

Oviposition experience promotes active reproductive behaviour in a synovigenic parasitoid

Zi-Yin Wang¹, Yu-Fan Wang¹, Si-Yu Yin¹, Peng-Cheng Liu¹, Hao-Yuan Hu¹

¹ Collaborative Innovation Centre of Recovery and Reconstruction of Degraded Ecosystem in Wanjiang Basin Co-founded by Anhui Province and Ministry of Education, The School of Ecology and Environment, Anhui Normal University, Wuhu, Anhui Province, China

Corresponding author: Peng-Cheng Liu (15952019586@163.com)

Academic editor: Zachary Lahey | Received 25 October 2022 | Accepted 6 December 2022 | Published 17 February 2023

<https://zoobank.org/F134A655-AB53-4393-82A5-79AD9B54DD98>

Citation: Wang Z-Y, Wang Y-F, Yin S-Y, Liu P-C, Hu H-Y (2023) Oviposition experience promotes active reproductive behaviour in a synovigenic parasitoid. *Journal of Hymenoptera Research* 95: 1–12. <https://doi.org/10.3897/jhr.95.96631>

Abstract

Parasitoids are important insects that are commonly released into the environment to reduce the population sizes of pest species. The lifetime reproductive success of parasitoids mainly depends on host availability and the availability of mature eggs. Consequently, it is predicted that female wasps must balance the risk of egg or host (time) limitation with maximized lifetime fecundity. Typically, synovigenic females, which continue to mature eggs throughout their lifetime, have been shown to adjust their egg production rate in response to environmental variations in host availability to reduce the risk of egg limitation. In this study, we found that in a synovigenic egg parasitoid, *Anastatus japonicus* (Hymenoptera: Eupelmidae), the oviposition experience of *Ana. japonicus* females significantly enhanced the egg load and increased the rate of mature egg production. However, in contrast to other studies, the experience of contact with a host did not significantly affect the egg load in females. This result suggests that the overall oviposition experience might induce an adjustment and accelerate egg maturation in *Ana. japonicus* and is likely more important in egg maturation than transitory host contact. In addition to affecting the egg load, oviposition experience influenced *Ana. japonicus* female reproductive behaviour, which shifted virgin female behavioural preferences from mating to oviposition and laying more eggs per clutch. Our study provides an optimal strategy for the post-oviposition release of *Ana. japonicus*, an egg parasitoid of several lepidopteran forest pests, to improve biocontrol effectiveness.

Keywords

Anastatus japonicus, biological control, egg limitation, egg load

Introduction

Reproduction is crucial for all animals. Insect parasitoids are insects that parasitise other organisms, and all invertebrate life stages, including the egg, larval/nymphal, pupal, and adult stages are susceptible to parasitisation. Because of their parasitic nature, an increasing number of species have been extensively released to reduce the population sizes of pest species (Hassan 1993; Zhishan et al. 2003; Asgari and Rivers 2011; Wang et al. 2019). Many studies on parasitoid wasps have focused on applied research, with the intent to improve the attack and control of pest populations by such species (Powell 1986; Wajnberg et al. 2008; Yang et al. 2014). Generally, the lifetime reproductive success of parasitoids mainly depends on host availability and the availability of mature eggs (Jervis et al. 2001; Tylianakis et al. 2004; Hougardy et al. 2005). In the field, parasitoids generally experience one of the two following situations. Either the number of mature eggs available for laying exceeds the number of oviposition opportunities or the number of oviposition opportunities exceeds the number of mature eggs available for laying; these are defined as host/time limitation and egg limitation, respectively (Godfray 1994; Richard and Casas 2012). However, a perfect match between the number of hosts and the availability of mature eggs is rare. Consequently, to maximize reproductive success, insect parasitoids are hypothesized to balance the risk of egg limitation and time limitation (Minkenberg et al. 1992; Rosenheim 1996; Heimpel et al. 1998; Rosenheim et al. 2008).

According to the type of egg production, parasitoids can be classified as pro-ovigenic or synovigenic. Pro-ovigenic species mature all or most of their lifetime complement of eggs prior to emergence from the host, whereas synovigenic species emerge with very few or no mature eggs, and egg maturation begins at eclosion and continues throughout adult life (Flanders 1950; Jervis et al. 2001). A number of internal and environmental factors have been shown to influence egg production and maturation in both pro-ovigenic and synovigenic species. Host resources greatly influence synovigenic females that adjust their egg production rate in response to host availability (Papaj 2000). For example, in the parasitoid *Eupelmus vuilleti* (Crawford) (Hymenoptera: Eupelmidae), contact with a host by the female antennae can accelerate egg maturation (Casas et al. 2009), and in the aphid parasitoid *Aphelinus albipodus* (Hayat & Fatima) (Hymenoptera: Aphelinidae), females mature eggs faster in the presence of preferred hosts (Wu and Heimpel 2007). In those studies, females were usually manipulated by a single contact with the host (i.e., antennal) to perceive the host's presence, and then egg loads were counted. However, contact or perceived contact with a host is only one component of complete oviposition behaviour. Therefore, this study mainly focused on the effect of complete oviposition behaviour on egg loads in female wasps.

Lymantria dispar (L.) (Lepidoptera: Erebidae) is a leaf-feeding insect that causes the large-scale defoliation of forest and urban trees worldwide during intermittent population outbreaks. *Anastatus japonicus* Ashmead (formerly *Anastatus dispar* Ruschka) (Hymenoptera: Eupelmidae) is a recorded egg parasitoid of *L. dispar* (Crossman 1925; Kurir 1944; Avci 2009; Alalouni et al. 2013) and is widely distributed in Europe

and Asia. In addition, due to its potential as a biological control agent of *L. dispar*, *Ana. japonicus* was imported to North America in the early 1900s (Crossman 1925; Yan et al. 1989) and achieved effective control efficiency. Field investigations revealed that, together with *Ooencyrtus kuvanae* (Howard) (Hymenoptera: Encyrtidae), which is also a primary egg parasitoid of *L. dispar*, parasitism rates might reach 20–40% (Hoy 1976; Reardon 1981; Brown and Cameron 1982; Brown 1984). In addition to *L. dispar*, several other noxious lepidopteran species that are primarily forest pests, including *Malacosoma neustria testacea* (Motschulsky), *Odonestis pruni* (Linnaeus), *Antheraea pernyi* (Guerin-Meneville), *Dendrolimus punctatus tabulaeformis* (Walker), and *Actias selene ningpoana* (Felder), can be parasitised (Yan et al. 1989; Li and Lou 1992; Li et al. 2001). Great efforts have been made to mass rear *Ana. japonicus* for the control of *Caligula japonica* (Moore) in China, as the eggs of *Ant. pernyi* are suitable factitious hosts (Yan et al. 1989). The lifetime fecundity of a female *Ana. japonicus* is several hundred offspring (Liu et al. 2015), and the offspring sex ratio is mainly influenced by host quality (i.e., size) (Liu et al. 2017). The egg maturation mode of *Ana. japonicus* is typically synovigenic, and previous studies found that females usually contained tens of mature eggs by dissecting the abdomen (Liu and Hao 2019). Hosts of *Ana. japonicus*, i.e., *L. dispar*, typically lay clutches containing hundreds or thousands of eggs; thus, the lifetime reproductive success of a female parasitoid is limited by the supply of mature eggs, i.e., egg limitation. Several synovigenic females have been shown to adjust their egg production rate in response to environmental variations in host availability (Papaj 2000; Wu and Heimpel 2007; Casas et al. 2009). During oviposition in a host, parasitoids may learn to recognize particular visual and olfactory host stimuli and use these cues to modify subsequent behaviours (Vet et al. 1995; Vinson 1998). Thus, in this study, the effect of the complete oviposition experience on egg load was studied in *Ana. japonicus*. In addition, the effect of contact with a host on egg load was tested, as well. Finally, the effects of oviposition experience on subsequent behaviour and capacity, e.g., behavioural choice and host exploration capacity, were also studied in *Ana. japonicus*.

Materials and methods

Host and parasitoid species

Ana. japonicus colonies were first established from a population reared on *L. dispar* egg masses collected in Tongliao city, China (43°62'N, 122°25'E) in December 2019, and the colony was subsequently maintained on *Ant. pernyi* eggs. Eggs of *Ant. pernyi* were obtained by laparotomizing adult female abdomens, and they were maintained at 0 °C (Wang et al. 2014). We isolated the parasitised host eggs of *Ant. pernyi* individually in polyethylene tubes (height: 7.5 cm; diameter: 1 cm), with the openings covered by a cotton ball to prevent any mating behaviour before the experiment began. A previous study showed that mating behaviour significantly increased the egg load (Liu and Hao 2019).

Egg loads in females with host contact experience and oviposition experience

A single, one-day-old, newly emerged *Ana. japonicus* virgin female was introduced into a Petri dish (height: 1.5 cm, diameter: 5 cm) with four eggs of *Ant. pernyi*; the Petri dishes were maintained at 26 ± 0.5 °C with $70 \pm 5\%$ relative humidity (RH). When the female made antennal contact with one of the hosts for more than 30 s, the behaviour was interrupted and the female was placed into a cylindrical plastic box (diameter: 5.0 cm, height 5.0 cm) for rearing. As a control treatment, no host eggs were provided to females. Female wasps aged 2 to 10 days were dissected for the determination of egg loads. Egg loads were measured in terms of the number of mature eggs in the ovaries. Honey water (honey:water = 4:6) was supplied on cotton balls as nutrition for adult females until dissection (Yan et al. 1989). The selected adults were euthanized by freezing at -80 °C, and then the abdomens were placed into a Petri dish with a saline solution. We counted the number of mature eggs by dissecting the abdomens using forceps under a microscope (Leica M205A, Germany). In total, 13–17 females were dissected for each treatment.

To acquire oviposition experience, a one-day-old virgin female was introduced into a Petri dish (height: 1.5 cm, diameter: 5 cm) with four host eggs. After completing an oviposition event in a host, the female was removed and reared in a cylindrical plastic box (diameter: 5.0 cm, height 5.0 cm); the treatment was considered “oviposition experience”. Based on preliminary experiments, an oviposition event was considered finished when the female completed oviposition (i.e., the female initiated parasitisation of a new host or moved away from the previously parasitised host for at least 1 min), and the duration of the oviposition event lasted for more than 10 min. As a control treatment, no host eggs were provided to females. Females aged 2 to 10 days and exposed to the above two treatments were dissected for the determination of egg loads, and they were fed honey water (honey: water = 4: 6) daily. In total, 13–17 females were used for each treatment.

Effect of oviposition experience on mate and oviposition choice behaviours

Previous studies revealed that newly eclosed females rarely lay offspring on the first day. Thus, in this study, two-day-old virgin females (with oviposition experience or without any experience) were introduced into a Petri dish (height: 1.5 cm, diameter: 5 cm) containing one newly eclosed virgin male and four fresh *Ant. pernyi* eggs for 60 min. The entire process was video recorded. In each dish, the first mating and oviposition events in the female were recorded.

Effect of oviposition experience on subsequent host exploration capacity

In this experiment, an artificial host clutch containing nine *Ant. pernyi* eggs was offered to two virgin females (with oviposition experience and without any experience); the females and egg clutch were placed into a Petri dish (height: 1.5 cm, diameter: 5 cm) to allow oviposition for three hours. In each dish, each host egg in the clutch was marked with a number (e.g., 1, 2...9). For easy differentiation, one randomly selected female

in each dish was marked with white (the other female was marked with green) acrylic paint on the back of the thorax. In total, the sample size was 16, and the entire process was video recorded. Similarly, successful oviposition in a host was considered when the oviposition process was complete and the duration of the oviposition event lasted for more than 10 min. In each dish, successful oviposition and the number of host eggs in which the marked wasps oviposited were determined by reviewing the recorded videos.

Statistical analysis

All analyses were performed with *R* software (version 2.14.1). In our study, the effects of female age and experience on egg load were analysed with generalized linear mixed models (GLMMs, lme4 package, Bates et al. 2018) with a Poisson distribution and log link function (Crawley 1993). When the ratio of residual deviance and residual *df* were >1 , the data exhibited overdispersion. Under this scenario, significance testing was performed using quasi-Poisson regression, and significance was assessed based on the *F* statistic (Crawley 1993, 2007). In each model, egg load was considered the response variable, and the factors of female age and oviposition experience were considered fixed effects. The criterion for significance was a *p* value < 0.01 when testing interactions (Crawley 2007). For the behavioural choice experiment, the preferences for mating and oviposition were analysed using sign tests, and a chi-square test was employed to determine the effect of the oviposition experience of females on preference. Finally, a paired-samples *t*-test was used to analyse the difference in the number of host eggs parasitised by females with oviposition experience and without oviposition experience.

Results

Egg loads in females with host contact experience and oviposition experience

On the second day, a few mature eggs (virgin females without any experience: 5.93 ± 1.22 ; virgin females with host contact experience: 6.08 ± 0.83) were observed in the ovaries. The GLMM analysis showed that the number of mature eggs in the females was significantly influenced by individual age ($F = 29.034$, $df_1 = 8$, $df_2 = 209$, $p < 0.001$) but not by contact with the host ($F = 0.034$, $df_1 = 1$, $df_2 = 209$, $p = 0.854$). In addition, there were no interaction effects of female experience status and age on the number of mature eggs ($F = 0.187$, $df_1 = 8$, $df_2 = 209$, $p = 0.992$). As shown in Fig. 1, daily egg loads increased from day 2 until day 5 and then plateaued from days 6–10.

The results showed that both age ($F = 10.653$, $df_1 = 8$, $df_2 = 214$, $p < 0.001$) and oviposition experience ($F = 39.891$, $df_1 = 1$, $df_2 = 214$, $p < 0.001$) had significant effects on the number of mature eggs in females. There were significant interaction effects between female experience status and age on the number of mature eggs ($F = 5.52$, $df_1 = 8$, $df_2 = 214$, $p < 0.001$). As shown in Fig. 1, daily egg loads in females with oviposition experience peaked at day 3, with 16.7 ± 1.12 eggs per female, while in females with and without host contact experience, the egg load peaked at approximately day 5.

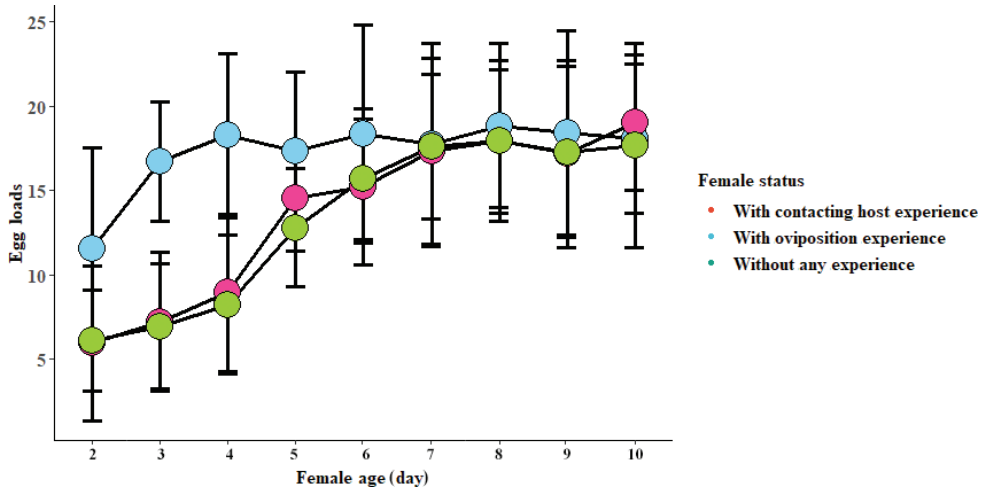


Figure 1. Mean egg loads (+SEs) over time of *Anastatus japonicus* females. Egg loads were measured in terms of the number of mature eggs in the ovaries. The age of measured females ranged from 2 to 10 days old.

Effect of oviposition experience on mate and oviposition choice behaviours

When mating and oviposition choices were presented to females without any experience, most females (29/30) successfully made a choice that preferred for mating ($n = 21$) ($Z = -2.228$, $p = 0.026$) (Fig. 2). In addition, all females with oviposition experience successfully made a distinct choice, while those without experience did not show any preference for mating ($n = 13$) or oviposition ($n = 17$) ($Z = -0.548$, $p = 0.584$) (Fig. 2). Thus, oviposition experience had a significant effect on the above choice results ($\chi^2 = 5.107$, $df = 1$, $p = 0.024$).

Effect of oviposition experience on subsequent host exploration capacity

When an artificial host clutch containing nine *Ant. pernyi* eggs was offered for oviposition, females with oviposition experience produced a mean of 1.78 ± 0.15 offspring (Fig. 3), which was significantly more than that produced by females without any oviposition experience (0.92 ± 0.12) (paired-samples t test, $t = 3.515$, $df = 8$, $p = 0.001$). In addition, among all the oviposition behaviours, conspecific superparasitism occurred only once (1/43) when two females in a single dish laid eggs in the same host.

Discussion

Anastatus japonicus is a typically synovigenic parasitoid that continuously matures eggs throughout its lifetime. Synovigenic females have been shown to adjust their egg production rate in response to host availability (Papaj 2000). Our study provides

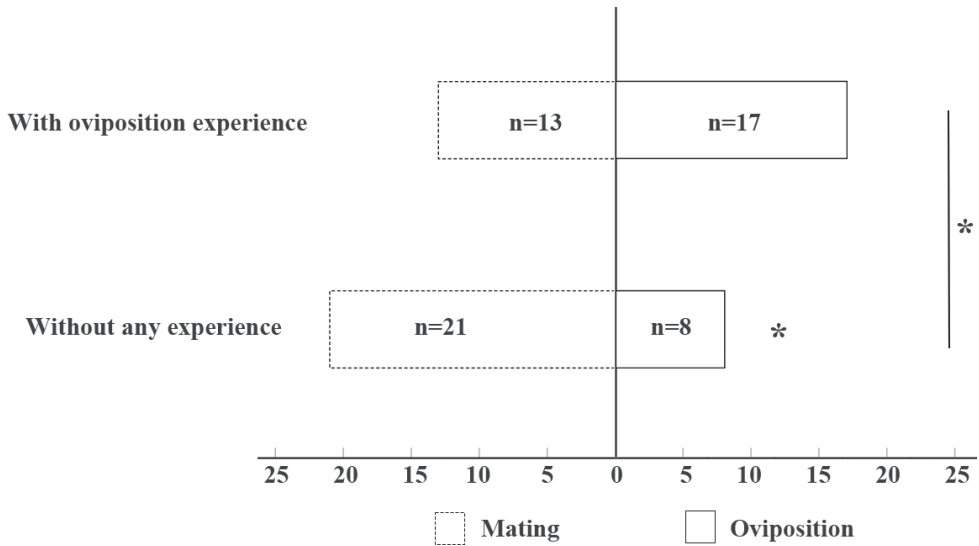


Figure 2. Effect of oviposition experience on mate and oviposition choice behaviours. * $p < 0.05$.

further evidence that the oviposition experience of *Ana. japonicus* females significantly enhances female egg load and rapidly increases the number of mature eggs (Fig. 1). Hosts are important resources for reproduction, and it is predicted that female wasps must balance the risks of egg and time limitation with maximum lifetime fecundity (Minkenberg et al. 1992; Rosenheim 1996; Heimpel et al. 1998; Rosenheim et al. 2008). Thus, *Ana. japonicus* females with oviposition experience are likely to reduce the risk of egg limitation by rapidly increasing their egg loads. Similar to the study in the parasitoid *E. vuilleti* (Crawford) (Casas et al. 2009), oviposition experience might initiate a hormonal cascade leading to egg maturation in *Ana. japonicus* and should be studied further. In contrast to a study in the parasitoid *E. vuilleti*, host contact experience in *Ana. japonicus* did not affect the egg loads in females. This result suggests that oviposition experience is likely more important in egg load maturation than transitory host contact in *Ana. japonicus*. A limitation of this study was that it did not consider the effects of host density in *Ana. japonicus*, as a fixed number of host eggs was provided. The density of hosts in the environment has been suggested to be directly linked to egg maturation rates in many studies (Rosenheim 1996; Rosenheim et al. 2000; Segoli and Rosenheim 2013). Usually, a high host density elicits production of a larger egg load (Bodin et al. 2009; Casas et al. 2009). However, a negative effect of host density on egg load was observed in the soybean aphid parasitoid *Binodoxys communis* (Gahan) (Dieckhoff et al. 2014). Thus, the effect of host density on egg load should be studied and considered in further research.

Hymenopterans are haplodiploid; thus, virgin females can produce male offspring before mating (Cook 1993; Heimpel and de Boer 2008). Hypothetically, virgin females need to evaluate the following trade-offs: (1) search for hosts and produce sons

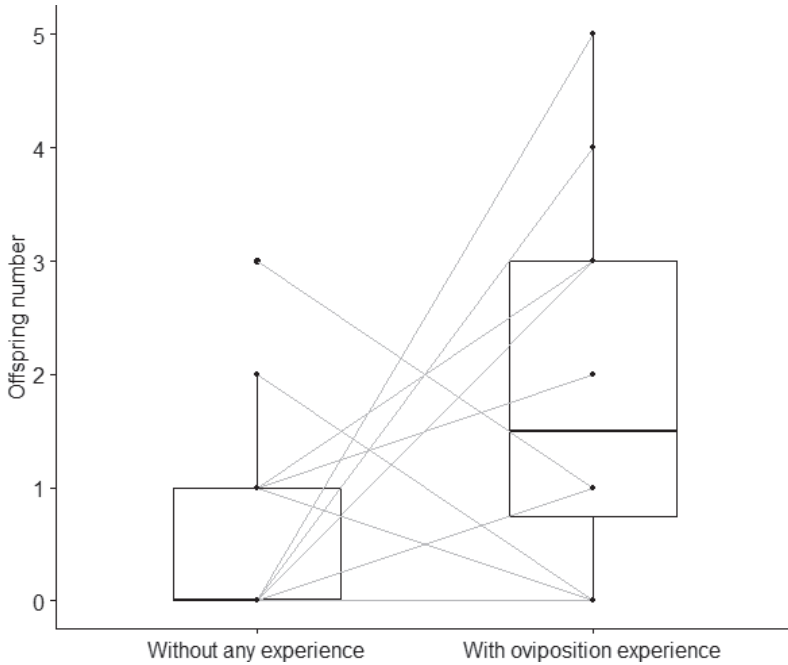


Figure 3. Box plot for paired data of offspring number laying by female with oviposition experience and female without any oviposition experience in a dish. Boxes: 25th and 75th percentiles; heavy line: median; whiskers: 1.5 times the interquartile range of the data.

immediately or (2) search for mates and perhaps produce both sons and daughters later in life (Godfray 1990; Godfray and Hardy 1993; Godfray 1994; Fauvergue et al. 2008). In *Ana. japonicus*, the results showed that virgin females preferred to complete mating first. A specific local mating system likely contributed to the preference for mating. It may be a result of long-term evolution that female dispersal occurs before mating. In addition, virgin *Ana. japonicus* may have lower fitness than mated females, that only produces male offspring. However, our study showed that the oviposition experience of females changed the behavioural preference from mating to oviposition. A potential explanation for oviposition experience influencing subsequent oviposition behaviour in *Ana. japonicus* females is that females with oviposition experience may fine-tune behaviours closely associated with reproduction (Pyle et al. 1991). Alternatively, compared to females without experience, those with oviposition experience had larger egg loads, indicating that these individuals had a higher risk of time limitation. Time-limited species often have large egg loads or the ability to quickly replenish their egg supply, so their reproductive success is proportional to the number of hosts they are able to attack during their lifetime (Stephens and Krebs 1986; Charnov and Stephens 1988).

Thus, oviposition experience of females changed the behavioural preference from mating to oviposition in our species, may be more expected to achieve the reproductive success in response to the risk of time limitation.

Generally, in addition to egg load, oviposition experience influenced female *Ana. japonicus* reproductive behaviour, shifting virgin female behavioural preference from mating to oviposition, allowing more eggs to be laid per host clutch. The change in behavioural preference from mating to oviposition may be a direct effect of oviposition experience in females. In our study, when an artificial host clutch containing nine *Anth. pernyi* eggs was offered for oviposition, females with oviposition experience laid a mean of 1.78 ± 0.15 eggs, which was significantly more than that laid by females without oviposition experience. In addition, during oviposition in a host, parasitoids learn to recognize particular visual and olfactory stimuli of the host and use these cues to modify subsequent behaviours (Vet et al. 1995; Vinson 1998). Thus, oviposition experience might also be associated with an increased hatch rate and increased host acceptability, resulting in more eggs laid per clutch. In addition, among all the oviposition behaviours observed in the current study, conspecific superparasitism occurred only once (1/43), as two females in a dish oviposited in the same host. Females exhibited a host discrimination ability and could identify parasitised hosts to avoid wasting eggs (Liu et al. 2018). Our experimental design including a large host number for females may also have contributed to the general absence of conspecific superparasitism.

Anastatus japonicus is an egg parasitoid of *L. dispar* (Crossman 1925; Kurir 1944; Avci 2009; Alalouni et al. 2013) and a potential biological control agent of this species in North America (Crossman, 1925; Yan et al. 1989). Great efforts have been made to mass rear *Ana. japonicus* for the control of *C. japonica* in addition to *L. dispar* in China, and the eggs of *Ant. pernyi* are suitable factitious hosts (Yan et al. 1989). Our study suggested that females with oviposition experience had a higher reproductive value, with larger egg loads and a preference for oviposition. Therefore, in the rearing of *Ana. japonicus* for biological control, hosts can be provided before the release of wasps so that the female wasps can gain oviposition experience. This will likely improve the reproductive value of the released female wasps so that the wasps can parasitize more hosts, improving the efficacy of biological control.

References

- Abe J, Innocent TM, Reece SE, West SA (2010) Virginity and the clutch size behavior of a parasitoid wasp where mothers mate their sons. *Behavioral Ecology* 21: 730–738. <https://doi.org/10.1093/beheco/arq046>
- Adamson M, Ludwig D (1993) Oedipal mating as a factor in sex allocation in haplodiploids. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences* 341(1296): 195–202. <https://doi.org/10.1098/rstb.1993.0103>
- Alalouni U, Schädler M, Brandl R (2013) Natural enemies and environmental factors affecting the population dynamics of the gypsy moth. *Journal of Applied Entomology* 137: 721–738. <https://doi.org/10.1111/jen.12072>
- Asgari S, Rivers DB (2011) Venom proteins from endoparasitoid wasps and their role in host-parasite interactions. *Annual Review of Entomology* 56(1): 313–335. <https://doi.org/10.1146/annurev-ento-120709-144849>

- Avci M (2009) Parasitoid complex and new host plants of the gypsy moth, *Lymantria dispar* L. in the Lakes district, Turkey. *Journal of Animal and Veterinary Advances* 8: 1402–1405.
- Bates D, Maechler M, Bolker B, Walker S, Christensen RHB, Singmann H, Dai B, Scheipl F, Grothendieck G, Green P, Fox J, Bauer A, Krivitsky PN (2018) Package ‘lme4’. Version 1(17): 437.
- Bodin A, Jaloux B, Delbecque JP, Vannier F, Monge JP, Mondy N (2009) Reproduction in a variable environment: How does *Eupelmus vuilleti*, a parasitoid wasp, adjust oogenesis to host availability? *Journal of Insect Physiology* 55(7): 643–648. <https://doi.org/10.1016/j.jinsphys.2009.04.003>
- Brown MW, Cameron EA (1982) Natural enemies of *Lymantria dispar* (Lep.: Lymantriidae) eggs in central Pennsylvania, USA, and a review of the world literature on natural enemies of *Lymantria dispar* eggs. *Entomophaga* 27: 311–322. <https://doi.org/10.1007/BF02374814>
- Brown MW (1984) Literature review of *Ooencyrtus kuvanae* (Hym.: Encyrtidae), an egg parasite of *Lymantria dispar* (Lep.: Lymantriidae). *Entomophaga* 29: 249–265. <https://doi.org/10.1007/BF02372112>
- Casas J, Vannier F, Mandon N, Delbecque JP, Giron D, Monge JP (2009) Mitigation of egg limitation in parasitoids: immediate hormonal response and enhanced oogenesis after host use. *Ecology* 90: 537–545. <https://doi.org/10.1890/08-0507.1>
- Charnov EL, Stephens DW (1988) On the evolution of host selection in solitary parasitoids. *The American Naturalist* 132(5): 707–722. <https://doi.org/10.1086/284883>
- Cook JM (1993) Sex determination in the Hymenoptera: a review of models and evidence. *Heredity* 71: 421–435. <https://doi.org/10.1038/hdy.1993.157>
- Crawley M (1993) *GLIM for Ecologists*. Blackwell Scientific, Oxford.
- Crawley M (2007) *The R Book*. Wiley, Chichester, 942 pp. <https://doi.org/10.1002/9780470515075>
- Crossman SS (1925) Two imported egg parasites of the gypsy moth, *Anastatus bifasciatus* Fonsc and *Schedius kuvanae* Howard. *Journal of Agricultural Research* 30: 643–675.
- Dieckhoff C, Theobald JC, Wäckers FL, Heimpel GE (2014) Egg load dynamics and the risk of egg and time limitation experienced by an aphid parasitoid in the field. *Ecology and Evolution* 4(10): 1739–1750. <https://doi.org/10.1002/ece3.1023>
- Fauvergue X, Genco AL, Pinto ML (2008) Virgins in the wild: mating status affects the behavior of a parasitoid foraging in the field. *Oecologia* 156: 913. <https://doi.org/10.1007/s00442-008-1037-7>
- Flanders SE (1950) Regulation of ovulation and egg disposal in the parasitic Hymenoptera. *Canadian Entomologist* 82: 134–140. <https://doi.org/10.4039/Ent82134-6>
- Godfray HCJ, Hardy ICW (1993) Sex ratio and virginity in haplodiploid insects. Chapman & Hall, London, 402–417. https://doi.org/10.1007/978-1-4684-1402-8_12
- Godfray HCJ (1990) The causes and consequences of constrained sex allocation in haplodiploid animals. *Journal of Evolutionary Biology* 3: 3–17. <https://doi.org/10.1046/j.1420-9101.1990.3010003.x>
- Godfray HCJ (1994) *Parasitoids: Behavioral and Evolutionary Ecology*. Princeton University Press, Princeton, 367 pp. <https://doi.org/10.1515/9780691207025>
- Hassan SA (1993) The mass rearing and utilization of *Trichogramma* to control lepidopterous pests: achievements and outlook. *Pesticide Science* 37(4): 387–391. <https://doi.org/10.1002/ps.2780370412>

- Heimpel GE, de Boer JG (2008) Sex determination in the Hymenoptera. *Annual Review of Entomology* 53: 209–230. <https://doi.org/10.1146/annurev.ento.53.103106.093441>
- Heimpel GE, Mangel M, Rosenheim JA (1998) Effects of time limitation and egg limitation on lifetime reproductive success of a parasitoid in the field. *The American Naturalist* 152: 273–289. <https://doi.org/10.1086/286167>
- Hougardy E, Bezemer TM, Mills NJ (2005) Effects of host deprivation and egg expenditure on the reproductive capacity of *Mastrus ridibundus*, an introduced parasitoid for the biological control of codling moth in California. *Biological Control* 33: 96–106. <https://doi.org/10.1016/j.biocontrol.2005.01.013>
- Hoy MA (1976) Establishment of gypsy moth parasitoids in North America: an evaluation of possible reasons for establishment or non-establishment. In: Anderson JF, Kaya HK (Ed.) *Perspectives in Forest Entomology*. Academic Press, New York, NY, USA, 215–232.
- Jervis MA, Heimpel GE, Ferns PN, Harvey JA, Kidd NAC (2001) Life-history strategies in parasitoid wasps: a comparative analysis of ‘ovigeny’. *Journal of Animal Ecology* 70: 442–458. <https://doi.org/10.1046/j.1365-2656.2001.00507.x>
- Kurir A (1944) *Anastatus disparis* Ruschka Eiparasit des *Lymantria dispar* L. *Journal of Applied Entomology* 30: 551–586. <https://doi.org/10.1111/j.1439-0418.1944.tb00613.x>
- Li BJ, Lou JX (1992) Preliminary studies on *Anastatus disparis* (Hymenoptera: Eupelmidae), an egg parasitoid of gypsy moth. *Chinese Journal of Biological Control* 8(3): 144.
- Liu PC, Hao DJ (2019) Behavioural and transcriptional changes in postmating females of an egg parasitoid wasp species. *Royal Society Open Science* 6(1): 181453. <https://doi.org/10.1098/rsos.181453>
- Liu PC, Luo J, Tian S, Wen SY, Wei JR, Hao DJ (2018) Facultative production of multiple-egg clutches in a quasi-gregarious parasitoid: fitness gains for offspring at low developmental temperature. *Behavioral Ecology and Sociobiology* 72: 39. <https://doi.org/10.1007/s00265-018-2458-x>
- Liu PC, Men J, Zhao B, Wei JR (2017) Fitness-related offspring sex allocation of *Anastatus disparis*, a gypsy moth egg parasitoid, on different-sized host species. *Entomologia Experimentalis et Applicata* 163: 281–286. <https://doi.org/10.1111/eea.12579>
- Liu PC, Wei JR, Wang JJ, Liu JX, Dong LJ (2015) Relationship between the environmental temperatures and development of *Anastatus disparis* (Ruschka) (Hymenoptera: Eupelmidae) and the sex ratio control of the offspring. *Forest pest and disease* 34: 9–14.
- Minkenbergo O, Tatar M, Rosenheim JA (1992) Egg load as a major source of variability in insect foraging and oviposition behavior. *Oikos* 65: 134–142. <https://doi.org/10.2307/3544896>
- Papaj DR (2000) Ovarian dynamics and host use. *Annual Review of Entomology* 45: 423–448. <https://doi.org/10.1146/annurev.ento.45.1.423>
- Powell W (1986) *Enhancing parasitoid activity in crops*. Academic Press, Orlando.
- Pyle P, Spear LB, Sydeman WJ, Ainley DG (1991) The effects of experience and age on the breeding performance of western gulls. *Auk* 108: 25–33.
- Reardon RC (1981) Alternative controls, parasites. In: Doane CC, ML McManus (Ed.) *The Gypsy Moth: Research Toward Integrated Pest Management*. Technical Bulletin USDA, Washington, DC, USA, 299–302.
- Richard R, Casas J (2012) A quantitative framework for ovarian dynamics. *Functional Ecology* 26: 1399–1408. <https://doi.org/10.1111/j.1365-2435.2012.02050.x>

- Rosenheim JA, Heimpel GE, Mangel M (2000) Egg maturation, egg resorption and the costliness of transient egg limitation in insects. *Proceedings of the Royal Society B: Biological Sciences* 267: 1565–1573. <https://doi.org/10.1098/rspb.2000.1179>
- Rosenheim JA, Jepsen SJ, Matthews CE, Smith DS, Rosenheim MR (2008) Time limitation, egg limitation, the cost of oviposition, and lifetime reproduction by an insect in nature. *The American Naturalist* 172: 486–496. <https://doi.org/10.1086/591677>
- Rosenheim JA (1996) An evolutionary argument for egg limitation. *Evolution* 50: 2089–2094. <https://doi.org/10.1111/j.1558-5646.1996.tb03595.x>
- Segoli M, Rosenheim JA (2013) The link between host density and egg production in a parasitoid insect: comparison between agricultural and natural habitats. *Functional Ecology* 27(5): 1224–1232. <https://doi.org/10.1111/1365-2435.12109>
- Stephens DW, Krebs JR (1986) *Foraging Theory*. Princeton University Press, Princeton, 262 pp.
- Tylianakis JM, Didham RK, Wratten SD (2004) Improved fitness of aphid parasitoids receiving resource subsidies. *Ecology* 85: 658–666. <https://doi.org/10.1890/03-0222>
- Vet LEM, Lewis WJ, Cardé RT (1995) Parasitoid foraging and learning. In: *Chemical Ecology of Insects 2*. Chapman & Hall, New York, 65–101. https://doi.org/10.1007/978-1-4615-1765-8_3
- Vinson SB (1998) The general host selection behavior of parasitoid Hymenoptera and a comparison of initial strategies utilized by larvaphagous and oophagous species. *Biological Control* 11: 79–96. <https://doi.org/10.1006/bcon.1997.0601>
- Wajnberg E, Bernstein C, Van Alphen J [Eds] (2008) *Behavioral ecology of insect parasitoids: from theoretical approaches to field applications*. John Wiley & Sons, 462 pp. <https://doi.org/10.1002/9780470696200>
- Wang JJ, Liu XB, Zhang YA, Wen C, Wei JR (2014) The reproductive capability of *Ooencyrtus kuvanae*, reared on eggs of the factitious host *Antheraea pernyi*. *Journal of Applied Entomology* 138: 267–272. <https://doi.org/10.1111/jen.12080>
- Wang ZZ, Liu YQ, Shi M, Huang JH, Chen XX (2019) Parasitoid wasps as effective biological control agents. *Journal of Integrative Agriculture* 18(4): 705–715. [https://doi.org/10.1016/S2095-3119\(18\)62078-7](https://doi.org/10.1016/S2095-3119(18)62078-7)
- Wu ZS, Heimpel GE (2007) Dynamic egg maturation strategies in an aphid parasitoid. *Physiological Entomology* 32: 143–149. <https://doi.org/10.1111/j.1365-3032.2007.00560.x>
- Yan JJ, Xu CH, Gao WC, Li GW, Yao DF, Zhang PY (1989) *Parasites and predators of forest pests*. China Forestry Publishing House, Beijing.
- Yang ZQ, Wang XY, Zhang YN (2014) Recent advances in biological control of important native and invasive forest pests in China. *Biological Control* 68: 117–128. <https://doi.org/10.1016/j.biocontrol.2013.06.010>
- Wu ZS, Hopper KR, Ode PJ, Fuester RW, Chen JH, Heimpel GE (2003) Complementary sex determination in hymenopteran parasitoids and its implications for biological control. *Insect Science* 10(2): 81–93. <https://doi.org/10.1111/j.1744-7917.2003.tb00369.x>