



# Host size and parasite density impact on the efficacy and reproductive output of *Pyemotes zhonghuajia*, a biological control agent of potato tuber moth

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## Abstract

The potato tuber moth (PTM), *Phthorimaea operculella* (Zeller), is a globally significant pest that attacks potatoes and many other Solanaceous crops. The ectoparasitic mite *Pyemotes zhonghuajia* Yu, Zhang & He is a promising biological control agent for PTM. This study investigated the effects of PTM larval body size (small and large) and *P. zhonghuajia* density (50, 150, and 250 mites) on host paralysis, as well as on the development and reproduction of *P. zhonghuajia*, aiming to optimize its mass production and application in PTM management. Our results showed that *P. zhonghuajia* females took significantly longer to paralyze and kill large PTM larvae at the lowest density (50 mites). Increasing mite density significantly decreased the parasitism rate per host, likely due to increased mutual interference among host-searching mites. However, the number of *P. zhonghuajia* females feeding on a single host increased significantly with mite density, resulting in smaller opisthosoma and fewer offsprings, suggesting food competition among females. Host size had a significant positive effect on opisthosoma size, offspring number per opisthosoma, and total offspring produced by *P. zhonghuajia* female, indicating that larger hosts provide more nutrients. The total number of offspring produced by *P. zhonghuajia* females from a host of a given size was similar across mite densities, suggesting that an optimal ratio of 50 *P. zhonghuajia* females per PTM larva is recommended for laboratory mass rearing and field augmentative release.

**Keywords** *Pyemotes zhonghuajia* · Host size · Parasitism density · Opisthosoma diameter · Reproduction

## Introduction

The potato tuber moth (PTM), *Phthorimaea operculella* Zeller (Lepidoptera: Gelechiidae), originated in Central and northern South America and has since globally colonized potato-growing areas in over 90 countries (Rondon 2010; Rondon and Gao 2018), facilitated by

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its high dispersal capacity and anthropogenic activities. PTM is active year-round in most tropical and subtropical regions. It causes significant economic losses by larvae feeding on potato leaves, stems, and tubers (Roux and Baumgärtner 1998; Hanafi 1999; Kroschel et al. 2020), and it increases the risk of fungal and bacterial pathogen infections in the field (Kroschel et al. 2020; Munyaneza and Bizimungu 2022). Moreover, PTM infestation can cause complete loss of potato tubers during storage (Rondon 2010). Climate change is expected to exacerbate the spread of PTM, further increasing economic losses in potato production (Kroschel et al. 2013). Currently, PTM management primarily relies on chemical pesticides such as chloranthraniliprole, cypermethrin, and quinalphos (Raj and Trivedi 1987; Shutko et al. 2021). However, long-term and frequent use has led to reduced control efficacy due to the rapid development of pesticide resistance in PTM populations (Kearar and Sadeh 2007; Baker et al. 2020; Mhatre et al. 2020). Biological control, using natural enemies such as parasitoids, predators, and microorganisms, offers an eco-friendly and effective alternative (Smith 1996; Kearar and Sadeh 2007; Rondon 2010; Ren et al. 2025; Zou et al. 2025).

The genus *Pyemotes* (family Pyemotidae, subclass Acari) comprises many cosmopolitan ectoparasitic mites capable of parasitizing various insect pests across multiple orders, including Coleoptera, Diptera, Hemiptera, Hymenoptera, Homoptera, Isoptera, Lepidoptera, Neuroptera, Strepsiptera, and Thysanoptera (Weiser and Hrdy 1962; Cross 1965; Cross et al. 1975; Moser 1975; Bruce and Wrensch 1990; Marei 1992; Zhong et al. 2007; He et al. 2019; Tian et al. 2020a; Song et al. 2022; Liu et al. 2023). *Pyemotes* mites are considered ideal biocontrol agents in pest management due to their high fecundity, short generation time, female-biased sex ratio, and strong toxicity to hosts (Tomalski et al. 1988; Liu et al. 2008). For example, *Pyemotes zhonghuajia* (Zhang, Yu, and He), a species endemic to China (Yu et al. 2010), has demonstrated exceptional efficacy in parasitizing a wide range of pests, including various agricultural and forestry pests across Lepidoptera (He et al. 2012; Tian et al. 2020a, b; Liu et al. 2020, 2023; Feng et al. 2022; Song et al. 2025), Coleoptera (He et al. 2019), and Diptera (Li et al. 2019; Song et al. 2022).

Species across the genus *Pyemotes* are viviparous, with their immature offspring developing inside the mother's opisthosoma (Chen et al. 2021). The offspring complete their immature development within 4–7 days, depending on environmental temperature (He et al. 2019). A single *P. zhonghuajia* female may produce 100–200 offspring with an extremely female-biased sex ratio (>90%) (He et al. 2019). Male offspring emerge earlier and mate with their siblings upon the emergence of the latter, after which the mated females immediately begin searching for hosts (Bruce 1989). *Pyemotes mites* demonstrate typical traits of parasitic organisms. Before feeding, females paralyze their hosts by injecting venomous saliva (Weiser and Sláma 1964; Tomalski et al. 1988; Chen et al. 2021; Song et al. 2022). A single adult female *P. zhonghuajia* can paralyze and kill a third-instar larva of *Spodoptera litura* (Fabricius) (Lepidoptera: Noctuidae), which is 680,000 times its own body weight, within 3 h (Chen et al. 2021). Liu et al. (2023) report that *P. zhonghuajia* females can kill all instar stages of PTM. Increasing mite density raises mortality rates of mature 4th-instar larvae and pupae. Exposure to *P. zhonghuajia* mites imposes significant negative sublethal effects on PTM pupation rate, female fecundity, and adult longevity. Moreover, these sublethal stresses are transgenerational, resulting in reduced reproduction in the offspring generation. Furthermore, predatory cues from PTM larvae parasitized and killed by *P. zhonghuajia* females may significantly reduce PTM egg hatch, larval pupation, and adult emergence rates (unpublished data). These findings indicate the high potential of *P. zhong-*

*huajia* as a biological control agent for PTM. However, current knowledge provides limited information to support the commercial mass rearing of *P. zhonghuajia*, which hinders the development of biological control programs.

Body size plays a critical role in determining the fitness of organisms, a well-established concept in entomology (Eijs and Van Alphen 1999; Mayhew and Glaizot 2001; Da Rocha et al. 2007). For parasitic species, body size is influenced not only by genetic and physiological mechanisms but also by host quality (MacKauer 1996; Samková et al. 2019). The ‘host size-quality’ hypothesis posits that host size, as a proxy for quality, directly influences the availability of resources necessary for the growth, development, and reproduction of parasitic natural enemies (Charnov et al. 1981; Charnov 1982; Blackburn 1991; Stenberg and Hambäck 2010; Ode and Hunter 2002; West and Sheldon 2002). When a host is immobilized or killed, its resources become finite, compelling parasites to maximize resource utilization to enhance their fitness (Paine et al. 2004; Lykouressis et al. 2009; Zhang et al. 2017). For gregarious parasitic species, parasite/parasitoid density also plays a significant role in shaping fitness outcomes (Waage and Godfray 1985; Harvey et al. 1998). Increasing parasite density leads to intensified competition, reducing individual body size or even causing developmental failure (Zaviezo and Mills 2000; Beckage and Gelman 2001; Bezemer and Mills 2003; Aspin et al. 2024; Bell et al. 2005). Such parasite-host mediated dynamics have been well studied in parasitoid wasps; however, less attention has been given to the parasitic mites, limiting our understanding of factors that determine their fitness under varying conditions of mite density and host size.

In this study, we investigated the effects of host body size and parasite density on host paralysis and mortality, as well as on the development, reproductive potential, and fitness of *P. zhonghuajia*. Our aim is to provide insights that will help optimize the production and application of *P. zhonghuajia*, thereby contributing to the sustainable management of agricultural and forestry pests.

## Materials and methods

### Organism colonies and experimental conditions

We established a colony of *P. operculella* from approximately 200 immature larvae collected in November 2020 from Puding County (105°27'49"E, 26°26'36"N), Anshun City, Guizhou Province, China. PTM larvae were reared on about 5 kg of potato tubers (*cv. Weiyu No. 7*) placed in a plastic box (24 cm × 29 cm × 22 cm), which was housed within a large mesh cage (35 cm × 35 cm × 35 cm, aperture size=0.125 mm). The potato tubers were stacked in two layers, separated by degreasing cotton that served as pupation sites. Newly emerged adults were captured using a 500-ml plastic cup and transferred to another large mesh cage for further breeding. Adult PTM were fed a 10% honey solution applied daily to gauze. The colony was maintained in a climate chamber at 25 ± 1 °C, 65 ± 5% RH, and a 16:8 h (L: D) photoperiod.

The colony of the ectoparasitic mite *P. zhonghuajia* was obtained from the Changli Institute of Pomology, Hebei Academy of Agriculture and Forestry Sciences. Mature 4th-instar PTM larvae were provided as hosts for the mites. This colony was maintained in a climatic cabinet (Ningbo Haishuchang Sea Industry & Trade, China, model RXZ-380 A-LED) at

$25 \pm 1$  °C,  $75 \pm 5\%$  RH, and a 16:8 h (L: D) photoperiod. All experiments were conducted under the same temperature, humidity, and photoperiod conditions.

## Preparation of PTM larvae and parasitic mites

To obtain 4th-instar PTM larvae of different body sizes, 40 newly emerged PTM adults (20 males and 20 females) were randomly collected and paired in 50-mL centrifuge tubes. The tube openings were sealed with two layers of 100-mesh gauze and secured with rubber bands. A 10% honey solution was applied to the upper gauze layer as food. Eggs laid on the lower gauze layer were collected daily and the layer replaced until sufficient eggs were obtained. Eggs hatched four days post-oviposition. 20, 60, or 100 1st-instar larvae were gently transferred onto a potato tuber ( $82.3 \pm 1.3$  g) using a fine brush. Each larval density treatment had five replicates. The potatoes were individually placed in plastic bowls (12.0 cm diameter  $\times$  5.2 cm height) standing on 50 g of sterile dry sand.

Larvae developed to the 4th instar and emerged from tubers after 14–17 days. Fifty 4th-instar larvae from each replicate were individually weighed using an electronic balance precise to 0.0001 mg. Based on their body mass distribution under different rearing densities (supplementary material 1), larvae reared at 20 and 100 individuals per tuber were classified as large and small hosts, respectively, and these two groups were subsequently used in the experiments.

To prepare *P. zhonghuajia* females for experiments, newly emerged female mites and mature 4th-instar PTM larvae were randomly collected from colonies at a ratio of 50:1 and transferred into a small cylinder (4.0 cm diameter  $\times$  1.2 cm height) fixed inside a Petri dish (9.0 cm diameter  $\times$  1.5 cm height) using a fine brush under an electronic microscope (AO-HK830T, Shenzhen Aosvi Optical Instrument Co., Ltd.). Female mites fed on the PTM larvae for approximately seven days; mature female offspring then emerged and dispersed from the cylinder. Ten 4th-instar PTM larvae were evenly placed around the cylinder. Parasitized PTM larvae were transferred to a new Petri dish to initiate a new culture. One 4th-instar larva could host approximately 150, up to 250, female mites. Thus, mite densities of 50, 150, and 250 were set for experiments.

## Experimental setup and data recording

To evaluate *P. zhonghuajia* performance in terms of paralysis, parasitism, development, reproduction, and offspring fitness on PTM larvae, six treatment combinations were tested: three mite densities (50, 150, and 250 female mites) crossed with two host body sizes (large and small). Each treatment included 15 replicates (4th-instar PTM larvae). For each replicate, the target number of female mites was carefully transferred under a microscope using a fine brush and introduced together with a single 4th-instar larva of the designated body size into a small cylindrical container.

Immediately after introduction, five larvae from each treatment were randomly selected. Every 5 min, they were observed under a stereomicroscope. A stopwatch was used to measure the time taken by *P. zhonghuajia* females to paralyze the host (defined as loss of mobil-

ity but still responding to gentle touch with a fine brush) and to kill the host (defined as no response to gentle touch) (Liu et al. 2023).

For the remaining replicates ( $n=10$ ), PTM larvae together with the feeding *P. zhonghuajia* females were maintained in the climate chamber under the conditions described above. During feeding, the mite opisthosoma enlarged in size until day 7, after which the opisthosoma size plateaued and the female began oviposition. From each treatment, 10 replicates (larvae) were randomly selected, and *P. zhonghuajia* females were gently brushed off their hosts under a microscope. For each replicate, the number of females with a bulged opisthosoma was counted, and the parasitism rate was calculated as the number of mites with bulged opisthosoma divided by the corresponding mite density for that treatment. The opisthosoma size of all *P. zhonghuajia* females was also measured.

To assess reproductive potential relative to opisthosoma size, four females were randomly selected from each replicate ( $n=20$  in total) after measuring opisthosoma size. Each opisthosoma was dissected individually in a water droplet under the microscope, and the number of offspring was counted. The total number of offspring produced per single PTM larva was estimated by multiplying the average number of offspring per opisthosoma by the number of *P. zhonghuajia* females parasitizing that larva.

## Data analysis

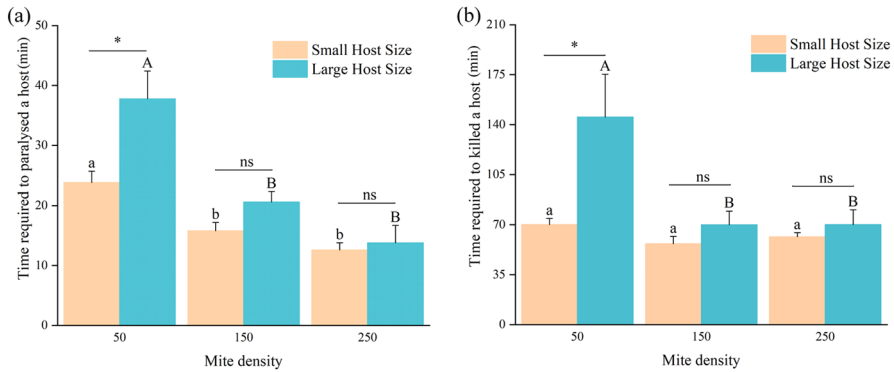
Analysis of variance (ANOVA, GLM Procedure) was used to analyze data on the time required by *P. zhonghuajia* females to paralyze and kill PTM larvae, the number of females feeding on a host, opisthosoma size, number of offspring per opisthosoma, and total offspring produced per host. Data on the proportion of *P. zhonghuajia* females parasitizing PTM larvae at different mite densities were analyzed using a generalized linear mixed model (GLIMMIX Procedure) with a binomial distribution and logit link function. Tukey's HSD test was applied for multiple comparisons among mite densities. Linear models were used to assess relationships between opisthosoma size and mite number, and between offspring number and opisthosoma size. All analyses were performed using SAS v.9.13 software (SAS Institute, Cary, NC, USA) with a significance level of  $\alpha=0.05$ .

## Results

### Mite density and host body size affecting host paralysis and mortality

*Pyemotes zhonghuajia* females at the lowest density (50 mites) required significantly longer time to paralyze hosts than higher densities of 150 and 250 mites, regardless of host body size ( $F_{2,12} = 13.79$  and  $13.98$  for small and large hosts, respectively;  $P < 0.001$ ) (Fig. 1a). At a mite density of 50, females took significantly longer to paralyze large hosts than small hosts ( $F_{1,8} = 7.75$ ,  $P = 0.0238$ ), but the paralysis time did not differ significantly between small and large hosts at densities of 150 and 250 ( $F_{1,8} = 4.61$  and  $0.15$  for densities of 150 and 250, respectively;  $P > 0.05$ ) (Fig. 1a).

The time required by *P. zhonghuajia* females to kill large hosts was significantly longer at the low mite density of 50 compared to higher densities of 150 and 250 ( $F_{2,12} = 5.18$ ,  $P = 0.0239$ ). For small hosts, killing time was similar across all mite densities ( $F_{2,12} = 2.56$ ,



**Fig. 1** Interactive effects of mite density and host body size on the time required by *P. zhonghuajia* females to paralyze (a) and kill (b) PTM larvae. For a given host size, columns with different letters indicate significant differences among mite densities (ANOVA:  $P < 0.05$ ), whereas identical letters indicate no significant difference. For a given mite density, an asterisk (\*) indicates a significant difference between host sizes ( $P < 0.05$ ), while “ns” denotes no significant difference

$P = 0.1183$ ) (Fig. 1b). Females also took significantly longer to kill large hosts than small hosts at the low mite density of 50 ( $F_{1,8} = 6.19$ ,  $P = 0.0376$ ), but no significant difference was found at mite densities of 150 and 250 ( $F_{1,8} = 1.46$  and  $0.64$ , respectively;  $P > 0.05$ ) (Fig. 1b).

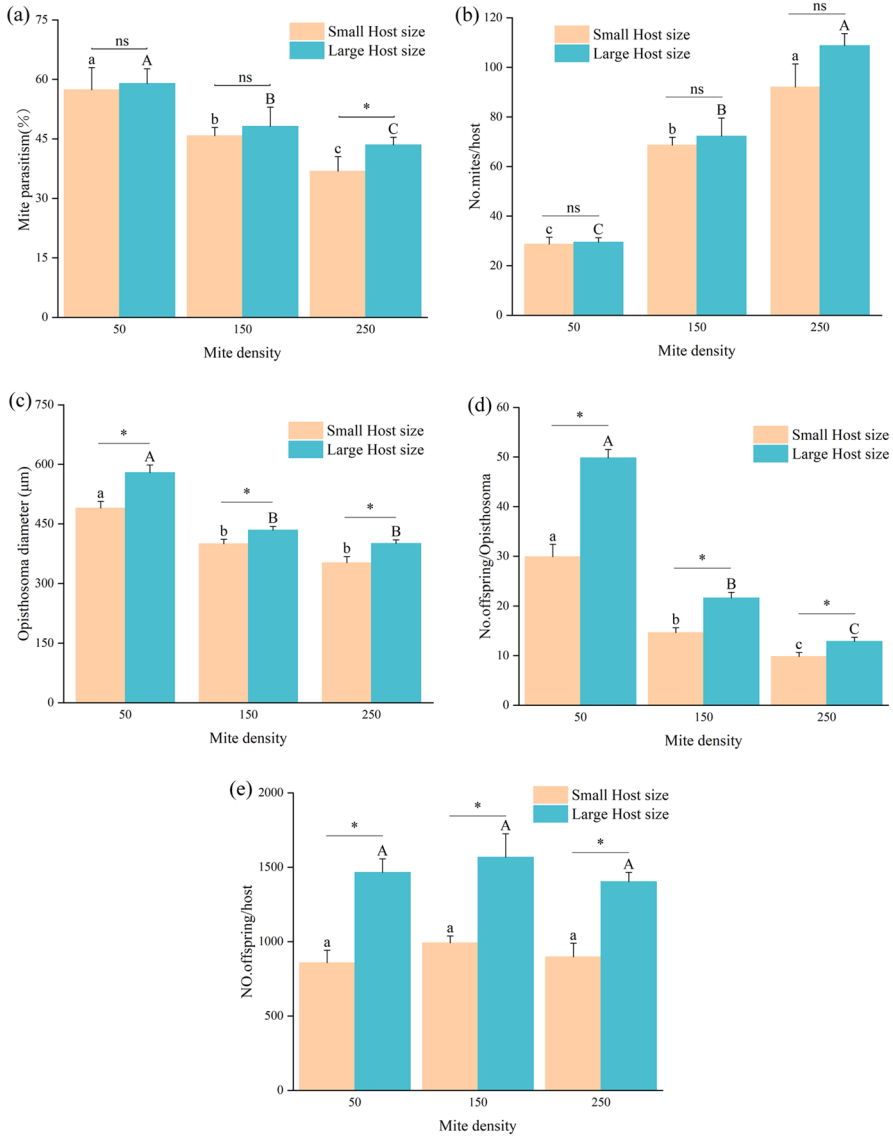
### Mite density and host body size affecting *P. zhonghuajia* female parasitization and fecundity

The proportion of *P. zhonghuajia* females successfully parasitizing hosts decreased significantly with increasing mite density, regardless of host size ( $F_{2,27} = 41.59$  and  $20.63$  for small and large hosts, respectively;  $P < 0.0001$ ) (Fig. 2a). At the highest mite density of 250, significantly more females parasitized large hosts than small hosts ( $F_{1,18} = 23.16$ ,  $P = 0.0001$ ). However, at mite densities of 50 and 150, no significant difference in parasitism rate was observed between small and large hosts ( $F_{1,18} = 0.26$  and  $1.73$ , respectively;  $P > 0.05$ ) (Fig. 2a).

The number of *P. zhonghuajia* females feeding on a host increased significantly with mite density ( $F_{2,27} = 29.41$  and  $59.62$  for small and large hosts, respectively;  $P < 0.0001$ ). However, for each mite density, the number of feeding females did not differ significantly between small and large hosts ( $F_{1,18} = 0.06$ ,  $0.21$ , and  $2.53$  for densities of 50, 150, and 250, respectively;  $P > 0.05$ ) (Fig. 2b).

Opisthosoma size was significantly larger at the low mite density of 50 compared to higher densities of 150 and 250, regardless of host size ( $F_{2,27} = 22.18$  and  $49.14$  for small and large hosts, respectively;  $P < 0.0001$ ). Additionally, opisthosoma size was significantly larger when females parasitized large hosts compared to small hosts across all mite densities ( $F_{1,18} = 11.98$ ,  $5.38$ , and  $7.30$  for densities of 50, 150, and 250, respectively;  $P < 0.05$ ) (Fig. 2c).

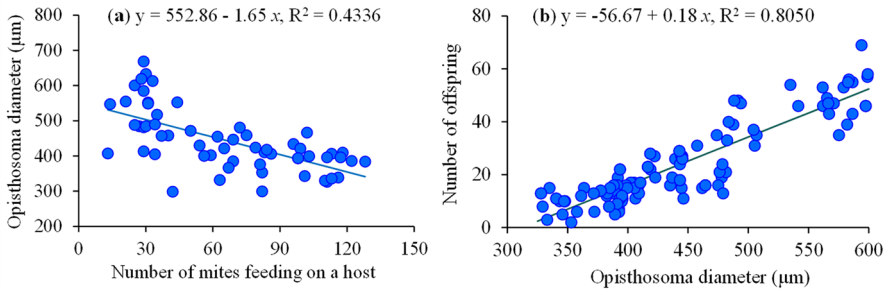
The number of mite offspring per opisthosoma decreased significantly with increasing mite density regardless of host size ( $F_{2,57} = 35.87$  and  $221.97$  for small and large hosts, respectively;  $P < 0.0001$ ). Offspring numbers were significantly higher when females para-



**Fig. 2** Effects of mite density and host body size on *P. zhonghuajia* female parasitism rate (a), number of mites feeding on a host (b), opisthosoma size (c), number of offspring per opisthosoma (d), total number of offspring per PTM larva (e). For a given host size, columns with different letters indicate significant differences among mite densities (ANOVA:  $P < 0.05$ ), whereas identical letters indicate no significant difference. For a given mite density, an asterisk (\*) indicates a significant difference between host sizes ( $P < 0.05$ ), while “ns” denotes no significant difference

sitized large hosts than small hosts at all mite densities ( $F_{1,38} = 42.31, 14.38, \text{ and } 6.69$  for densities of 50, 150, and 250, respectively;  $P < 0.05$ ) (Fig. 2d).

The total number of mite offspring that developed from a single PTM larva did not differ significantly among mite densities for either small or large hosts ( $F_{2,27} = 0.80 \text{ and } 0.56$  for



**Fig. 3** Relationships between opisthosoma size and number of mites feeding on a host (a), and between number of offspring and opisthosoma size (b)

**Table 1** Relationship between opisthosoma size and offspring production in *P. zhonghuajia*

| Opisthosoma size (Mean ± SE) | 95% CI        | N  | Offspring per Opisthosoma (Mean ± SE) | 95% CI      |
|------------------------------|---------------|----|---------------------------------------|-------------|
| 348.40 ± 3.34                | 341.40–355.39 | 20 | 7.85 ± 0.74                           | 6.30–9.40   |
| 394.21 ± 2.60                | 388.76–399.65 | 20 | 14.65 ± 1.41                          | 11.70–17.60 |
| 437.56 ± 2.72                | 431.88–443.24 | 20 | 21.65 ± 1.19                          | 19.16–24.14 |
| 480.52 ± 3.62                | 472.95–488.09 | 20 | 29.90 ± 2.54                          | 24.58–35.22 |
| 576.53 ± 4.05                | 568.05–585.01 | 20 | 49.85 ± 1.72                          | 46.26–53.44 |

Note: Opisthosoma size is expressed in µm, and offspring number is presented as Mean ± SE

small and large hosts, respectively;  $P > 0.05$ ). However, significantly more offspring were produced when *P. zhonghuajia* females parasitized large hosts compared to small ones ( $F_{1,38} = 24.18, 12.29, \text{ and } 20.83$  for mite densities of 50, 150, and 250, respectively;  $P < 0.01$ ) (Fig. 2e).

### Relationship between opisthosoma size and mite number, and between offspring number and opisthosoma size

Opisthosoma size significantly decreased with increasing numbers of females feeding on a host ( $F_{1,58} = 44.41, P < 0.0001$ ) (Fig. 3a). The exact measurements of opisthosoma size and the corresponding number of offspring are summarized in Table 1. Regression analysis showed that the number of offspring increased significantly with increasing opisthosoma size ( $F_{1,118} = 487.10, P < 0.0001$ ) (Fig. 3b).

### Discussion

Ectoparasitic mites, such as species in the *Pyemotes* genus, need to paralyze and kill their hosts by injecting venomous saliva before feeding (Weiser and Sláma 1964; Tomalski et al. 1988; Chen et al. 2021; Song et al. 2022). However, this venomous injection elicits immune responses in the hosts, activating both hemocytes-based and humoral immunity (Shi et al. 2022), as has been widely documented in various ectoparasitoid–host systems (e.g., Cai et

al. 2004; Er et al. 2010; Teng et al. 2016; Li et al. 2018; Yang et al. 2019; Shi et al. 2022), including the interaction between the ectoparasitic mite *P. zhonghuaia* and the fall armyworm *Spodoptera frugiperda* (Song et al. 2024).

Our results show that *P. zhonghuaia* females required significantly more time to paralyze and kill large PTM larvae than small ones, especially at low mite density (i.e., 50 mites) (Fig. 1), even though the number of mites per host was similar for each density treatment (Fig. 2b). These findings suggest a body size-dependent immune response in PTM larvae to mite attack, which may represent a general rule in animals (Brooks 2023; Ejsmond et al. 2023). Moreover, the longer time taken to reduce larger PTM larvae may also result from their greater robustness. For example, in the gregarious ectoparasitoid *Sclerodermus harmandi*, females take longer to lay eggs on larger *Monochamus alternatus* larvae (Liu et al. 2011). Prior work also shows that parasitism by *P. zhonghuaia* may suppress host immunity by reducing total hemolymph protein content in the beetle *Semanotus bifasciatus* (Zhou et al. 2010). It is therefore not surprising that higher volumes of venomous saliva, injected by more mites at higher densities (150 and 250), significantly shortened the time required to paralyze and kill hosts, particularly smaller ones (Fig. 1). Thus, large PTM larvae may mount stronger antipredator responses via both enhanced physiological immunity and physical vigor, even though they ultimately cannot escape parasitism.

Mutual interference among host-searching predators or parasitoids can reduce foraging efficiency, thereby lowering parasitism or predation rates (e.g., Beddington 1975; Visser et al. 1999; Skalski and Gilliam 2001; DeLong and Vasseur 2011; Mougi 2022; Alebraheem 2023; Ishaque et al. 2023; Clemente et al. 2024). Additionally, many studies have shown that ectoparasite abundance tends to increase with host body size, as larger hosts are easier targets and provide more space and resources (Poulin and Rohde 1997; Grutter and Poulin 1998; Poulin 1999; Henri and Van Veen F 2011; Henriksen et al. 2023). In our study, parasitism rates by *P. zhonghuaia* significantly declined with increasing mite density (Fig. 2a), indicating possible mutual interference, especially at the highest density. Interestingly, this reduction in parasitism rate did not result in fewer mites feeding on the host; in fact, the number of feeding females increased with mite density, regardless of host size (Fig. 2b). This suggests that the success of *P. zhonghuaia* in locating and feeding on hosts is density-dependent, rather than host-size-dependent. Future research into the functional and numerical responses of *P. zhonghuaia* relative to host and mite densities will help to clarify its foraging efficiency and biological control potential.

*Pyemotes mites* are idiobiont ectoparasitoids that permanently paralyze their hosts, thereby arresting host growth and development. Consequently, host size at parasitism integrates both resource quantity and host quality, including nutritional composition and physiological condition (Holmes et al. 2023). In lepidopteran larvae, larger or later-instar individuals typically contain higher protein and lipid reserves, which are critical for somatic growth and egg production in ectoparasitoids (Hu et al. 2002; Farahani et al. 2016). Because host quality is effectively fixed at parasitism in idiobiont systems, variation in initial host size can have disproportionate effects on maternal performance and reproductive output (Wang and Messing 2004; Harvey et al. 2013). In our study, the significant decrease in opisthosoma size with increasing mite density (Fig. 2c) and number of feeding females (Fig. 3a) suggests strong nutrient limitation under intensified intraspecific competition. By contrast, larger PTM larvae functioned as higher-quality food sources, supporting significantly larger opisthosoma size (Fig. 2c), higher numbers of offspring per opisthosoma (Fig. 2d), a posi-

tive relationship between offspring number and opisthosoma size (Fig. 3b), and a greater total number of offspring per host larva (Fig. 2e). Similar size- and quality-dependent patterns have been reported in other idiobiont ectoparasitoids attacking lepidopteran hosts, where larger larvae support greater brood sizes and enhanced female fecundity (Wang and Messing 2004; Harvey 2005; Silva-Torres et al. 2009; Harvey et al. 2013; Knapp and Knappová 2013; Zermoglio et al. 2024). Although larger hosts may require greater venom investment to overcome stronger immune and physical defenses, their superior nutritional value appears to offset these initial costs, ultimately resulting in higher reproductive returns (Beckage and Gelman 2004; Harvey 2005; Pennacchio and Strand 2006; Jarvis et al. 2008).

The ratio of natural enemies to hosts is a critical factor in optimizing the mass rearing of biological control agents. Both excessive and insufficient predator densities can increase costs and reduce rearing efficiency due to the need to rear both hosts and predators. In augmentative biological control programs, the release rate of natural enemies significantly influences control efficacy, particularly against lepidopteran pests (Crowder 2007; Tian et al. 2020a, b; Feng et al. 2022; Liu et al. 2023). Our findings show that for both host sizes, the total number of offspring produced was not significantly different among the three mite densities (Fig. 2e), suggesting that a ratio of 50 *P. zhonghuaqia* females per PTM larva could be optimal for laboratory mass rearing and field releases. Further experiments are needed to evaluate the rearing efficiency and biological control effectiveness of *P. zhonghuaqia* across a range of release ratios.

## Conclusion

*Pyemotes zhonghuaqia* females typically take longer to paralyze and kill large PTM larvae at the low mite density of 50 individuals. This may be attributed to two main factors. First, fewer mites on a host at low density results in a lower volume of venomous saliva being injected. Second, larger PTM larvae elicit stronger immune responses to attacks by *P. zhonghuaqia* females. Although parasitism rates decrease at higher mite densities due to increased mutual interference, the number of *P. zhonghuaqia* females feeding on each host increases. This leads to smaller opisthosoma sizes and fewer offspring per opisthosoma, indicating intraspecific competition for food among the mites. Host size positively affects opisthosoma size, the number of offspring per opisthosoma, and the total offspring produced per host, suggesting that larger hosts provide more nutritional resources for offspring development. Despite the significantly reduced number of mites feeding per host at higher densities, the total number of offspring produced from a host of a given size remains similar across densities. These findings suggest that a ratio of 50 *P. zhonghuaqia* females per PTM larva may represent an optimal balance for laboratory mass rearing and field augmentative release.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s10493-026-01120-3>.

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**Author contributions** Chenming Xiao performed the fieldwork, analysed and wrote the paper. Xiongzhaoh He contributed to critical analysis of the results and writing the paper. Chenming Xiao, ChengXu Wu, MaoFa

Yang, JianFeng Liu and FangLing Xu conceived and designed the study. Chenming Xiao, Xuelin Li, Di Fan, Long Zhang, Xiongzhao He, Guy Smagghe, and Jifeng Hu processed the samples and performed analyses. All authors read and approved the final version of the manuscript.

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**Data availability** We declare all data is being provided within this manuscript.

## Declarations

**Competing interests** The authors declare no competing interests.

**Declaration of generative AI** We did not use generative AI to write this manuscript.

**Ethical approval** This is an observational study. The Institute of Biological Sciences Research Ethics Committee has confirmed that no ethical approval is required.

**Supplementary Information** Data on host body size, Opisthosoma diameter of *Pyemotes zhonghuajia*, and the corresponding offspring number are provided on the last page of the article.

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