Entomologia Experimentalis et Applicata
Experimental and Applied Entomology

WILEY

ORIGINAL ARTICLE

Foraging Egg Parasitoids Benefit From the Presence of Potential Competitors

Prabitha Mohan[1,2] | Vanshika Pal[1,3] | Abhyudai Singh[4] | Saskya van Nouhuys[1]

[1]Centre for Ecological Sciences, Indian Institute of Science, Bangalore, India | [2]Tata Institute for Genetics and Society, Bengaluru Life Science Cluster (BLiSC), Bengaluru, India | [3]Division of Biological and Life Sciences, School of Arts and Sciences, Ahmedabad University, Ahmedabad, India | [4]Department of Electrical and Computer Engineering, University of Delaware, Newark, Delaware, USA

Correspondence: Saskya van Nouhuys (saskya@iisc.ac.in)

Received: 29 November 2025 | **Revised:** 9 April 2026 | **Accepted:** 16 April 2026

Keywords: competition | exploitative competition | foraging behaviour | intraspecific competition | performance traits | resource use | superparasitism | *Trichogramma chilonis*

ABSTRACT

Competition is generally considered a negative interaction that lowers the fitness of individuals. Studies of competition and fitness traits in parasitoids have primarily focused on interference competition, with less attention paid to parasitoids under exploitative competition. Theoretical studies predict that interference competition will decrease the resource utilisation by parasitoids, while exploitative competition will not. In our study, we investigated the impact of intraspecific exploitative competition among parasitoids on fitness traits, including resource utilisation, the percentage of offspring that emerged from parasitised eggs, and the percentage of female offspring produced from parasitised eggs. We investigated whether these fitness traits were influenced by the presence of conspecific foraging females, as well as by parasitoid and resource densities. Since we were studying the effect of exploitative competition, we used a non-aggressive egg parasitoid, *Trichogramma chilonis*. The host was the stored grain pest, *Corcyra cephalonica*. We found that *T. chilonis* resource utilisation increased in the presence of conspecifics. However, the density of those conspecifics and the resource density did not affect resource utilisation. The presence of conspecific foraging females did not affect the rate of offspring survival. However, at a lower resource density, offspring survival was higher than under resource-abundant conditions. We explored this counterintuitive pattern using a simple mathematical model, which shows that superparasitism, occurring at low host density, can lead to high emergence. This is because, given only some progeny survive, the chance of parasitoid emergence increases with the number of eggs laid in the host. The secondary sex ratio of the progeny was unaffected by the presence of conspecifics or by parasitoid or resource densities. We conclude that for *T. chilonis*, the presence of competitors has a positive effect. Its high performance under competitive conditions may contribute to its efficiency as a biological control agent.

1 | Introduction

Competition is an important biotic factor that is considered a key driver of population dynamics, patterns of species coexistence, and community structure (Bernhardt et al. 2020). Competition can alter the behaviour and life history traits of organisms (Kaplan and Denno 2007; Wauters et al. 2019; Ode et al. 2022) and is generally considered a negative interaction because of its negative fitness consequences (Cody et al. 1975; Forsman et al. 2002; Koutsidi et al. 2024). For instance, under interspecific competition with *Eretmocerus hayati* Rose and Zolnerowich (Hymenoptera: Aphelinidae), *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae) produces more eggs, but of smaller egg size, which results in a low offspring survival rate (Fan et al. 2025). The intensity of competition is affected by both the density of competitors and the availability of

resources (Johnson et al. 2004; Hasegawa and Yamamoto 2009; Pekkonen et al. 2013; Riley and Dybdahl 2015; Wang and Callaway 2021; Tao et al. 2024). For instance, in mosquitoes, density-dependent competition as a result of limited food availability can cause increased juvenile mortality, delayed pupation, and reduced adult longevity (Agnew et al. 2002; Than et al. 2020).

Parasitoid wasps experience more intense competition compared to other higher trophic-level animals because, unlike predators, individual parasitoids rely on a single host for all the resources necessary for their development (Ode et al. 2022). Resource competition happens at various stages of a parasitoid's lifecycle, including both extrinsic competition between adult females for oviposition and intrinsic competition between juveniles inside or on a host for nutrition (Harvey et al. 2013; Cusumano et al. 2016; Ode et al. 2022). Both extrinsic and intrinsic competition can happen between individuals of the same species (intraspecific competition) or between individuals of different species (interspecific competition).

Competition affects several fitness traits of parasitoids, including developmental time, offspring survival, and body size (Harvey et al. 2013, 2019; Visser et al. 2014; Cusumano et al. 2015). Intrinsic competition among multiple parasitoid larvae within a host can cause resource limitation, leading to long development time and small offspring size (Harvey et al. 2009). Under low resource availability, interspecific competition can cause offspring mortality through superparasitism, which in some situations can be advantageous at the individual or population level (van Alphen and Visser 1990; Xu et al. 2013). Competition among adult female parasitoids can also cause a shift in their offspring's primary sex ratio (the sex of eggs laid) by increasing the proportion of males because, at low resource availability, males, which require lower resource requirements, may be more likely to survive than females (Hamilton 1967; King 1993; King and Seidl 1993; Brodeur and Boivin 2004).

Adult female parasitoids foraging for hosts behave differently depending on the density of conspecifics and the density of host resources available (Xu et al. 2013; Couchoux and van Nouhuys 2014; Cusumano et al. 2016; De Rijk et al. 2016). Studies of egg parasitoids show that the number of eggs parasitised by a single female often increases with increasing host and parasitoid density (Kfir 1981, 1983). However, some parasitoids reduce their host patch exploitation time, leaving the patch early in the presence of conspecifics to avoid direct competition (Wajnberg et al. 2000; Robert et al. 2016; Kishani Farahani et al. 2019). For example, the patch exploitation time of a pupal parasitoid, *Pachycrepoideus vindemmiae* Rondani (Hymenoptera: Pteromalidae), decreases with increasing competitors to avoid direct competition (Goubault et al. 2005).

Competition among adult parasitoid females can be divided into interference or exploitative (Cusumano et al. 2016; Ode et al. 2022). Under intraspecific interference competition, parasitoid adult females may either chase away their competitors or physically combat them to guard their host resources (Batchelor et al. 2005; Nakamatsu et al. 2009). Under intraspecific exploitative competition, they will alter their foraging activity spatially or temporally to reduce the direct interaction (Ode et al. 2022). Theoretical models predict that the rate of resource use of parasitoids decreases under interference competition, yet remains unaffected under exploitative competition (Robert et al. 2016). However, empirical evidence of behaviour during exploitative competition and its consequences is scarce (Robert et al. 2016). In this study, we investigated the impact of intraspecific exploitative competition on resource utilisation, the percentage of offspring that emerge, and the secondary sex ratio of offspring produced.

We used a non-aggressive egg parasitoid, *Trichogramma chilonis* Ishii (Hymenoptera: Trichogrammatidae) and eggs of the stored grain pest *Corcyra cephalonica* Stainton (Lepidoptera: Pyralidae) for the study. *Trichogramma chilonis* is a biocontrol agent widely used against pest Lepidoptera species such as *Plutella xylostella* Linnaeus (Lepidoptera: Plutellidae), *Trichoplusia ni* Hübner (Lepidoptera: Noctuidae), and *Crocidolomia pavonana* Fabricius (Lepidoptera: Crambidae) (Miura et al. 1994; Miura and Kobayashi 1998; Singhamuni et al. 2015). Parasitism of *C. cephalonica* eggs, by *T. chilonis* usually produces only a single offspring from one host egg (Chowdhury et al. 2016; Manisha et al. 2020). Experienced *T. chilonis* females can discriminate parasitised from unparasitised eggs using their antennal perception and tend to lay eggs on unparasitised host eggs (Wang et al. 2016).

To study competition, we subjected the wasps to differing resource availability (host egg density) and conspecific density. We hypothesised that individual wasps would parasitise more eggs in the presence of conspecifics. This strategy may help offset the potential loss of their offspring due to superparasitism (Ives 1989). Resource utilisation would be higher under the lower resource condition due to greater competitive pressure. Consequently, we expected the number of eggs parasitised per female parasitoid to increase with increasing parasitoid density and decreasing resource density. We also expected the secondary sex ratio to be less female-biased as the number of conspecifics increased and resource density decreased. Finally, since we found in this study that the percentage of offspring emergence from parasitised eggs increased with parasitoid density under limited resource conditions, we developed a simple probabilistic model to explore the idea that this could be explained by survival under superparasitism, which increases when resources are limited.

2 | Methods

2.1 | Insect Rearing

The initial cultures of the parasitoid *T. chilonis* and its host *C. cephalonica* were obtained from the ICAR-National Bureau of Agricultural Insect Resources, Bengaluru, India, and Cryptox Biosolutions, Kanyakumari, India. The cultures were reared under laboratory conditions at 25°C ± 2°C, 65% ± 5% relative humidity, 12L:12D conditions. The rearing of both insects was based on the protocol published by the Directorate of Plant Protection, Quarantine & Storage, Department of Agriculture & Farmers Welfare, Ministry of Agriculture & Farmers Welfare, Government of India (n.d.). *Corcyra cephalonica* was

TABLE 1 | The number of replicate experimental trials for each measure of parasitoid performance at each parasitoid density and host density treatment. In the host abundant (HA) conditions, host egg availability increases with parasitoid density. In the host limited (HL) condition, the number of host eggs available does not increase with parasitoid density.

	Parasitoid density						
	Control	HA			HL		
Traits	**1 female**	**2 females**	**4 females**	**8 females**	**2 females**	**4 females**	**8 females**
Resource utilisation	78	30	37	21	47	38	20
Total offspring emergence	31	29	35	20	44	38	20
Percentage of female offspring emergence	31	29	35	20	44	38	20

reared on a Sorghum and groundnut-based diet in plastic containers covered with muslin cloth. The moths emerging from these boxes were collected and transferred to breeding cages. The breeding cages were custom-made inverted industrial funnels of a diameter of 200 mm. The wider part of the funnel was covered with mesh, and the moths were transferred through the tail of the funnel. A cotton ball soaked in a 50% honey solution was kept on the top of the funnel tail, which was covered with mesh to prevent moths from escaping. The breeding cage was kept in a plastic tray. The loosely connected *C. cephalonica* eggs that fell into the tray and on the mesh on the widest part of the funnel were removed using a paintbrush, and the eggs collected were stored in a refrigerator at 4°C. The parasitoids were reared on eggs of *C. cephalonica* that had been UV-sterilised to kill the host embryo. The sterilised eggs were pasted on paper cards (hereafter called egg cards) and placed in plastic boxes containing adult parasitoids for parasitisation. The adult parasitoids were also provided with a 50% honey solution. Egg cards for experiments were made by pasting 24-h-old *C. cephalonica* eggs to a $1cm^2$ card and then sterilising the eggs on the card.

2.2 | Experimental Design

To study the effects of parasitoid density, all the test parameters (resource utilisation, the percentage of offspring that emerged, and the secondary sex ratio of offspring) were observed under densities of one, two, four, and eight females. To study the impact of resource density, all the test parameters were observed under Host Abundant (HA) and Host Limited (HL) conditions (Figure S1). In HL conditions, the resource density was kept constant irrespective of the parasitoid density. The size of egg cards for the control and Host Limited (HL) conditions was fixed at $1cm^2$ (containing 500–600 eggs). For the Host Abundant (HA) condition, the size of the card increases with increasing parasitoid density to avoid resource constraints, i.e., $2\times1cm^2$, $4\times1cm^2$ and $8\times1cm^2$, respectively, for 2, 4 and 8 parasitoid densities (Figure S1).

Twenty-four hours before doing the experiments, newly emerged (> 8 h) and mated female parasitoids were introduced into a 35 × 10mm Cell Culture Dishes (Thermo Fisher Scientific, USA) for acclimatization. After 24 h, egg cards were introduced into the Petri dishes containing wasps for each experimental trial. The parasitisation was allowed for 2 h, after which the wasps were removed. Since the $8\times1\,cm^2$ egg cards for eight female densities in HA conditions are larger than the size of the 35 × 10 mm Cell Culture dishes, the wasps and egg cards for this treatment were placed in larger Petri dishes of size 90 × 14 mm (Tarsons Products Pvt. Ltd., India). After the experiment, the egg cards were stored at ambient room temperature during parasitoid development. The number of eggs parasitised in each Petri dish was counted after 4 days, when the parasitised eggs turned from white to black. The wasp offspring emerged from the parasitised eggs within 9 days of parasitisation. The number of offspring that emerged and their sex were recorded after 10 days. All experiments were performed starting at 10:00 am (4 h after light-on) to minimise temporal effects on parasitoid behaviour.

2.3 | Resource Utilisation Analysis

The resource utilisation was studied by comparing the number of eggs parasitised per female under competitive and non-competitive conditions. To examine whether the presence of competitor(s) affects resource utilisation, the number of eggs parasitised per female at 2, 4, and 8 female densities was compared with the non-competitive one-female condition ($n = 78$). We studied the effect of parasitoid density on resource utilisation by comparing the number of eggs parasitised per female between 2, 4, and 8 parasitoid densities. Finally, we also analysed the impact of resource abundance on resource utilisation by using two resource availability conditions- Host Abundant (HA) and Host Limited (RC). The sample sizes used for the study are shown in Table 1.

2.4 | Percentage of Total Offspring and Female Emergence

The percentage of parasitised eggs from which the adult offspring emerged (percentage of total emergence) and the percentage of female offspring that emerged were used to represent juvenile survival and secondary sex ratio, respectively. The impact of the presence of a competitor on the juvenile survival and offspring secondary sex ratio was compared between competitive (2, 4, and 8 female density) and non-competitive one-female conditions ($n = 31$). The impact of parasitoid density (2, 4 and 8 females) and resource density (HA and HL) on performance traits was also compared in this study. The sample sizes for both performance traits are given in Table 1.

2.5 | Statistical Analysis

The resource utilisation per female in the presence and absence of conspecifics was compared using the nonparametric Mann–Whitney *U* test. The resource utilisation per female was compared across varying parasitoid densities in two different resource conditions using the nonparametric Kruskal-Wallis Test and Dunn's test. The effect of different resource abundances (HL vs. HA) on resource utilisation (number of eggs parasitised) was compared using the Student's *t*-test and Mann–Whitney *U* test.

Juvenile survival and the secondary sex ratio across different parasitoid densities were compared using the Kruskal-Wallis test. Dunn's test was conducted as a post hoc analysis. Similarly, the effects of resource abundance on the juvenile survival and secondary sex ratio were compared using the Mann–Whitney *U* test and Welch's *t*-test. The statistical analyses were done using R version 4.3.3 (R Core Team 2024).

2.6 | Mathematical Model of Progeny Emergence Rate Under Resource-Constrained Conditions

We hypothesise that superparasitism (multiple females laying eggs in the same host) of hosts that are among the failed 25% parasitism may increase the likelihood that at least one offspring successfully emerges. Consequently, this could raise the overall emergence rate. To investigate this possibility, we modelled the relationship between offspring emergence rate and the number of females foraging together, across a range of host egg densities. The model incorporated oviposition rates and survival (emergence) data from our observations.

Let there be M high-quality host eggs that are parasitised by N wasps with p being the probability of an individual host egg being parasitised by a single wasp. Then, the probability that a host is parasitised by i of the N parasitoids is given by the Binomial distribution:

$$\frac{N!}{i!(N-i)!}p^i\,(1-p)^{N-i}, i \in \{0,1,\ \ldots\ N\}.$$

Plugging in $i = 0$ gives probability that an egg escapes parasitism,

$$(1-p)^N$$

and yields the following average number of parasitised high-quality hosts ($i \geq 1$)

$$M\left(1-(1-p)^N\right).$$

For a given number of adult female wasp $N \in \{1,2,4,8\}$, the probability p is chosen to match the parasitised eggs per wasp seen in the data (Figure 1), 7 parasitised eggs for a single wasp ($N = 1$) and 20 eggs per wasp for $N \in \{2,4,8\}$.

Also based on the data (Figure 3), we set the juvenile parasitoid survival probability inside the host egg to be $s = 0.75$ when the egg is parasitised by a single wasp. Assuming a random model of juvenile wasp survival, an egg parasitised by i wasps will have adult offspring emergence with probability

$$\left(1-(1-s)^i\right), i \in \{1,\ \ldots\ N\}.$$

This gives the probability of adult wasp emergence from a parasitised egg to be 75% (as expected for $i = 1$ when there are no superparasitism), and with superparasitism 94% (for $i = 2$) and 98% (for $i = 3$).

The fraction of parasitised eggs resulting in parasitoid emergence is now given by

$$\frac{\sum_{i=1}^{N}\frac{M\,N!}{i!(N-i)!}p^i\,(1-p)^{N-i}\left(1-(1-s)^i\right)}{M\left(1-(1-p)^N\right)}.$$

Recall from above that the probability p is dependent on M as the number of parasitised eggs per wasp is fixed.

3 | Results

3.1 | Effect of Competition on Resource Utilisation

The number of eggs parasitised per female in the presence of conspecifics (20.42 ± 10.15) was approximately 3.3 times higher than in the absence of conspecifics (6.14 ± 10.18, $W = 2332.5$, $p < 0.0001$, Figure 1). The same trend was observed in the resource utilisation per female across varying parasitoid densities at both HL and HA resource conditions.

In Host Abundant (HA) condition resource utilisation by parasitoids foraging alone was lower than when foraging with others ($\chi^2(3) = 66.5$, $p \leq 0.0001$, Figure 2a). That is, post hoc analysis pairwise comparisons using Dunn's test indicate a significant difference between 1–2 ($Z = 5.15$, $p \leq 0.0001$), 1–4 ($Z = 7.54$, $p \leq 0.0001$), 1–8 ($Z = 3.14$, $p = 0.01$). However, there was no significant difference among the multiple female treatments (2–4 and 2–8 female parasitoid) except between 4 and 8 ($Z = -2.68$, $p = 0.04$) females. In Host Limited (HL) condition resource utilisation by parasitoids alone was lower also than when foraging with others ($\chi^2(3) = 67.2$, $p \leq 0.0001$, Figure 2b), post hoc analysis pairwise comparisons using Dunn's test indicate a significant difference between 1 and 2 ($Z = 6.23$, $p \leq 0.0001$), 1–4 ($Z = 6.89$, $p \leq 0.0001$), and 1–8 ($Z = 4.29$, $p \leq 0.0001$). And again, there was no significant difference among the multiple parasitoid treatments (2–4, 2–8 and 4–8 female parasitoid densities). In the HA condition, the number of eggs parasitised at two female density is 18.5 ± 9.38, four female density is 23.95 ± 8.98, and eight female density is 13.67 ± 6.84. Similarly, in the HL condition, the number of eggs parasitised per female at two female density is 20.79 ± 13.94, four female density is 22.93 ± 7.17, and eight female density is 19.01 ± 6.61.

We also found that, averaging over the female densities, resource density did not significantly affect resource utilisation in the parasitoids ($t(191) = -1.20$, $p = 0.23$). The mean resource utilisation in the HA condition was 19.47 ± 9.43; in the HL condition, it was 21.23 ± 10.69. However, the pairwise comparison across different parasitoid densities showed lower resource utilisation at the eight female density ($t(39) = -2.5407$, $p = 0.01$) under the HA condition than the HL condition, while

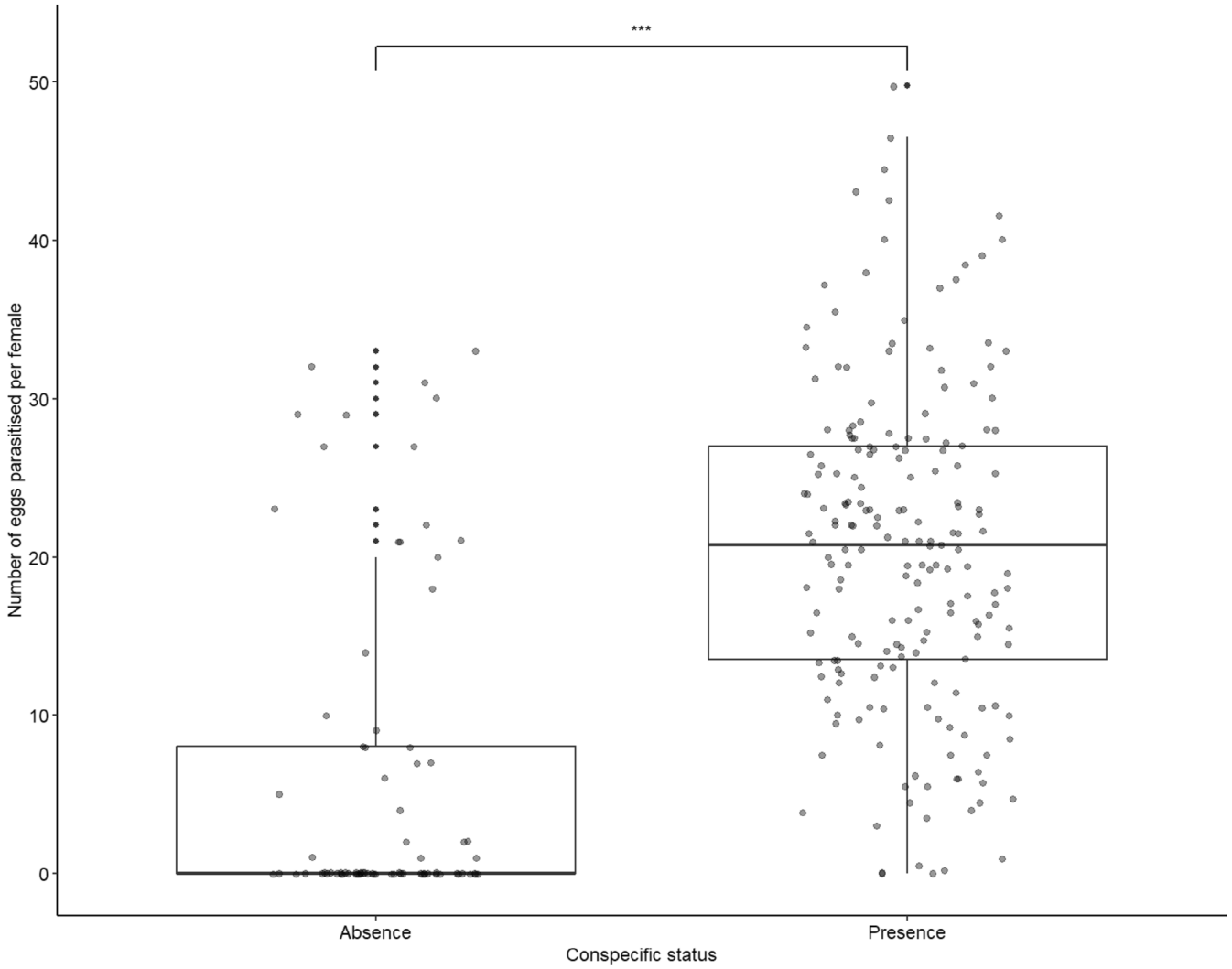

FIGURE 1 | Impact of presence of conspecifics on resource utilisation irrespective of resource or parasitoid densities: The number of eggs parasitised per female wasp in the presence and absence of conspecifics. Box plots represent the interquartile range, with the thick horizontal line indicating the median. The whiskers represent the data range, and individual jitter points represent each data point. Brackets indicate comparisons between groups. The number of asterisks, '***', indicates a higher level of significance (≤ 0.001).

no significant difference was observed between two female ($W = 648$, $p = 0.55$) and four female densities ($t(73) = 0.3269$, $p = 0.74$) (Figure S2).

3.2 | Effect of Competition on Juvenile Survival and the Secondary Sex Ratio

The juvenile survival was not affected by the presence of conspecific foraging parasitoids or by the parasitoid densities in the HL condition ($\chi^2(3) = 1.85$, $p = 0.60$; Figure 3b). However, the juvenile survival in the HA condition differed with parasitoid density ($\chi^2(3) = 8.53$, $p = 0.03$; Figure 3a). Post hoc Dunn's tests showed that the juvenile survival significantly differed between the parasitoid densities of 1 and 4 ($Z = 2.68$, $p = 0.04$), and not significant difference is observed between 1 and 2 ($Z = 0.43$, $p = 0.66$), 1–8 ($Z = 1.31$, $p = 0.75$), 2–4 ($Z = 2.19$, $p = 0.14$), 2–8 ($Z = 0.90$, $p = 0.72$), and 4–8 ($Z = -1.02$, $p = 0.92$) female densities. The average juvenile survival when there is only one female wasp was 75.5 ± 25.2. In the HA condition, the average juvenile survival in the two-female, four-female, and eight-female conditions, respectively, is 73.2 ± 23.9, 60.5 ± 26.7, and 69.8 ± 20.7. For the HL condition, juvenile survival under two females is 84.2 ± 16.9, under four females is 85 ± 13.7, and under eight females is 87.5 ± 5.7.

Juvenile survival was 1.2× higher in the HL conditions than in the HA conditions ($W = 2098$, $p < 0.0001$; Figure 4a). The average juvenile survival in the HA condition was 67.1 ± 24.5, and the HL condition was 85.1 ± 14.1. Similarly, the pairwise comparisons across different parasitoid densities also showed significant differences at two ($W = 439$, $p = 0.02$), four ($W = 231$, $p < 0.0001$), and eight female densities ($t(47.6) = -2.2182$, $p = 0.03$; Figure 4b).

On average, the secondary sex ratio at one female density is 68.75 ± 24.17. The secondary sex ratio is not affected by the presence of conspecific females or by the parasitoid density in either the HA ($\chi^2(3) = 3.36$, $p = 0.33$) and HL ($\chi^2(3) = 5.50$, $p = 0.13$) conditions (Figure S3). Similarly, resource density also did not affect the secondary sex ratio ($W = 4076$, $p = 0.57$;

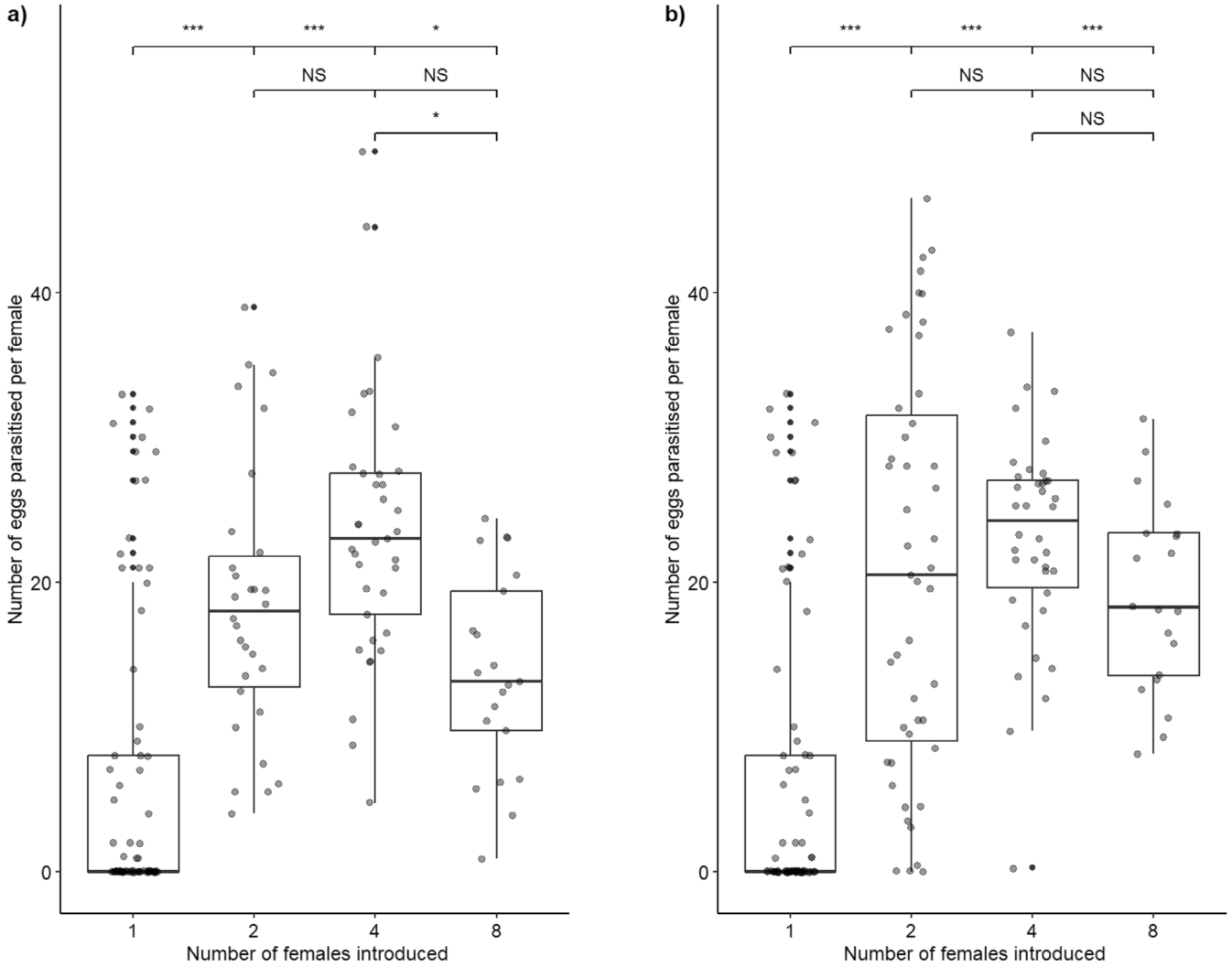

FIGURE 2 | Impact of parasitoid density on resource utilisation under different host density conditions: The number of eggs parasitised per female wasp is shown across varying parasitoid densities (1, 2, 4, and 8 females) under (a) Host Abundant (HA) and (b) Host-Limited (HL) conditions. Box plots represent the interquartile range, with the thick horizontal line indicating the median. The whiskers represent the data range, and individual jitter points represent each data point. Brackets indicate pairwise comparisons between density groups. The number of asterisks indicates the level of significance; '*' indicates marginal significance of ≤0.05 and '***' indicates higher significance of ≤0.001; 'NS' indicates no significant difference.

Figure S4). In the HA condition, the average secondary sex ratio across 2, 4, and 8 female densities was 65.61 ± 12.69, 65.21 ± 21.92, and 59.83 ± 18.76, respectively. Similarly, in the HL condition, the average secondary sex ratio across 2, 4, and 8 female densities is 66.61 ± 16.51, 67.22 ± 15.09, and 62.58 ± 9.76, respectively.

3.3 | Mathematical Model of Progeny Emergence Rate Under Resource-Constrained Conditions

The pattern of increased emergence rate of adult progeny wasps under host resources-limited conditions (HL) (Figure 4) could be due to increased superparasitism at lower host egg density. Typically, only one *T. chilonis* individual emerges from a parasitised host (Chowdhury et al. 2016; Manisha et al. 2020). Under single-female conditions, the average emergence rate was approximately 75%, indicating that about 25% of parasitised eggs failed to yield adult progeny (Figure 3). This suggests that parasitism was unsuccessful in roughly a quarter of cases. Using a simple mathematical model, plot the relationship between the proportion of parasitised eggs from which adult wasps emerge, and the density of high-quality host eggs, for 1, 2, 4, 8 female parasitoids (Figure 5). This shows that increasing superparasitism, driven by multiple wasps parasitising a low number of high-quality eggs, can enhance the percentage parasitoid emergence to up to 90% ($N = 8, M = 200$) from its basal value of 75% ($N = 1$), which is similar to what we found in the empirical study with resource constraint (Figure 4).

4 | Discussion

Contrary to theoretical predictions about intraspecific competition (Robert et al. 2016), we found that the egg parasitoid *T. chilonis* parasitised more eggs in the presence of conspecifics than when alone. However, neither parasitoid density nor resource density affected the number of eggs parasitised per female. Our

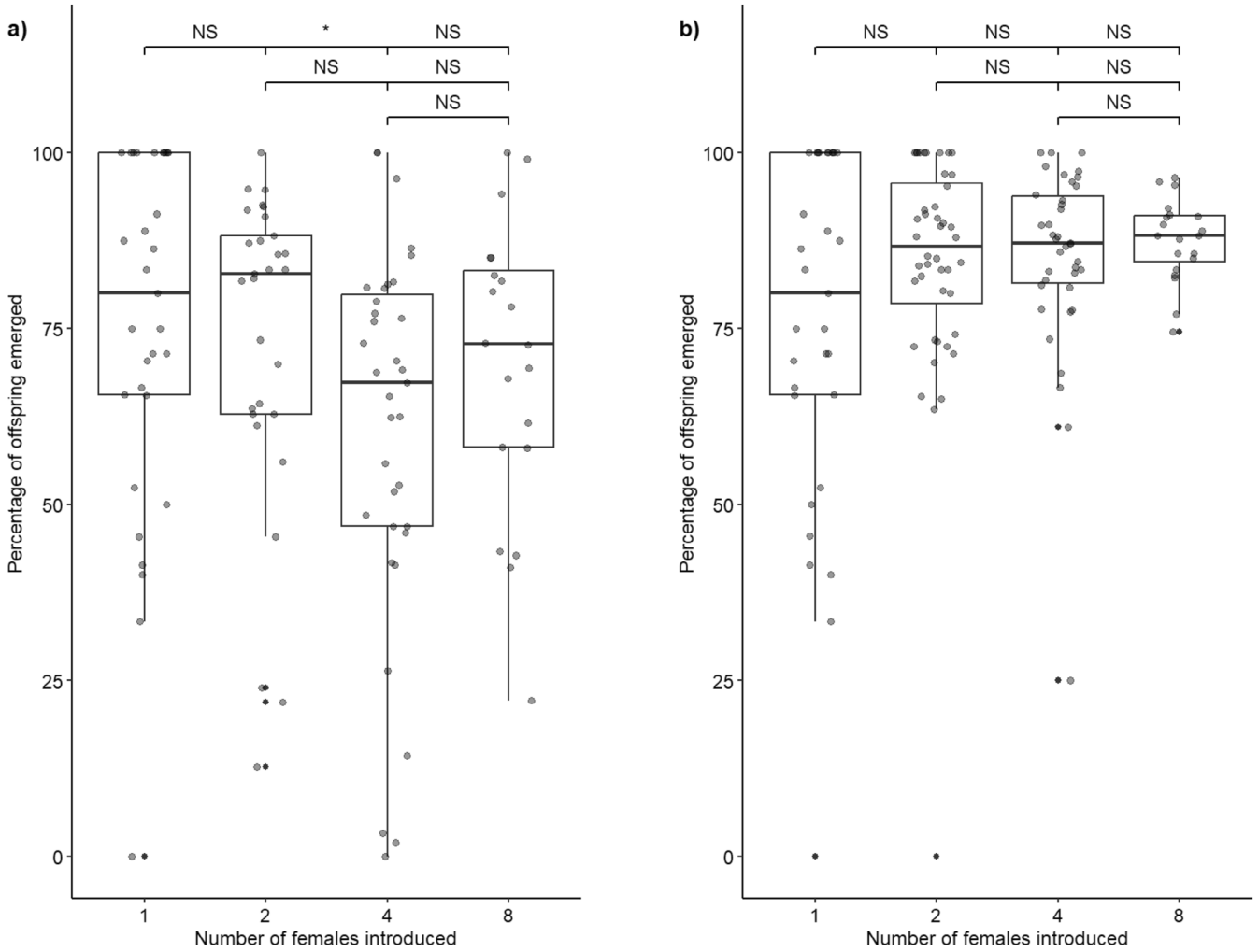

FIGURE 3 | Impact of parasitoid density on percentage of offspring emerged under two different host density conditions: The percentage of offspring emerged is shown across varying parasitoid densities (1, 2, 4, and 8 females) under (a) Host Abundant (HA) and (b) Host-Limited (HL) conditions. Box plots represent the interquartile range, with the thick horizontal line indicating the median. The whiskers represent the data range, and individual jitter points represent each data point. Brackets indicate pairwise comparisons between density groups. The number of asterisks indicates the level of significance, '*' indicates marginal significance of ≤ 0.05 and 'NS' indicates no significant difference.

experiments showed that juvenile survival (the percentage of offspring that emerged) was high at low resource density. Through a simple mathematical model, we further demonstrated that superparasitism under these conditions can drive high population-level emergence. In this study, we also found that the secondary sex ratio (percentage of female offspring emerged) was neither affected by the presence of conspecifics nor by the density of parasitoids or resources.

Previous studies of other parasitoid species have shown that the foraging decisions are affected by the presence of conspecific competitors (Ives 1989; Visser et al. 1999; Harvey et al. 2013). Yet, the direction of this effect differs based on the competing species. For instance, studies on clutch size decisions of the solitary parasitoid *Comperiella bifasciata* Howard (Hymenoptera: Encyrtidae) show that females that were kept together with conspecifics before parasitisation laid more eggs than females kept alone (Visser and Rosenheim 1998). However, females of the gregarious parasitoid *Aphaereta minuta* Nees (Hymenoptera: Braconidae), kept with conspecifics before parasitisation, produced smaller clutches than those kept alone (Visser 1996). The patch allocation time, which is a component of the foraging decision of parasitoids, is also influenced by the presence of conspecifics and has been found to increase or decrease with competition (Visser et al. 1992). The parasitoid *Hyposoter horticola* Gravenhorst (Hymenoptera: Ichneumonidae) revisits patches more frequently in the presence of a conspecific competitor than in the absence of a competitor (Couchoux and van Nouhuys 2014). On the other hand, the pupal parasitoid *P. vindemmiae* spent less time in patches when the number of competitors increased (Goubault et al. 2005). The effect of the presence of conspecifics on resource utilisation also differs among non-aggressive parasitoids related to those used in our study. In the case of *Trichogramma pintoi* Voegelé and *T. minutum* Riley (Hymenoptera: Trichogrammatidae), *T. pintoi* shortened patch residence time under competition, whereas *T. minutum* did not modify patch residence time in response to competition, leading Robert et al. (2016) to conclude that resource utilisation of adult parasitoids towards the presence of a competitor is parasitoid species-specific. Thus, we also

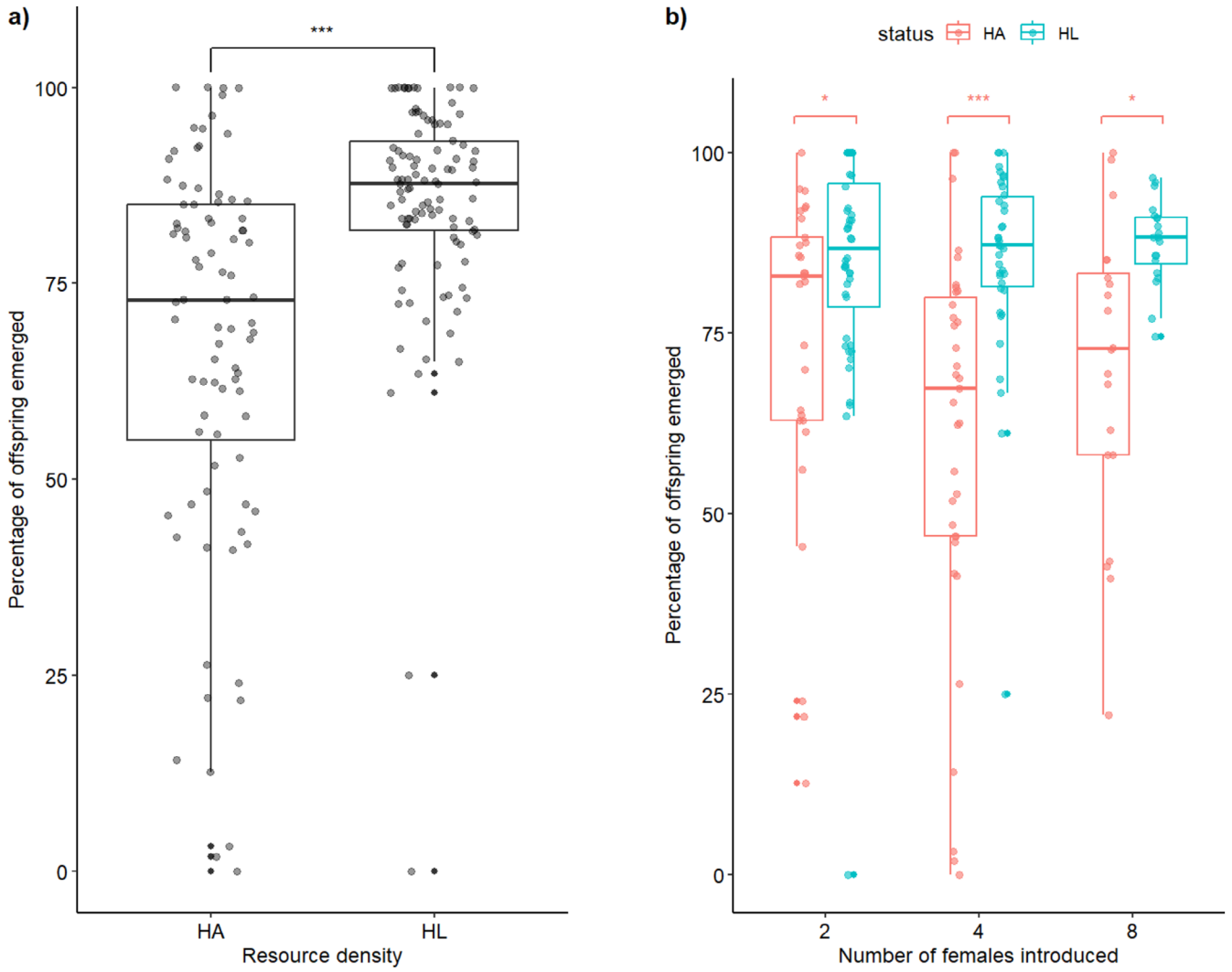

FIGURE 4 | Comparison of percentage of offspring that emerged across two different resource density conditions: (a) Overall comparison of percentage of offspring that emerged between Host Abundance (HA) and Host-limited (HL) conditions. (b) Pairwise comparisons between HA (red) and HL (blue) conditions across three parasitoid densities (2, 4, and 8 females). Box plots represent the interquartile range, with the thick horizontal line indicating the median. The whiskers represent the data range, and individual jitter points represent each data point. Brackets indicate pairwise comparisons between density groups. The number of asterisks indicates the level of significance; '*' indicates significance of ≤0.05, '***' indicates significance of ≤0.001.

conclude that the response of *T. chilonis* to resource utilisation in the presence of a conspecific might be a species-specific response.

One possible reason for increased resource utilisation is to compensate for the potential decline in individual fitness due to superparasitism. The ability of *T. chilonis* to distinguish between parasitised and unparasitised eggs increases with ovipositional experience, and those with no ovipositional experience tend to parasitise unparasitised eggs or previously parasitised eggs with the same probability (Miura et al. 1994). This suggests that the observed increase in resource utilisation may be an adaptive strategy, allowing *T. chilonis* to maximise individual reproductive success despite potential loss due to superparasitism.

While the presence of a conspecific significantly increased the number of eggs parasitised per female, increasing parasitoid density beyond two did not further increase their resource utilisation. However, we observed an upward trend in parasitism as female density increased from two to four, followed by a decline at eight, at both resource densities. Contrary to what we found, Yan et al. (2023) found a decreasing trend in parasitism per female *T. pintoi*, with increasing parasitoid densities (Yan et al. 2023). Similarly, Kfir (1981) found that per female parasitism by *T. pretiosum* declined when parasitoid density increased from 2 to 4, but did not significantly vary when the parasitoid density increased from 4 to 16 (Kfir 1981). In *T. chilonis*, the decline in the number of eggs parasitised per female is significant only between 4 and 8 female densities compared to 2–4 and 2–8 in the HA condition. One reason for the very low parasitisation at the 8-female density in the HA condition could be the increase in the enclosure's spatial scale to accommodate a large number of egg cards under resource abundance. For *Trichogramma*, differences in the temporal and spatial distributions of resources can affect their host-finding success (Burte et al. 2023). Overall, we conclude that increasing parasitoid density beyond

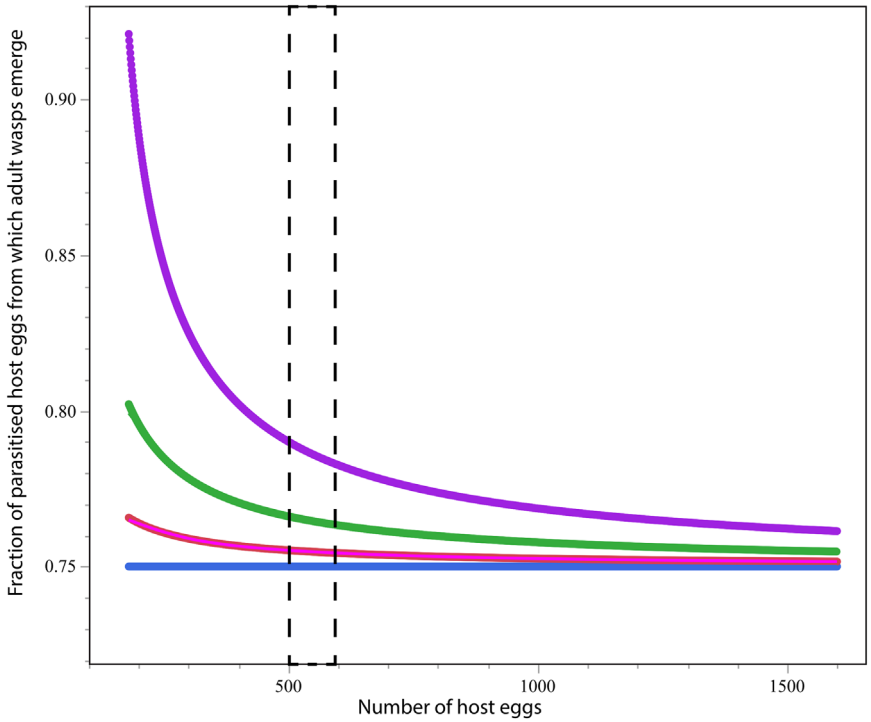

FIGURE 5 | The association of the fraction of parasitised eggs yielding adult parasitoids with host egg availability in the model. The coloured curves represent different numbers of foraging wasps (1: Blue, 2: Pink, 4: Green, 8: Purple). The dashed rectangle marks the resource-constrained conditions in the experimental study.

two females does not significantly affect resource utilisation by *T. chilonis*. While it remains uncertain whether female wasps perceive conspecific presence through visual, olfactory, or tactile senses (Pexton and Mayhew 2005), our study suggests that *T. chilonis* may not detect the number of conspecifics around them, at least up to eight females, but can recognise when at least one conspecific is in the vicinity, likely through odour cues (Gonthier et al. 2023).

The number of eggs parasitised per female was the same when offered abundant (HA) or limited (HL) resource density. A previous study of the functional response of *T. chilonis* on *C. cephalonica* found that *T. chilonis* follows Hollings type II functional response (Qin et al. 2023). In parasitoids following type II functional response, the individual parasitisation rate increases at lower host densities, while it decreases at higher host densities (Holling 1966; Tazerouni et al. 2019). For another *Trichogramma* parasitoid, which follows type II functional response, *T. pretiosum*, above the host density of 300 eggs, the number of eggs parasitised per female reaches a plateau in the functional response curve in all 2, 4 and 8 parasitoid densities (Kfir 1983). It is possible that we did not detect an effect of resource density because egg density was high (500–600 eggs per 1 cm^2 card) even under the resource-condition. However, since there was an increase in resource use in response to the presence of conspecifics, it may be that the wasps use the presence of competitors, rather than the density of host eggs, as a signal of declining host availability (van Alphen and Visser 1990).

One outcome of competition for parasitoids is superparasitism, in which a female lays eggs in a previously parasitised host. This can lead to the mortality of offspring if only one can develop. We found that neither the presence of a competitor nor higher parasitoid density affected offspring survival (percentage emergence). However, juvenile survival was higher when resources were constrained than when resources were abundant. As resource density decreases, we expect the rate of superparasitism to increase (Kraft and Van Nouhuys 2013). While generally, superparasitism is detrimental at the individual level for solitary parasitoids, it can be adaptive at the population level, as it increases the probability of at least one offspring emerging from a parasitised host (Mackauer and Chau 2001). This may be true in our system, where not all parasitism leads to successful parasitoid development even when a host is singly parasitised and the wasps are foraging simultaneously. Using a simple probabilistic model, we demonstrated that if the foraging parasitoids do not avoid superparasitism, the emergence rate is high when multiple wasps forage. It also decreases with increasing host density as superparasitism decreases. The resource-constrained condition with multiple foraging females qualitatively matches the model. This suggests that the parasitoid females may not be avoiding superparasitism, perhaps because they are still naïve. While individual success declines with superparasitism, at the population level it results in a high parasitism rate, which would be advantageous for biological control.

Parasitoid wasps are Hymenoptera and thus have a haplodiploid sex-determination system, allowing mated females to control the sex of their offspring. Many exhibit a female-biased sex ratio because, where resources are sufficient, it is advantageous to have more daughters (Somjee et al. 2011). In our study, there was a female bias, which was not affected by resource density, suggesting no perceived variation in host quality. According to Local Mate Competition theory, the proportion of male offspring

produced should increase with the number of foundress females visiting a patch, and the offspring sex ratio should change from female-biased toward a sex ratio of 1:1 (Hamilton 1967). For instance, *Trichogramma pretiosum* Riley (Hymenoptera: Trichogrammatidae) (Luck et al. 2001) and *T. evanescens* (Waage and Lane 1984) show lower female sex bias with increasing patch foundress number. Two other *Trichogramma* species, *T. minutum* and *T. pintoi*, produced more male offspring when the parasitoid density was 10 females in a patch than when they were alone (Martel and Boivin 2004). In *T. pintoi*, the percentage of male offspring increased at a maternal density greater than four (Yan et al. 2023). In our study, we observed no male bias at higher founder density, which may be due to the abundance of available resources in both resource conditions.

Understanding the effect of competition on resource utilisation and other performance traits gives us insights into the population dynamics of parasitoids, as well as pest control efficiency (Courchamp et al. 1999; Bográn et al. 2002; Ode and Hardy 2008; Bompard et al. 2013). When taken together with previously studied parasitoids exhibiting exploitative competition, it is evident that the presence of competitors can have both positive and negative effects on resource utilisation and other performance traits, which differ across parasitoid species. One of the reasons is that it is difficult to come up with a pattern because there are few documented studies of exploitative competition among parasitoids. In our study, we found that in the presence of conspecifics, *T. chilonis* increases its resource utilisation. Similarly, the percentage of offspring that survive to emerge is higher when resources are more limited. Thus, *T. chilonis* can perform relatively well under intraspecific competitive conditions. This might be one of the reasons for the high performance of *T. chilonis* in augmentative biological control against many pest species (Sharma et al. 2020; Li et al. 2024).

Author Contributions

Prabitha Mohan: conceptualization, methodology, data curation, investigation, formal analysis, funding acquisition, visualization, project administration, writing – original draft, writing – review and editing. **Saskya van Nouhuys:** conceptualization, methodology, formal analysis, supervision, visualization, project administration, writing – review and editing, resources. **Vanshika Pal:** data curation, investigation, writing – review and editing. **Abhyudai Singh:** investigation, writing – review and editing.

Acknowledgements

We acknowledge Prof. Kavita Iswaran for her suggestions on statistical analysis, Tapasya THapa and Shreya Gangwal for their assistance in rearing the insect culture, and the Population and Community Ecology lab members for their ideas and discussions. We also acknowledge the two editorial reviewers whose suggestions improve the quality of this article. P.M. acknowledges the National Postdoctoral Fellowship from the Anusandhan National Research Foundation for funding the research, as well as the Centre for Ecological Sciences, Indian Institute of Science, for providing the facility. P.M. also thanks Prajit J, Central University of Kerala, for the suggestions and discussions.

Funding

This work was funded by Anusandhan National Research Foundation (Grant No: PDF/2022/002896), Government of India.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that supports the findings of this study are available in the Supporting Information of this article.

References

Agnew, P., M. Hide, C. Sidobre, and Y. Michalakis. 2002. "A Minimalist Approach to the Effects of Density-Dependent Competition on Insect Life-History Traits." *Ecological Entomology* 27: 396–402.

Anonymous Mass Production Protocol of Bio-Agents. n.d. "Directorate of Plant Protection Quarantine and Storage, Department of Agriculture & Farmers Welfare, Ministry of Agriculture & Farmers Welfare, Government of India."

Batchelor, T. P., I. C. W. Hardy, J. F. Barrera, and G. Pérez-Lachaud. 2005. "Insect Gladiators II: Competitive Interactions Within and Between Bethylid Parasitoid Species of the Coffee Berry Borer, *Hypothenemus hampei* (Coleoptera: Scolytidae)." *Biological Control* 33: 194–202.

Bernhardt, J. R., P. Kratina, A. L. Pereira, M. Tamminen, M. K. Thomas, and A. Narwani. 2020. "The Evolution of Competitive Ability for Essential Resources." *Philosophical Transactions of the Royal Society, B: Biological Sciences* 375: 20190247.

Bográn, C. E., K. M. Heinz, and M. A. Ciomperlik. 2002. "Interspecific Competition Among Insect Parasitoids: Field Experiments With Whiteflies as Hosts in Cotton." *Ecology* 83: 653–668.

Bompard, A., I. Amat, X. Fauvergue, and T. Spataro. 2013. "Host-Parasitoid Dynamics and the Success of Biological Control When Parasitoids Are Prone to Allee Effects." *PLoS One* 8: e76768.

Brodeur, J., and G. Boivin. 2004. "Functional Ecology of Immature Parasitoids." *Annual Review of Entomology* 49: 27–49.

Burte, V., M. Cointe, G. Perez, L. Mailleret, and V. Calcagno. 2023. "When Complex Movement Yields Simple Dispersal: Behavioural Heterogeneity, Spatial Spread and Parasitism in Groups of Micro-Wasps." *Movement Ecology* 11: 13.

Chowdhury, Z., S. Alam, C. Dash, M. Maleque, and A. Akhter. 2016. "Determination of Parasitism Efficacy and Development of Effective Field Release Technique for *Trichogramma* spp. (Trichogrammatidae: Hymenoptera)." *American Journal of Experimental Agriculture* 10: 1–7.

Cody, M., R. MacArthur, and J. Diamond. 1975. *Ecology and Evolution of Communities*. Harvard University Press.

Couchoux, C., and S. van Nouhuys. 2014. "Effects of Intraspecific Competition and Host-Parasitoid Developmental Timing on Foraging Behaviour of a Parasitoid Wasp." *Journal of Insect Behavior* 27: 283–301.

Courchamp, F., T. Clutton-Brock, and B. Grenfell. 1999. "Inverse Density Dependence and the Allee Effect." *Trends in Ecology & Evolution* 14: 405–410.

Cusumano, A., E. Peri, G. Boivin, and S. Colazza. 2015. "Fitness Costs of Intrinsic Competition in Two Egg Parasitoids of a True Bug." *Journal of Insect Physiology* 81: 52–59.

Cusumano, A., E. Peri, and S. Colazza. 2016. "Interspecific Competition/Facilitation Among Insect Parasitoids." *Current Opinion in Insect Science* 14: 12–16.

De Rijk, M., X. Zhang, J. A. H. Van Der Loo, B. Engel, M. Dicke, and E. H. Poelman. 2016. "Density-Mediated Indirect Interactions Alter Host Foraging Behaviour of Parasitoids Without Altering Foraging Efficiency." *Ecological Entomology* 41: 562–571.

Fan, Z.-Y., M. M. Khan, X.-L. Lv, et al. 2025. "Behavioral and Physiological Responses of the Aphelinid Parasitoid, *Encarsia formosa*, to Interspecific Competitors." *Communications Biology* 9: 143.

Forsman, J. T., J.-T. Seppänen, and M. Mönkkönen. 2002. "Positive Fitness Consequences of Interspecific Interaction With a Potential Competitor. Proceedings of the Royal Society of London." *Series B: Biological Sciences* 269: 1619–1623.

Gonthier, J., Y. B. Zhang, G. F. Zhang, J. Romeis, and J. Collatz. 2023. "Odor Learning Improves Efficacy of Egg Parasitoids as Biocontrol Agents Against *Tuta absoluta*." *Journal of Pest Science* 96: 105–117.

Goubault, M., Y. Outreman, D. Poinsot, and A. M. Cortesero. 2005. "Patch Exploitation Strategies of Parasitic Wasps Under Intraspecific Competition." *Behavioral Ecology* 16: 693–701.

Hamilton, W. D. 1967. "Extraordinary Sex Ratios." *Science* 156: 477–488.

Harvey, J. A., L. de Haan, O. Verdeny-Vilalta, B. Visser, and R. Gols. 2019. "Reproduction and Offspring Sex Ratios Differ Markedly Among Closely Related Hyperparasitoids Living in the Same Microhabitats." *Journal of Insect Behavior* 32: 243–251.

Harvey, J. A., R. Gols, and M. R. Strand. 2009. "Intrinsic Competition and Its Effects on the Survival and Development of Three Species of Endoparasitoid Wasps." *Entomologia Experimentalis et Applicata* 130: 238–248.

Harvey, J. A., E. H. Poelman, and T. Tanaka. 2013. "Intrinsic Inter- and Intraspecific Competition in Parasitoid Wasps." *Annual Review of Entomology* 58: 333–351.

Hasegawa, K., and S. Yamamoto. 2009. "Effects of Competitor Density and Physical Habitat Structure on the Competitive Intensity of Territorial White Spotted Charr *Salvelinus leucomaenis*." *Journal of Fish Biology* 74: 213–219.

Holling, C. S. 1966. "The Functional Response of Invertebrate Predators to Prey Density." *Memoirs of the Entomological Society of Canada* 98: 5–86.

Ives, A. R. 1989. "The Optimal Clutch Size of Insects When Many Females Oviposit Per Patch. Source." *American Naturalist* 133: 671–687.

Johnson, C. A., J. W. A. Grant, and L. A. Giraldeau. 2004. "The Effect of Patch Size and Competitor Number on Aggression Among Foraging House Sparrows." *Behavioral Ecology* 15: 412–418.

Kaplan, I., and R. F. Denno. 2007. "Interspecific Interactions in Phytophagous Insects Revisited: A Quantitative Assessment of Competition Theory." *Ecology Letters* 10: 977–994.

Kfir, R. 1981. "Effect of Hosts and Parasite Density on the Egg Parasite *Trichogramma pretiosum* [Hym.: Trichogrammatidae]." *Entomophaga* 26: 445–451.

Kfir, R. 1983. "Functional Response to Host Density by the Egg Parasite *Trichogramma pretiosum*." *Entomophaga* 28: 345–353.

King, B. H. 1993. *Sex-Ratio Manipulation by Parasitoid Wasps. Evolution and Diversity of Sex Ratio in Insects and Mites*, edited by D. L. Wrensch and M. Ebbert, 418–441. Chapman and Hall.

King, B. H., and S. E. Seidl. 1993. "Sex Ratio Response of the Parasitoid Wasp *Muscidifurax raptor* to Other Females." *Oecologia* 94: 428–433.

Kishani Farahani, H., Y. Moghadassi, L. Alford, and J. van Baaren. 2019. "Effect of Interference and Exploitative Competition on Associative Learning by a Parasitoid Wasp: A Mechanism for Ideal Free Distribution?" *Animal Behaviour* 151: 157–163.

Koutsidi, M., A. Lazaris, P. Peristeraki, G. Tserpes, and E. Tzanatos. 2024. "Quantification of Intraspecific and Interspecific Competition in Fish Species of the Aegean Sea." *ICES Journal of Marine Science* 81: 334–347.

Kraft, T. S., and S. Van Nouhuys. 2013. "The Effect of Multi-Species Host Density on Superparasitism and Sex Ratio in a Gregarious Parasitoid." *Ecological Entomology* 38: 138–146.

Li, X., T. Chen, L. Chen, et al. 2024. "*Trichogramma chilonis* Is a Promising Biocontrol Agent Against *Tuta absoluta* in China: Results From Laboratory and Greenhouse Experiments." *Entomologia Generalis* 44: 357–365.

Luck, R. F., J. A. M. Janssen, J. D. Pinto, and E. R. Oatman. 2001. "Precise Sex Allocation, Local Mate Competition, and Sex Ratio Shifts in the Parasitoid Wasp *Trichogramma pretiosum*." *Behavioral Ecology and Sociobiology* 49: 311–321.

Mackauer, M., and A. Chau. 2001. "Adaptive Self Superparasitism in a Solitary Parasitoid Wasp: The Influence of Clutch Size on Offspring Size." *Functional Ecology* 15: 335–343.

Manisha, B. L., M. M. Visalakshi, D. V. Sairam Kumar, and P. Kishore Varma. 2020. "Resource Efficient and Cost-Reduction Technology for *Trichogramma chilonis* Ishii (Hymenoptera: Trichogrammatidae) Production." *Journal of Biological Control* 34: 43–46.

Martel, V., and G. Boivin. 2004. "Impact of Competition on Sex Allocation by *Trichogramma*." *Entomologia Experimentalis et Applicata* 111: 29–35.

Miura, K., and M. Kobayashi. 1998. "Effects of Host-Egg Age on the Parasitism by *Trichogramma chilonis* Ishii (Hymenoptera: Trichogrammatidae), an Egg Parasitoid of the Diamondback Moth." *Applied Entomology and Zoology* 33: 219–222.

Miura, K., S. Matsuda, and M. Kobayashi. 1994. "Discrimination Between Parasitized and Unparasitized Hosts in an Egg Parasitoid, *Trichogramma chilonis* Ishii (Hymenoptera: Trichogrammatidae)." *Applied Entomology and Zoology* 29: 317–322.

Nakamatsu, Y., J. A. Harvey, and T. Tanaka. 2009. "Intraspecific Competition Between Adult Females of the Hyperparasitoid *Trichomalopsis apanteloctena* (Hymenoptera: Chelonidae), for Domination of *Cotesia kariyai* (Hymenoptera: Braconidae) Cocoons." *Annals of the Entomological Society of America* 102: 172–180.

Ode, P. J., and I. C. W. Hardy. 2008. *Parasitoid Sex Ratios and Biological Control. Behavioral Ecology of Insect Parasitoids*, edited by É. Wajnberg, C. Bernstein, and J. van Alphen, 253–291. Wiley.

Ode, P. J., D. K. Vyas, and J. A. Harvey. 2022. "Extrinsic Inter- and Intraspecific Competition in Parasitoid Wasps." *Annual Review of Entomology* 67: 305–328.

Pekkonen, M., T. Ketola, and J. T. Laakso. 2013. "Resource Availability and Competition Shape the Evolution of Survival and Growth Ability in a Bacterial Community." *PLoS One* 8: e76471.

Pexton, J. J., and P. J. Mayhew. 2005. "Clutch Size Adjustment, Information Use and the Evolution of Gregarious Development in Parasitoid Wasps." *Behavioral Ecology and Sociobiology* 58: 99–110.

Qin, Z., D. Li, Y. Luo, and A. G. S. Cuthbertson. 2023. "Impact of Different *Trichogramma chilonis* Populations From Sugarcane Fields on Parasitism of *Corcyra cephalonica*." *Journal of Applied Entomology* 147: 819–824.

R Core Team. 2024. "R: A Language and Environment for Statistical Computing, R Foundation for Statistical Computing, Vienna, Austria." https://www.R-project.org.

Riley, L. A., and M. F. Dybdahl. 2015. "The Roles of Resource Availability and Competition in Mediating Growth Rates of Invasive and Native Freshwater Snails." *Freshwater Biology* 60: 1308–1315.

Robert, F. A., J. Brodeur, and G. Boivin. 2016. "Patch Exploitation by Non-Aggressive Parasitoids Under Intra- and Interspecific Competition." *Entomologia Experimentalis et Applicata* 159: 92–101.

Sharma, S., P. S. Shera, R. Kaur, and K. S. Sangha. 2020. "Evaluation of Augmentative Biological Control Strategy Against Major Borer Insect

Pests of Sugarcane—A Large-Scale Field Appraisal." *Egyptian Journal of Biological Pest Control* 30: 127.

Singhamuni, S. A. A., M. I. U. F. Jayasuriya, K. S. Hemachandra, and U. G. A. I. Sirisena. 2015. "Evaluation of the Potential of *Trichogramma chilonis* Ishii (Hymenoptera: Trichogrammatidae) as a Bio-Control Agent for *Trichoplusia ni*, Cabbage Semi-Looper." *Tropical Agricultural Research* 26: 223–236.

Somjee, U., K. Ablard, B. Crespi, P. W. Schaefer, and G. Gries. 2011. "Local Mate Competition in the Solitary Parasitoid Wasp *Ooencyrtus kuvanae*." *Behavioral Ecology and Sociobiology* 65: 1071–1077.

Tao, Z., C. Shen, W. Qin, et al. 2024. "Fluctuations in Resource Availability Shape the Competitive Balance Among Non-Native Plant Species." *Ecological Applications* 34: e2795.

Tazerouni, Z., A. A. Talebi, and M. Rezaei. 2019. *Functional Response of Parasitoids: Its Impact on Biological Control. Parasitoids: Biology, Behavior and Ecology*, edited by E. Donnelly, 1–119. Nova Science Publishers.

Than, A. T., F. Ponton, and J. Morimoto. 2020. "Integrative Developmental Ecology: A Review of Density-Dependent Effects on Life-History Traits and Host-Microbe Interactions in Non-Social Holometabolous Insects." *Evolutionary Ecology* 34: 659–680.

van Alphen, J. J. M., and M. E. Visser. 1990. "Superparasitism as an Adaptive Strategy for Insect Parasitoids." *Annual Review of Entomology* 35: 59–79.

Visser, B., C. Le Lann, H. Snaas, I. C. W. Hardy, and J. A. Harvey. 2014. "Consequences of Resource Competition for Sex Allocation and Discriminative Behaviors in a Hyperparasitoid Wasp." *Behavioral Ecology and Sociobiology* 68: 105–113.

Visser, M. E. 1996. "The Influence of Competition Between Foragers on Clutch Size Decisions in an Insect Parasitoid With Scramble Larval Competition." *Behavioral Ecology* 7: 109–114.

Visser, M. E., T. H. Jones, and G. Driessen. 1999. "Interference Among Insect Parasitoids: A Multi-Patch Experiment." *Journal of Animal Ecology* 68: 108–120.

Visser, M. E., and J. A. Rosenheim. 1998. "The Influence of Competition Between Foragers on Clutch Size Decisions in Insect Parasitoids." *Biological Control* 11: 169–174.

Visser, M. E., J. J. M. van Alphen, and H. W. Nell. 1992. "Adaptive Superparasitism and Patch Time Allocation in Solitary Parasitoids: The Influence of Pre-Patch Experience." *Behavioral Ecology and Sociobiology* 31: 163–171.

Waage, J. K., and J. A. Lane. 1984. "The Reproductive Strategy of a Parasitic Wasp: II. Sex Allocation and Local Mate Competition in *Trichogramma evanescens*." *Journal of Animal Ecology* 53: 417–426.

Wajnberg, E., X. Fauvergue, and O. Pons. 2000. "Patch Leaving Decision Rules and the Marginal Value Theorem: An Experimental Analysis and a Simulation Model." *Behavioral Ecology* 11: 577–586.

Wang, D., L. Lü, Y. He, Q. Shi, C. Tu, and J. Gu. 2016. "Mate Choice and Host Discrimination Behavior of the Parasitoid *Trichogramma chilonis*." *Bulletin of Entomological Research* 106: 530–537.

Wang, S., and R. M. Callaway. 2021. "Plasticity in Response to Plant–Plant Interactions and Water Availability." *Ecology* 102: e03361.

Wauters, L. A., M. V. Mazzamuto, F. Santicchia, S. Van Dongen, D. G. Preatoni, and A. Martinoli. 2019. "Interspecific Competition Affects the Expression of Personality-Traits in Natural Populations." *Scientific Reports* 9: 11189.

Xu, H. Y., N. W. Yang, and F. H. Wan. 2013. "Competitive Interactions Between Parasitoids Provide New Insight Into Host Suppression." *PLoS One* 8: e82003.

Yan, Z., J. J. Yue, and Y. Y. Zhang. 2023. "Biotic and Abiotic Factors That Affect Parasitism in *Trichogramma pintoi* (Hymenoptera: Trichogrammatidae) as a Biocontrol Agent Against *Heortia vitessoides* (Lepidoptera: Pyralidae)." *Environmental Entomology* 52: 301–308.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** Data for Foraging egg parasitoids benefit from the presence of potential competitors. **Figure S1:** Graphical representation showing resource distribution under two different resource densities: Host Abundant (HA) and Host Limited (HL) conditions. Each egg card (orange square) contains 500–600 *C. cephalonica* eggs. **Figure S2:** Comparison of resource utilisation across two different resource density conditions. (a) Overall comparison of the number of eggs parasitised per female between Host Abundance (HA) and Host-limited (HL) conditions. (b) Pairwise comparisons between HA (red) and HL (blue) conditions across three parasitoid densities (2, 4, and 8 females). Box plots illustrate the interquartile range, with the thick horizontal line representing the median. Whiskers extend to the data range (minimum and maximum values), and individual jitter points represent each observed data. Brackets indicate pairwise comparisons between groups. The number of asterisks indicates the level of significance; "*' indicates significance of ≤ 0.05, NS indicates no significance. **Figure S3:** Impact of parasitoid density on percentage of female offspring emerged under two different host density conditions: The percentage of female offspring emerged under (a) Host Abundant (HA), and (b) Host Limited (HL) conditions. Box plots illustrate the interquartile range, with the thick horizontal line representing the median. Whiskers extend to the data range (minimum and maximum values), and individual jitter points represent each observed data point. Brackets indicate pairwise comparisons between density groups. NS indicates no significant difference. **Figure S4:** Comparison of the percentage of female offspring that emerged across two different resource density conditions: (a) Overall comparison of the percentage of female offspring produced between Host Abundance (HA) and Host-limited (HL) conditions. (b) Pairwise comparisons between HA (red) and HL (blue) conditions across three parasitoid densities (2, 4, and 8 females). Box plots illustrate the interquartile range, with the thick horizontal line representing the median. Whiskers extend to the data range (minimum and maximum values), and individual jitter points represent each observed data point. Brackets indicate pairwise comparisons between groups. NS indicates no significant difference.