied in a timely manner or applied repeatedly, leading to the development of pesticide resistance in the pest (Wang et al. 2012). Furthermore, pesticide applications could disrupt established IPM for other pests, increase chemical residues, negatively affect pollinators and other beneficial or non-target organisms, and cause harm to the environment and human health (Weisenburger 1993; Desneux et al. 2007; Qu et al. 2015). Although some entomopathogenic fungi, bacteria and viruses have been tested for the control of this pest, these pathogens yielded unsatisfactory results (Tetsu et al. 1974; Liu and Luo 2008). Under this scenario, it is urgently needed to develop effective but also environmentally friendly control strategies for this pest.

Biological control with insect parasitoids to control forest pests has been practiced from a long time (Fischbein and Corley 2015). Among insect natural enemies, egg parasitoids would be ideal agents for the control of insect pests as they kill host pests before the pests cause potential damage to host plants. Indeed, many egg parasitoids such as trichogrammatids have been widely mass-produced and released for the control of Lepidopteran pests globally including China (Smith 1996; Mills 2010; Huang et al. 2020; Zang et al. 2021). For example, the egg parasitoid *Anastatus japonicus* Ashmead (Hymenoptera:

Eupelmidae) (later identified as *A. fulloi* Sheng & Wang) has been mass-produced and released annually to control the litchi stink bug *Tessaratoma papillosa* Stål (Hemiptera: Tessaratomidae) in China since the late 1960s (Li et al. 2014). Recently, the egg parasitoids *Trissolcus japonicus* Ashmead (Hymenoptera: Scelionidae) and *A. bifasciatus* Geoffroy are considered as candidate biological control agents for inundative releases against the invasive brown marmorated stink bug *Halyomorpha halys* (Stål) (Hemiptera: Pentatomidae) in North America and Europe (Talamas et al. 2015; Stahl et al. 2018a, b; Abram et al. 2019). We surveyed indigenous egg parasitoids associated with JGS in walnut orchards in northwestern China in 2017 and 2018, and collected seven parasitoid species from parasitized JGS eggs, namely *Anastatus fulloi* Sheng & Wang, *A. gansuensis* Chen & Zang, *A. japonicus*, *A. meilingensis* Sheng & Yu, *Mesocomys albitarsis* (Ashmead) and *M. trabalae* Yao, Yang & Zhao (all Hymenoptera: Eupelmidae), and *Aprostocetus brevipedicellus* Yang and Cao (Hymenoptera: Eulophidae) species (Chen et al. 2020). Parasitism rates of JGS egg masses (individual eggs) ranged from 0.55% (0.01%) to 30.41% (3.59%) in the fields (Chen et al. 2020). Among them, *A. fulloi* is a widely distributed and well-studied species as a biological control agent of various lepidopteran and pentatomid (Hemiptera) eggs (Li et al. 2014). *Mesocomys albitarsis* was reported as a major egg parasitoid of JGS in Japan (Clausen 1927). All of them were newly reported on JGS in northwestern China, and *A. gansuensis* was a newly described species (Chen et al. 2019). This field survey indicated the potential of these locally occurring egg parasitoids for the biological control of JGS. Indigenous parasitoids have already adapted to local ecological conditions and if they can adapt to newly emerging or invading pests, they may be manipulated to suppress the pests through conservative and augmentative biological control (Yuan et al. 2012; Fischbein et al. 2019). One of such examples is the fall webworm moth *Hyphantria cunea* Drury (Lepidoptera: Erebidae), an exotic and invasive pest that has been successfully controlled by the indigenous pupal parasitoid *Chouioia cunea* Yang (Hymenoptera: Eulophidae) in China (Yang et al. 2006).

The production of natural enemies for use in biological control programs is often rather expensive, where the attempt to acquire a cost-effective production system is the main objective of many biological control programs (Watt et al. 2015). The Chinese oak silkworm *Antheraea pernyi* Guérin-Méneville (Lepidoptera: Saturniidae) has been considered as an ideal factitious host for the mass production of *A. fulloi* and *Pseudanastatus albitarsis* (= *M. albitarsis*) to control *T. papillosa* and *Dendrolimus punctatus* Walker (Lepidoptera: Lasiocampidae), respectively (Teng and Ni 1989; Li et al. 2014), because of its high parasitism rates, low rearing costs, and easy storage and transportation (Li

et al. 2019; Iqbal et al. 2019). However, the suitability of *A. pernyi* eggs as a rearing host for other egg parasitoids has not yet been evaluated. This study aimed to identify the most suitable agents for biological control of JGS among six recently discovered indigenous eupelmid egg parasitoids: *A. fulloi*, *A. gansuensis*, *A. japonicus*, *A. meilingensis*, *M. albitarsis* and *M. trabalae* using *A. pernyi* egg as a factitious host. The eulophid *A. brevipedicellus* was not tested because of its low field parasitism on individual JGS eggs (< 1.1%) or egg masses (< 2.2%) during the field surveys (Chen et al. 2020). Specifically, we comparatively evaluated their relative performances on differently aged JGS eggs in terms of the number of parasitized eggs and offspring fitness. Augmentative or inundative release programs rely on not only selection of parasitoid species that preferentially attack target pests and are well adapted to the agroecosystem of the target pests, but also efficient mass-rearing systems to produce large numbers of high-quality parasitoids (Smith 1996). Age-related development changes in host, both physiological and morphological, can result in variable host quality and influence a parasitoid's host acceptance for oviposition and suitability for offspring (Nurindah et al. 1999; Li et al. 2014; Stahl et al. 2018a; Iqbal et al. 2019). This is particularly true for parasitoids attacking static developmental stages such as egg and pupa, as the quantity of resources available for the development of parasitoid progeny is determined at the time of parasitism (Vinson 1976; Pizzol et al. 2012; Zhang et al. 2014; Hou et al. 2018). Therefore, we also compared the effect of host age on the performances of these parasitoids. This information will help select suitable host age for the rearing or timing of field release of these parasitoids.

## Materials and methods

### Parasitoids

Laboratory colonies of the six eupelmid egg parasitoids (*Anastatus fulloi*, *A. gansuensis*, *A. japonicus*, *A. meilingensis*, *Mesocoms albitarsis* and *M. trabalae*) were established

with adult wasps emerged from field-collected and parasitized JGS egg masses in walnut orchards in 2017 in Kangxian (105–106°E, 32.9–33.7°N), northwestern China. Each species was identified based on the morphological characteristics as described by Gibson (1995, 1997, 2011) and Gibson and Fusu (2016). All six species were further verified using voucher specimens as identified by Dr. Gibson in 2018. The cytochrome oxidase subunit I gene (COI) sequences of the four *Anastatus* species were also analyzed according to Hebert et al. (2003). All voucher specimens were deposited in the Institute of Biological Control collection, Jilin Agricultural University at Changchun, China (for additional information of these parasitoids, see Table 1).

Each parasitoid colony was initiated with 30 wasps and maintained on the factitious host *A. pernyi* eggs under controlled conditions (25 ± 1 °C, 70 ± 5% RH and 14L:10D). Mature *A. pernyi* moths were dissected to collect host eggs. The eggs were washed with distilled water and then air dried at normal room temperatures (Iqbal et al. 2019). Fifty eggs were glued on an egg card (5.0 × 1.0 cm) and then exposed to individual females in small glass tubes (10.0 × 1.5 cm) covered with fine mesh for 24 h. Exposed eggs were held until the emergence of wasps. All six eupelmid egg parasitoids had been reared for five generations prior to their use in this study and rejuvenated every three to five generations by transferring them to rear on JGS eggs.

### Host insect

JGS is a univoltine species; it lays eggs in the fall and overwinters as eggs in diapause from September to April of the following year in Kangxian, China (Yang et al. 2008b). JGS cocoons were collected in walnut orchards in Kangxian (33° 26' 33.81" N, 105° 41' 52.10" E) during the middle of June 2019. Approximately, 300 cocoons were collected and placed in a plastic container (25.5 × 25.5 × 5 cm) inside an insect cage (30 × 30 × 30 cm). The cocoons were maintained in an open insectary so that they were exposed to similar field conditions (23–29 °C, 60–85% RH and natural photoperiod) and emerged as field populations did from June

**Table 1** Detailed information on six eupelmid egg parasitoid species tested in this study

Parasitoid species	GenBank accession number	Indigenous host <sup>a</sup>	Other hosts recorded (references)
<i>A. fulloi</i>	MK604241	<i>Caligula japonica</i>	<i>Erthesina fullo</i> (Sheng et al. 1997)
<i>A. gansuensis</i>	MK373759	<i>C. japonica</i>	
<i>A. japonicus</i>	MK604240	<i>C. japonica</i>	<i>Antherea pernyi</i> (Zhao et al. 2019)
<i>A. meilingensis</i>	MK604242	<i>C. japonica</i>	<i>Dendrolimus punctatus</i> , <i>D. kikuchii</i> (Sheng and Yu 1998)
<i>M. albitarsis</i>	–	<i>C. japonica</i>	<i>Dendrolimus spectabilis</i> (Hirose 1964)
<i>M. trabalae</i>	–	<i>C. japonica</i>	<i>Trabala vishnou</i> (Yao et al. 2009)

<sup>a</sup>Host species from which the parasitoid was originally collected for this study (Chen et al. 2019, 2020)

to September. Newly emerged adults were paired and kept in insect rearing cages (50×50×50 cm). The adults were monitored daily for oviposition, and newly laid eggs were collected and kept under the same conditions as described above until they reached required ages (see below) for experiments.

## Experimental setup

Experiments were conducted under laboratory conditions (25±1 °C, 70±5% RH and 14L:10D). To determine the performance of each of the six egg parasitoids on different-aged JGS eggs, four different ages (0, 10, 20 and 30-d old) of JGS eggs were selected to cover a wide range of aged hosts that could be attacked by these parasitoids in the field. Because adult JGS females start oviposition in September in Kangxian, China, where monthly field temperatures vary from 8 to 28 °C (mean 15.5 °C) in September and 2 to 21 °C (mean 11.5 °C) in October based on weather data available at <https://www.tianqi.com>. Field temperatures drop dramatically after October (≈ 30-d old of early laid JGS eggs) when these parasitoids are likely no longer active in the field (Fang et al. 1995). Newly emerged adult wasps (<6 h old) were collected and held in a group of ten pairs (except for *A. gansuensis*, which produces by parthenogenesis) in a cylindrical and transparent plastic container (9.0×14.0 cm, diameter×height) covered with fine mesh for 3 d to allow mating, with 30% honey solution provided as food for the parasitoids. All tests used 3-d old and mated female wasps. Our preliminary observations found that all the six parasitoids could not parasitize more than 30 eggs per female wasp per 24 h, therefore, female wasps were individually exposed to 50 host eggs of 0, 10, 20 or 30 d-old in a no choice test (i.e., with unlimited access to hosts). The host eggs were glued on a strip-shaped egg card (5.0×1.0 cm) and exposed to the parasitoid in a small glass tube (10.0×1.5 cm) covered with fine mesh. The test procedures were similar for each parasitoid species at each tested host age.

A replicate was discarded if the wasp was found dead at the end of the 24-h exposure. Following the 24-h exposure, the wasps were removed, and all exposed eggs were checked daily for the emergence of wasps until no wasps emerged for a consecutive of 20 d. Finally, all host eggs without a parasitoid emergence hole were dissected under a stereomicroscope to determine the fate of each egg, i.e., either dead and unparasitized or parasitized with a recognizable dead parasitoid larva, a dead or live parasitoid pupa or a developed but dead adult inside the host egg. Images (examples) were taken for these different scenarios using a Nikon camera and/or Keyence VHX-2000 digital microscope. There were 15 valid replicates for each parasitoid species and host age treatment.

For each treatment replicate, we calculated the number of parasitized eggs (= number of host eggs with a parasitoid emergence hole + number of host eggs containing a parasitoid larva, pupa or adult), percentage of offspring emergence (= number of host eggs with a parasitoid emergence hole × 100/number of parasitized eggs), percentage of female progeny (= number of emerged and unemerged adult females × 100/total number of emerged and unemerged adults) and developmental time (*d*) of individual wasps from the oviposition to adult emergence. Also, the percentages of offspring died as larvae, undeveloped (dead and diapause) as pupae and dead as adults inside the hosts were calculated by dividing the numbers of dead larvae, undeveloped pupae and dead adults by the total number of parasitized host eggs, respectively.

## Data analyses

A two-way analysis of variance (ANOVA) was used to compare the performances of the six egg parasitoids, considering the effects of both parasitoid species (six levels) and host age (four levels), as well as their interaction on the number of parasitized hosts, developmental time, percent offspring emergence, percent female progeny and percentage of offspring dead as larvae, undeveloped as pupae or dead as adults inside the hosts. Prior to the ANOVAs, the percentage data were arcsine square-root-transformed to normalize variances and checked for the normality of residuals and homoscedasticity with Shapiro–Wilk tests. When the ANOVAs revealed significant effects of the factors, means were separated by Tukey's Honestly Significant Difference (HSD) test with an alpha equal to 0.05. All data analyses were performed using the SAS statistical software package (SAS Institute 2010, Cary, NC, USA).

## Results

### Number of parasitized eggs

All six parasitoids successfully parasitized JGS eggs of four tested ages, but the number of parasitized eggs was affected by parasitoid species, host age and their interaction (Table 2). The numbers of parasitized eggs (averaged from 2.60 to 23.53 eggs) was generally followed (in decreasing order) by *A. japonicus*, *M. albitarsis*, *M. trabalae*, *A. fulloi*, *A. meilingensis* and *A. gansuensis* at each host age (0-d old:  $F_{5,84} = 34.63$ ,  $P < 0.001$ ; 10-d old:  $F_{5,84} = 22.32$ ,  $P < 0.001$ ; 20-d old  $F_{5,84} = 61.62$ ,  $P < 0.001$ ; 30-d old:  $F_{5,84} = 48.87$ ,  $P < 0.001$ ) (Fig. 1a). All four *Anastatus* species parasitized more old (30 d, or 20 and 30 d) than younger (0, 10 and 20 d, or 0 and 10 d) eggs (*A. fulloi*:  $F_{3,56} = 15.62$ ,  $P < 0.001$ ; *A. gansuensis*:

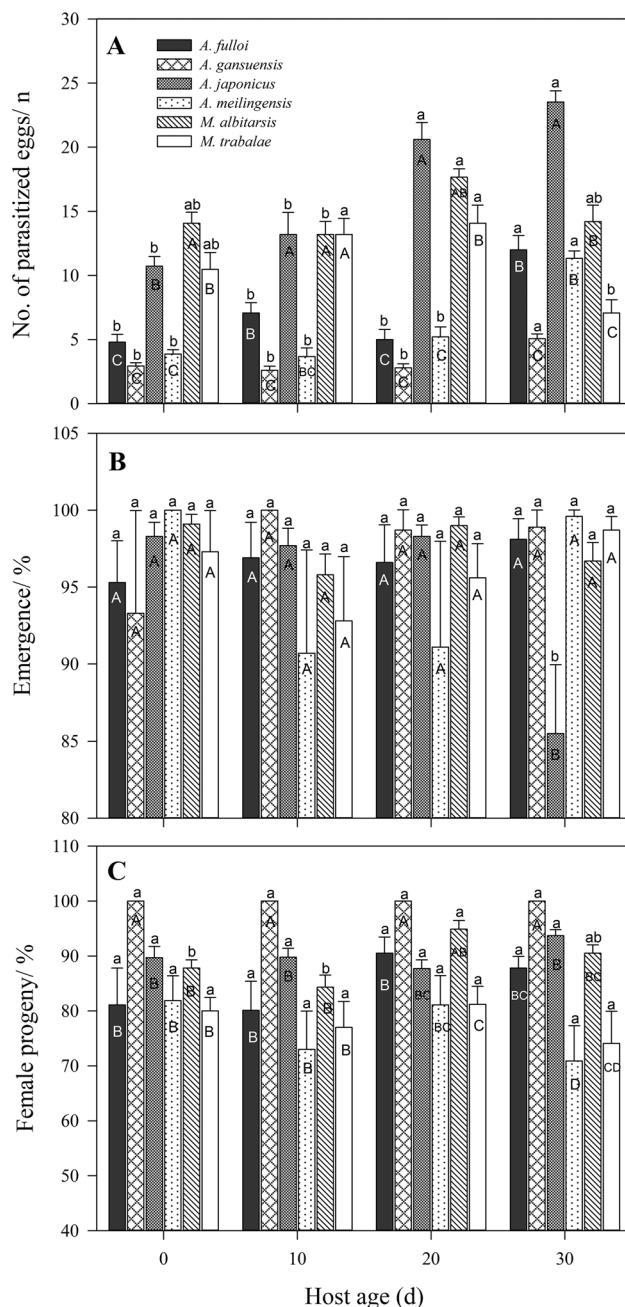
**Table 2** Results of two-way ANOVAs testing the effects of parasitoid species (PS), host age (HA) of *C. japonica* egg as well as their interaction on the performances of six eupelmid egg parasitoids in terms of the number of parasitized eggs, offspring emergence, developmental time and percent female progeny and the percentage of offspring dead as larvae, undeveloped as pupae or unemerged (dead) as adults inside the hosts

Performance parameters	Source	Df	MS	F	P
Number of host eggs parasitized	PS	5	1696.34	129.14	<0.001
	HA	3	353.68	26.92	<0.001
	PS×HA	15	156.86	11.94	<0.001
Offspring emergence (%)	PS	5	169.35	1.21	0.303
	HA	3	102.18	0.73	0.534
	PS×HA	15	273.51	1.96	0.018
Developmental time (d)	PS	5	323.43	287.60	<0.001
	HA	3	25.31	22.51	<0.001
	PS×HA	15	2.57	2.28	0.004
Female progeny (%)	PS	5	5121.99	31.52	<0.001
	HA	3	293.36	1.81	0.146
	PS×HA	15	226.96	1.40	0.146
Dead as larvae (%)	PS	5	66.67	1.02	0.408
	HA	3	18.12	0.28	0.842
	PS×HA	15	127.85	1.95	0.018
Undeveloped as pupae (%)	PS	5	324.29	7.70	<0.001
	HA	3	60.98	1.45	0.229
	PS×HA	15	186.56	4.43	<0.001
Dead as unemerged adults (%)	PS	5	10.62	0.51	0.770
	HA	3	12.34	0.59	0.622
	PS×HA	15	20.57	0.98	0.471

$F_{3,56} = 13.31, P < 0.001$ ; *A. japonicus*:  $F_{3,56} = 24.10, P < 0.001$ ; *A. meilingensis*:  $F_{3,56} = 33.48, P < 0.001$  (Fig. 1a). However, *M. albitarsis* parasitized similar numbers of eggs at various ages, except that it parasitized more 20-d old than 10-d old eggs ( $F_{3,56} = 4.09, P = 0.011$ ), and *M. trabalaе* parasitized more young (0, 10 and 20-d old) than old (30 d) eggs ( $F_{3,56} = 6.28, P = 0.001$ ) (Fig. 1a).

**Developmental time**

Developmental time from oviposition to adult emergence was also affected by parasitoid species, host age and their interaction (Table 2). It was similar among different host ages for *A. fulloi* ( $F_{3,56} = 0.94, P = 0.430$ ) and *A. gansuensis* ( $F_{3,56} = 2.69, P = 0.055$ ), but generally increased with increasing host ages for *A. japonicus* ( $F_{3,56} = 5.32, P = 0.003$ ), *A. meilingensis* ( $F_{3,56} = 13.50, P < 0.001$ ), *M. albitarsis* ( $F_{3,56} = 12.32, P < 0.001$ ) and *M. trabalaе* ( $F_{3,56} = 13.75, P < 0.001$ ) (Table 3). Among parasitoid species, the developmental time was different at each host age (0-d old:  $F_{5,84} = 192.55, P < 0.001$ ; 10-d old:  $F_{5,84} = 49.18,$



**Fig. 1** Effects of host age of *C. japonica* eggs on the number of parasitized eggs (a), percent emergence (b) and percent female progeny (c) of each of the six eupelmid egg parasitoids. Bars refer to means ± SE. The different lower-case letters above the same patterned bars indicate significant differences among different host ages for each parasitoid species, while the different upper-case letters above the bars indicate significant differences among different parasitoid species at each host age ( $P < 0.05$ , Tukey’s test)

$P < 0.001$ ; 20-d old:  $F_{5,84} = 77.35, P < 0.001$ ; 30-d old:  $F_{5,84} = 59.87, P < 0.001$ ). Overall, *A. gansuensis* developed slowly while *M. albitarsis* developed fast when compared to other four parasitoid species (Table 3).

**Table 3** Developmental time and percentage of offspring dead as larvae, undeveloped as pupae or dead as adults by each of six eupelmid egg parasitoid species on different-aged *C. japonica* eggs

Performance parameters	Parasitoid species	Host egg age (d) <sup>a</sup>			
		0	10	20	30
Developmental time (d)	<i>A. fulloi</i>	24.34±0.28 a B	24.61±0.30 a B	24.76±0.36 a B	25.08±0.33 a B
	<i>A. gansuensis</i>	26.01±0.22 ab A	26.19±0.14 ab A	25.84±0.16 b A	26.50±0.15 a A
	<i>A. japonicus</i>	22.54±0.12 b C	24.05±0.70 ab BC	23.45±0.38 ab C	25.22±0.55 a B
	<i>A. meilingensis</i>	20.58±0.17 c D	20.94±0.21 bc D	21.63±0.24 b D	22.52±0.29 a C
	<i>M. albitarsis</i>	19.25±0.10 b E	20.00±0.09 a D	19.54±0.10 b E	19.93±0.12 a D
	<i>M. trabalaе</i>	22.06±0.10 c C	22.89±0.11 ab C	22.66±0.17 b CD	23.28±0.16 a C
Dead as larvae (%)	<i>A. fulloi</i>	0.00±0.00 a A	0.00±0.00 a A	2.83±2.26 a A	0.00±0.00 a B
	<i>A. gansuensis</i>	6.67±6.67 a A	0.00±0.00 a A	1.33±1.33 a A	0.00±0.00 a B
	<i>A. japonicus</i>	0.00±0.00 a A	0.00±0.00 a A	0.00±0.00 a A	0.86±0.47 a B
	<i>A. meilingensis</i>	0.00±0.00 a A	9.33±6.72 a A	3.33±3.33 a A	0.42±0.42 a B
	<i>M. albitarsis</i>	0.00±0.00 b A	0.00±0.00 b A	0.00±0.00 b A	3.30±1.19 a A
	<i>M. trabalaе</i>	0.00±0.00 a A	1.85±1.39 a A	0.00±0.00 a A	0.00±0.00 a B
Undeveloped as pupae (%) <sup>b</sup>	<i>A. fulloi</i>	4.72±2.72 a A	0.83±0.83 a A	0.61±0.61 a AB	0.83±0.83 a B
	<i>A. gansuensis</i>	0.00±0.00 a B	0.00±0.00 a A	0.00±0.00 a B	0.00±0.00 a B
	<i>A. japonicus</i>	1.22±0.84 b B	1.61±0.98 b A	1.46±0.72 b AB	13.15±4.57 a A
	<i>A. meilingensis</i>	0.00±0.00 a B	0.00±0.00 a A	0.00±0.00 a B	0.00±0.00 a B
	<i>M. albitarsis</i>	0.00±0.00 b B	3.83±1.28 a A	1.04±0.56 b AB	0.00±0.00 b B
	<i>M. trabalaе</i>	0.00±0.00 a B	3.48±2.67 a A	4.40±2.23 a A	1.30±0.89 a B
Dead as unemerged adults (%)	<i>A. fulloi</i>	0.00±0.00 a A	2.22±2.22 a A	0.00±0.00 a A	1.11±1.11 a A
	<i>A. gansuensis</i>	0.00±0.00 a A	0.00±0.00 a A	0.00±0.00 a A	1.11±1.11 a A
	<i>A. japonicus</i>	0.48±0.48 a A	0.68±0.47 a A	0.28±0.28 a A	0.48±0.33 a A
	<i>A. meilingensis</i>	0.00±0.00 a A	0.00±0.00 a A	2.22±2.22 a A	0.00±0.00 a A
	<i>M. albitarsis</i>	0.90±0.62 a A	0.35±0.35 a A	0.00±0.00 a A	0.00±0.00 a A
	<i>M. trabalaе</i>	2.67±2.67 a A	1.84±1.12 a A	0.00±0.00 a A	0.00±0.00 a A

<sup>a</sup>Values (mean±SE) followed by the different upper-case letters within a column and the different lower-case letters within a row indicate significant different among parasitoid species and host ages, respectively ( $P < 0.05$ , Tukey's HSD test)

<sup>b</sup>All undeveloped *A. japonicus* pupae were alive (in diapause) while all undeveloped pupae of other parasitoid species were dead at the time of dissections

### Offspring survival and emergence

During the dissections, dead larvae, pupae or adults were found inside the hosts in all parasitoid species, except that all undeveloped *A. japonicus* were alive (in diapause) and no *A. gansuensis* and *A. meilingensis* pupae were dead (Table 3). Overall, percentages of offspring dead as larvae (0.0–9.3%), dead as pupae (0.0–4.7%), diapausing as pupae (1.2–13.1%) or dead as adults (0.0–2.7%) were low in all treatments (Table 3).

The percentage of offspring dead at the larval stage was not affected by parasitoid species and host age but was affected by the interaction of these two factors (Table 2). It was similar for *A. fulloi* ( $F_{3,56} = 1.56$ ,  $P = 0.208$ ), *A. gansuensis* ( $F_{3,56} = 0.87$ ,  $P = 0.460$ ), *A. meilingensis* ( $F_{3,56} = 1.31$ ,  $P = 0.280$ ) and *M. trabalaе* ( $F_{3,56} = 1.75$ ,  $P = 0.167$ ), but different for *A. japonicus* ( $F_{3,56} = 3.42$ ,  $P = 0.023$ ) and *M. albitarsis* ( $F_{3,56} = 7.72$ ,  $P < 0.001$ ) among different host ages

(Table 3). It was also similar in 0 d ( $F_{5,84} = 1.00$ ,  $P = 0.423$ ), 10 d ( $F_{5,84} = 1.77$ ,  $P = 0.127$ ) and 20 d ( $F_{5,84} = 0.77$ ,  $P = 0.575$ ) old eggs among different parasitoid species (Table 3). However, a higher percentage of *M. albitarsis* offspring dead as larvae in 30-d old than other aged eggs ( $F_{5,84} = 5.54$ ,  $P < 0.001$ ) (Table 3).

The percentage of undeveloped pupae was affected by parasitoid species but was not affected by host age or the interaction of these two factors (Table 2). It was similar for *A. fulloi* ( $F_{3,56} = 1.72$ ,  $P = 0.174$ ) or *M. trabalaе* ( $F_{3,56} = 1.25$ ,  $P = 0.300$ ) among different host eggs (Table 3). However, a higher percentage of *A. japonicus* pupae failed to develop in 30-d old than other aged eggs ( $F_{3,56} = 5.95$ ,  $P < 0.001$ ), and a lower percentage of *M. albitarsis* pupae failed to develop in 10-d old than other aged eggs ( $F_{3,56} = 6.72$ ,  $P < 0.001$ ). The percentage of undeveloped pupae was different in 0-d old ( $F_{5,84} = 2.65$ ,  $P = 0.029$ ), 20 d-old ( $F_{5,84} = 2.63$ ,  $P = 0.029$ ) and 30-d old ( $F_{5,84} = 7.31$ ,  $P < 0.001$ ) eggs, but was similar

in 10-d old ( $F_{5,84} = 1.64$ ,  $P = 0.159$ ) eggs among different parasitoid species (Table 3). There was no significant effect of host age, parasitoid species or their interaction on the percentage of unemerged adult wasps (Tables 2–3).

Consequently, offspring emergence was high (> 90%) in all treatments (Fig. 1b). Neither parasitoid species nor host age affected offspring emergence (Table 2). There was, however, an interactive effect between the parasitoid species and host age on the offspring emergence. It was no different for *A. fulloi* ( $F_{3,56} = 0.19$ ,  $P = 0.905$ ), *A. gansuensis* ( $F_{3,56} = 0.75$ ,  $P = 0.527$ ), *A. meilingensis* ( $F_{3,56} = 1.23$ ,  $P = 0.309$ ), *M. albitarsis* ( $F_{3,56} = 2.41$ ,  $P = 0.077$ ) or *M. trabalaе* ( $F_{3,56} = 0.91$ ,  $P = 0.442$ ) among different host ages (Fig. 1b). However, offspring emergence of *A. japonicus* was lower from the oldest (30-d old) than young (0, 10, or 20-d old) eggs ( $F_{3,56} = 7.03$ ,  $P = 0.0004$ ) (Fig. 1b), and this was largely due to the diapause of undeveloped pupae.

### Offspring sex ratio

Regardless of the host age, all six parasitoids were strongly female biased (> 70% females), except for *A. gansuensis* which produced 100% female offspring (Fig. 1c). Percentage of female progeny was affected by parasitoid species only (Table 2). It was no different for *A. fulloi* ( $F_{3,56} = 1.07$ ,  $P = 0.368$ ), *A. gansuensis* ( $F_{3,56} = 0.88$ ,  $P = 0.527$ ), *A. japonicus* ( $F_{3,56} = 2.14$ ,  $P = 0.105$ ), *A. meilingensis* ( $F_{3,56} = 1.38$ ,  $P = 0.260$ ), or *M. trabalaе* ( $F_{3,56} = 0.13$ ,  $P = 0.942$ ) among different host ages. However, *M. albitarsis* produced more female biased progeny from 20-d old than 0 or 10-d-old eggs ( $F_{3,56} = 7.74$ ,  $P < 0.001$ ). Overall, *A. gansuensis*, *A. japonicus*, and *M. albitarsis* produced more female biased progeny than the other three parasitoid species at all host ages (0-d old:  $F_{5,84} = 6.99$ ,  $P < 0.001$ ; 10-d old:  $F_{5,84} = 6.57$ ,  $P < 0.001$ ; 20-d old:  $F_{5,84} = 10.35$ ,  $P < 0.001$ ; 30-d old:  $F_{5,84} = 14.12$ ,  $P < 0.001$ ).

### Discussion

We compared the relative performances of six indigenous eupelmid egg parasitoids on different-aged JGS eggs, with an effort to identify the best candidate agents for the control of this emerging pest as well as suitable host ages for improving rearing and field release protocols of selected parasitoids. We demonstrated successful parasitism of JGS eggs by all six parasitoids and the suitability of various-aged JGS eggs for these parasitoids.

Eggs (except for diapausing eggs) develop in a short period of time and the quality of a host egg as a resource for an egg parasitoid decreases rapidly as the egg ages. Also, host eggs could become less acceptable due to increased hardness of the eggshell or less detectable due to fading

host recognition cues over time (Vinson 1998). Therefore, many egg parasitoids preferentially oviposit in young eggs, and young eggs can be more suitable than old eggs for the development of parasitoid offspring (Vinson 1998; Zhang et al. 2014; Hou et al. 2018). For example, *Trichogramma ostriniaе* Pang & Chen, *T. japonicum* Ashmend, *T. dendrolimi* Matsumura, and *T. chilonis* Ishii (all Hymenoptera: Trichogrammatidae) all showed an oviposition preference for young eggs of *Chilo suppressalis* (Walker) (Lepidoptera: Crambidae) and *Mythimna separata* (Walker) (Lepidoptera: Noctuidae) (Zhang et al. 2014; Hou et al. 2018). However, in this study, we found (1) the effect JGS egg age on the preference of the six tested egg parasitoids (in terms of the number of parasitized hosts) varied with the species of parasitoid; the four *Anastatus* species preferred old than young eggs while the two *Mesocomyx* appeared not to show a strong host age preference or preferred less for the oldest eggs; and (2) various-aged eggs seem to be suitable for all six parasitoids, as offspring survival was high (> 90%) and all parasitoids were female-biased at all host ages, although there exist slight variations in these fitness parameters across parasitoid species or host ages.

There may be several reasons why these six parasitoids did not show a strong preference for young JGS eggs and why various-aged eggs were suitable for these parasitoids. First, the JGS eggs used in this study were in diapause. Despite these eggs were differently aged, they likely offered nutrition of similar quality for the development of the parasitoids. Second, JGS egg has a hard surface (Fig. 2), and there must exist variations among the six parasitoid species in their abilities to penetrate the shell of JGS egg. Old JGS eggs could be hard to be penetrated by the *Mesocomyx*, or they may take longer to parasitize the old than young eggs (host handling time); both situations would result in reduced parasitization efficiency on old host eggs. However, this may be not the case for the *Anastatus*. Instead, it could be an advantage for the *Anastatus* to accept old rather than young eggs if there is no difference in host handling time among different host eggs and no obvious fitness costs for offspring development in old hosts (as showed here). Because these eggs parasitoids likely overwinter synchronously with their host eggs for several months in the field, old eggs could be more resistant to unpredictable environmental conditions. Similar results were observed in the egg parasitoid *Telenomus euproctidis* Wilcox (Hymenoptera: Scelionidae), whose offspring had high survival in overwintering eggs of *Euproctis pseudoconspersa* Strand (Lepidoptera: Erebiidae) (Ai et al. 2000). In general, all six egg parasitoids were still rather flexible in accepting JGS eggs, and this flexibility would allow them to explore a wide range of aged and diapausing JGS eggs. We must point out that it is possible that some individual parasitoids might had died at the egg stage, but they could be unrecognizable in the dead hosts during





**Fig. 2** Images of an adult female parasitizing *C. japonica* egg (a), emerged adults (b), dead larva (c), and alive (in diapause) pre-pupa (d) and pupa (e) of *A. japonicus*

the dissections. Thus, offspring survival could be slightly overestimated. Given the overall low percentages of dead host eggs across all parasitoid species and host age treatments (<10%), any differences resulting from the overestimation could be negligible.

Relatively, *A. gansuensis* developed slowly while *M. albitarsis* developed faster when compared to the other four parasitoid species that had similar developmental times. The developmental time was independent of host age in *A. fulloi* and *A. gansuensis* but slightly increased with host age in the other four parasitoids. To maximize their chances of successful parasitism, egg parasitoids often delay host development or speed up progeny development when ovipositing in an older host (Vinson 1998). For example, development of *A. bifasciatus* was delayed when attacking old eggs of *Thaumetopoea solitaria* (Freyer) (Lepidoptera: Notodontidae) or *H. halys* eggs (Boyadzhiev et al. 2017; Stahl et al. 2018b). As discussed above, diapausing JGS eggs may do not undergo significant changes of host quality over time, and for this reason, these parasitoids may be unnecessary to adjust their developmental times. Dead adults of all the six parasitoids were found inside JGS eggs, and this happened apparently because some adult wasps were unable to successfully gnaw a hole out of the eggs. This also occurred in other parasitoids such as *T. ostrinae*, *T. embryophagum* Hartig, and *T. piceum* Dyurich, where adult wasps failed to form an emergence hole for emergence (e.g., Hassan et al.

2004; Li et al. 2019). We suspect that adult wasps of these four species may take longer to emerge from old than young host eggs.

Interestingly, *A. gansuensis* produced all female offspring on JGS eggs. It could occasionally produce a few male offspring as we recently noticed that this parasitoid had a 113:1 ratio of female to male offspring when reared from *A. pernyi* eggs (Chen et al. unpubl. data). The parthenogenetic reproduction of *A. gansuensis* is an advantage if the parasitoid must be mass reared, because it would be cheaper to produce than sexual forms. Most hymenopteran species are haplodiploid, i.e., male (haploid) developed from unfertilized eggs while female (diploid) developed from fertilized eggs (Heimpel and de Boer 2008). Female-producing parthenogenesis (thelytoky) can be genetic or due to infections by endosymbiotic bacteria of the genera *Cardinium*, *Wolbachia*, and *Rickettsia* (Simon et al. 2003; Rabeling and Kronauer 2013; Monti et al. 2016). For example, parthenogenetic reproductions in *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae) (Zchori-Fein et al. 2001), *Plagiomerus diaspidis* Crawford (Hymenoptera: Encyrtidae) (Zchori-Fein and Perlman 2004) and *Leptocybe invasa* Fisher & La Salle (Hymenoptera: Eulophidae) (Nugnes et al. 2015) were associated with the infection of *Wolbachia*, *Cardinium*, and *Rickettsia*, respectively. Whether or not the *A. gansuensis* population was infested by endosymbionts is unknown and this deserves further study.

It is likely that these six egg parasitoids diapause in host eggs when they attack the hosts in later fall. Diapause does occur under a combination of low temperature and short photoperiod in several closely related species such as *M. pulchriceps* Cameron (Vanden Berg 1971), *A. umae* Bouček (= *A. madagascariensis* Risbec) (Narasimham and Sankaran 1982), and *A. bifasciatus* (Stahl et al. 2018b). Among the six parasitoid species, *A. japonicus* was previously reported to enter diapause as pre-pupae in *A. pernyi* eggs in China (Zhao et al. 2019) or as mature larvae inside the gypsy moth eggs in Ontario, Canada (Sullivan et al. 1977). The different diapausing stages as reported in the two studies could be due to different adaptations by two different geographical populations to the local environments. However, the tested laboratory conditions in the current study would not favor diapause, still, a small portion of *A. japonicus* went diapause as pre-pupae. This partial diapause of *A. japonicus* seems to be induced by the diapausing hosts. This also occurred in other parasitoids. For example, *Encarsia scapeata* Rivnay entered diapause when it was reared on diapausing host *Bemisia tabaci* Gennadius (Hemiptera: Aleyrodidae) (Gerling et al. 2009). Partial diapause could be an adaptive “risk-spreading” strategy for the parasitoid to cope with unpredictable environments (Hopper 1999).

In conclusion, all the six egg parasitoids have the potential for conservative and augmentative biological control of JGS. Fast development in *M. albitarsis*, parthenogenetic reproduction in *A. gansuensis* and partial diapause in *A. japonicus* all could be important attributes as biological control agents. Overall, *A. japonicus*, *M. albitarsis* and *M. tralalae* are recommended as the best candidate agents. These parasitoids could be mass-reared and released during the fall for the suppression of diapausing JGS eggs. It is also worth of mentioning that these parasitoids can be reared on the factitious host *A. pernyi* as we showed here that the tested parasitoids reared from *A. pernyi* eggs effectively parasitized JGS eggs. *Antheraea pernyi* eggs ( $104.96 \pm 0.57$  eggs /g) were about twice larger than JGS eggs ( $297.62 \pm 0.49$  eggs /g), and consequently, female parasitoids (e.g., *M. tralalae*) developed from the *A. pernyi* eggs ( $4.657 \pm 0.017$  um) were about twice larger than those reared from the JGS eggs ( $2.058 \pm 0.015$  um) (Chen et al. unpubl. data). In general, the body size of adult parasitoids is often positively correlated with many other fitness components (e.g., Quicke 1997; Morris and Fellowes 2002; Wang and Messing 2004). However, further detailed studies are needed for a better understanding of the effect of natal host on the parasitoids’ demographic parameters (e.g., intrinsic rate of increase) and other fitness attributes. Further studies are also needed to demonstrate the efficiency of these parasitoids against JGS via augmentative release in the field.

## Author contributions

LSZ, YMC and ND scoped and designed research. YMC, XRQ and ZYR conducted experiments and collected the data. YMC and XW performed data analyses. YMC and AI wrote the early draft. LSZ, XW and THL edited it. All authors read and approved the manuscript.

**Acknowledgments** We are grateful to Dr. Gary Gibson (Honorary Research Associate, Agriculture and Agri-Food Canada, Canadian National Collection of insects) for the identification of six Eupelmidae species. This research was funded by the National Key R&D Program of China (Nos: 2017YFE0104900 and 2017YFD0201000), and Gansu Provincial Fiscal Science and Technology Award and Compensation Project (2018-01).

## Compliance with ethical standards

**Conflict of interest** The authors declare no conflicts of interest.

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