Effects of Host Density on Pre-oviposition Behavior and Reproductive Output in Two Drosophila Pupal Parasitoids

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***Abstract*—Parasitoids are important biological control agents that can help suppress pest populations and reduce the crop and fruit losses, thereby contributing to maintenance of production. Given this, host availability is an important factor that may influence the oviposition decision and behavior of parasitoids. However, different parasitoid species may differ in how they respond to changes in host density due to their physiological state and reproductive strategies. This study investigated the effect of host density on pre-oviposition behavior and estimated oviposition output of two Drosophila pupal parasitoids: *Pachycrepoideus vindemmiae* and *Trichopria drosophilae*. Unmated female parasitoids were exposed to either 10 or 40 *Drosophila melanogaster* pupae, and the oviposition latency was recorded over multiple observational days. Reproductive output was estimated from the difference between the initial number of pupae and the number of *D. melanogaster* individuals that emerged. *P. vindemmiae* exhibited a significantly longer oviposition latency under high host density across observational days, whereas *T. drosophilae* showed a more variable response, with the significance of the difference changing among days. Despite the longer latency observed in *P. vindemmiae*, females exposed to a higher host density showed a greater estimated reproductive output. These differences mean that host density influences parasitoid oviposition behavior, but the response differs among species in many aspects.**

Keywords*—host density, parasitoids, oviposition latency, *P. vindemmiae*, *T. drosophilae

I. Introduction

A. Parasitoids and Host Interactions

Parasitoids are insects that live in close association with their hosts and depend on host resources for the development of their offspring [1]. Female parasitoids lay their eggs on or inside hosts, and the developing larvae consume host tissues, eventually leading to host death [1]. Due to their ability to regulate host populations, parasitoids play an important role in maintaining ecosystem stability and have been widely used as biological control agents [2]. Many agricultural pests, including fruit flies, cause significant damage to crops and reduce agricultural productivity [3]. Therefore, parasitoids have become an important alternative method for pest management by reducing pest populations naturally [2]. In particular, parasitoids of drosophilid flies have attracted attention as potential biological control agents against agricultural pests such as *Drosophila suzukii* [4, 5]. In addition, parasitoid–host interactions can influence food web structure, species diversity, and ecological balance within terrestrial ecosystems [1].

The reproductive success of female parasitoids is strongly influenced by their oviposition decisions. Successful reproduction is essential for females to pass their genes to future generations. In the oviposition process, there are four main stages: drumming, drilling, oviposition, and marking [6]. Before the first stage of oviposition, females must locate suitable hosts, assess host suitability, and avoid hosts that have already been parasitized [7–9]. These decisions are important because the quality and availability of hosts directly affect offspring survival and female reproductive fitness [1]. After accepting a host, females insert their ovipositor into the host and deposit their eggs inside or on the host depending on their parasitism strategy [10, 11].

B. Host Density and Parasitoid Oviposition Behavior

Host density is an important environmental factor that can influence parasitoid foraging and oviposition behavior. Changes in host density can alter host encounter rates, patch quality, and the potential reproductive benefits of exploiting a patch [8, 12]. Parasitoids may adjust their responses to host availability depending on the distribution and abundance of hosts, although the direction and magnitude of these responses can vary among species and ecological contexts [13, 14]. Therefore, changes in host density may influence the time females spend before oviposition as well as their subsequent reproductive investment.

Apart from environmental factors, mating status may also influence parasitoid oviposition behavior. Many parasitoids exhibit haplodiploid sex determination [1]. As a result, unmated females can only produce male offspring, while mated females can produce both male and female offspring [15, 16]. This difference may influence reproductive decisions because females may allocate their time and resources differently depending on

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their reproductive state [17]. Therefore, mating status should be taken into account when investigating oviposition behaviors in parasitoids.

C. Reproductive Strategies of *P. vindemmiae* and *T. drosophilae*

Trichopria drosophilae and *Pachycrepoideus vindemmiae* are two important pupal parasitoids that have attracted attention due to their potential applications in biological control [5, 18, 19]. Both species are capable of attacking drosophilid hosts and have been studied for their parasitism ability, host preference, and reproductive characteristics [4, 20]. Although previous studies have provided important information about their host discrimination and reproductive strategies, relatively little is known about how host density influences their behavioral responses before oviposition.

D. Research Gap and Hypothesis

Previous studies have focused on factors such as host quality, host age, and previous parasitism status, whereas the influence of host density on oviposition latency, which is defined as the time elapsed from the first physical contact between the female parasitoid and a host to the initiation of oviposition. remains less explored [8]. This oviposition latency has previously been used to quantify the time required for parasitoids to proceed from host encounter or inspection to oviposition [21, 22]. This period represents the decision-making process before egg deposition occurs. It reflects how quickly females respond to a potential host and whether they decide to initiate an oviposition attempt under specific environmental conditions [23]. However, it does not include host evaluation that occurs after oviposition behavior has already started, such as assessment during ovipositor insertion [21, 22]. Understanding how females adjust their latency under different host densities may provide further insights into how parasitoids balance decision accuracy and reproductive efficiency. Therefore, studying oviposition latency can improve our understanding of parasitoid decision-making and host selection strategies.

The objective of this study is to investigate the effect of host density on the oviposition behavior of *T. drosophilae* and *P. vindemmiae*. Specifically, this study compares oviposition latency between the two species under low and high host density conditions to determine whether unmated females modify their pre-oviposition behavior according to host availability. The study hypothesizes that unmated females of both species will exhibit different latency responses under different host densities, reflecting adaptive oviposition strategies in response to environmental variation.

II. Methods

A. Insects

The parasitoids used in this study were *P. vindemmiae* Rondani (Hymenoptera: Pteromalidae) and *T. drosophilae* Perkins (Hymenoptera: Diapriidae), two species of parasitoids that utilize Drosophila pupae as hosts. *D. melanogaster* Meigen (Diptera: Drosophilidae) was used as the host species in this study. All three species were collected from Zijin Mountain, Nanjing, Jiangsu Province, China, in 2025.

B. Parasitoids and Host Preparation

Colonies of *T. drosophilae* and *P. vindemmiae* were maintained using *D. melanogaster* pupae. All insects were reared under controlled laboratory conditions at 25°C ± 0.1°C, 60% ± 5% relative humidity, and a 16-hour light, 8-hour dark photoperiod, following the standard rearing protocol used in the Nanjing University Laboratory of Environmental Science.

The newly emerged female parasitoids were collected and maintained individually in 1.5 mL centrifuge tubes. A cotton ball soaked with 10% sucrose solution was provided as an energy source before experimentation. Only virgin females were used to eliminate variation associated with mating status. Moreover, females 1 day old were selected to minimize age-related differences resulting from different reproductive strategies.

C. Experimental Design

The study on oviposition behavior was conducted using two host-density treatments. The low host density contained 10 *D. melanogaster* pupae, whereas the high host density contained 40 *D. melanogaster* pupae. The host pupae were transferred into a standard Drosophila vial, and a cotton plug was placed at the top of the vial to allow ventilation and prevent parasitoids from escaping from the vial. Then one parasitoid was introduced into each vial, and the oviposition behavior was recorded under both host density conditions. The procedure was repeated 20 times.

D. Measurement of Oviposition Latency

After the introduction of the parasitoids, females were observed for 150 minutes. Oviposition latency, defined as the time interval between the first physical contact with a host and the initiation of oviposition, was continuously recorded for 10 days to assess pre-oviposition behavior.

After 24 hours of exposure, parasitoids were transferred into new vials containing fresh host pupae, and the same observation procedure was repeated every day. This process was continued throughout the experimental period to monitor oviposition behavior and reproductive activity of individual females.

For each female parasitoid, the time required before oviposition and the estimated number of parasitoids' hatching were recorded.

E. Estimation of Reproductive Output

The estimated number of parasitized hosts was determined by subtracting the number of *D. melanogaster* remaining in each tube at the end of the experimental period from the initial number of hosts provided. This calculation assumes that each host that was no longer present had been successfully parasitized and subsequently produced a parasitoid. Therefore, the resulting value was used as an estimate of parasitoid emergence rather than a direct measurement of the

number of eggs deposited or the number of parasitoids that successfully developed. The estimated number was calculated using the following:

Estimated number of parasitoids emerged = Initial number of *D. melanogaster* pupae − Number of *D. melanogaster* remaining after the experimental period

This estimation provided a consistent measure for comparing reproductive output between the different host-density treatments [24]. However, because host mortality may also result from host-feeding or other non-reproductive effects, this measure should be interpreted as an indirect estimate rather than a direct count of parasitoid emergence [4, 25].

F. Statistical Analysis

Data from *T. drosophilae* and *P. vindemmiae* were recorded separately to distinguish between species-specific responses to host density differences. The statistical analysis was conducted using R software (version 4.4.1). Differences in oviposition latency between host-density treatments were analyzed using appropriate statistical tests after testing the data distribution and variance across the different data sets. Results were presented as mean ± Standard Error of the Mean (SEM), and statistical significance was determined at $P < 0.05$.

III. Results

A. Effect of Host Density on Oviposition Latency and Species-Specific Responses

The oviposition latency of both parasitoid species varied between the two host-density treatments, although the responses differed between species and across days.

As shown in Fig. 1A, *P. vindemmiae* females exposed to the higher host density showed longer oviposition latency times than those exposed to the low host-density treatment. The difference between the two treatments was statistically significant for all five observation days ($P < 0.001$). The greatest differences were observed on Days 1, 3, and 4, where females in the high-density treatment showed substantially greater variation and generally longer latency times than females in the low-density treatment.

As shown in Fig. 1B, for *T. drosophilae*, the effect of host density varied across observation days. On Day 1, females exposed to 10 hosts showed significantly longer latency times than those exposed to 40 hosts ($P < 0.001$). On Day 2, the difference between treatments was also significant ($P < 0.05$), with the high-density treatment showing a higher latency time. No significant difference was observed between the two host-density treatments on Day 3. On Days 4 and 5, females exposed to 40 hosts showed significantly longer latency times than those exposed to 10 hosts ($P < 0.001$).

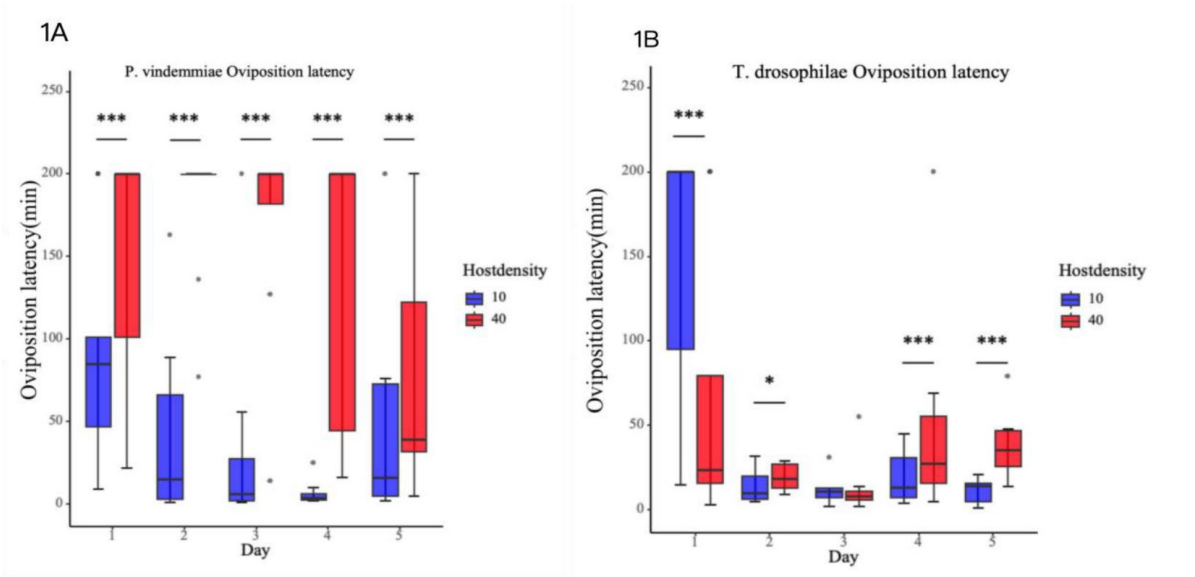


Fig. 1. Oviposition latency of *P. vindemmiae* (A) and *T. drosophilae* (B) under low (10 hosts) and high (40 hosts) host-density treatments across five days of parasitism. Oviposition latency was defined as the time interval between the first contact with a host and the initiation of oviposition. Bars represent mean ± SEM ($n = 9$ independent trials). *$P < 0.05$; *$P < 0.001$.

Overall, *P. vindemmiae* exhibited a more consistent increase in latency time under high host density, whereas the response of *T. drosophilae* varied across days.

B. Estimated Reproductive Output in Species-Specific Responses

The estimated number of eggs laid also varied between host-density treatments and across parasitism days.

As shown in Fig. 2C, *P. vindemmiae* females exposed to 40 hosts consistently laid more eggs than females exposed to 10 hosts throughout the 10-day observation period. Under the high-density treatment, the estimated number of eggs laid increased from approximately 18 eggs on Day 1 to approximately 28 eggs on Day 6. Egg production subsequently fluctuated, reaching approximately 28 eggs on Day 9 before decreasing to approximately 24 eggs on Day 10. In contrast, females

under the low-density treatment maintained relatively stable egg production levels of approximately 8–10 eggs per day.

As shown in Fig. 2D, *T. drosophilae* females exposed to 40 hosts also laid substantially more eggs than those exposed to 10 hosts throughout the observation period. Under high host density, estimated egg production decreased from approximately 28 eggs on Day 1 to approximately 19 eggs on Day 3, followed by fluctuations between approximately 17 and 22 eggs during the remaining observation period. Under low host density, egg production remained relatively stable, ranging from approximately 6 to 10 eggs per day.

Overall, both parasitoid species showed higher estimated egg production under the high-density treatment than under the low-density treatment. *P. vindemmiae* showed a gradual increase in egg production during the first several days under high host density, whereas *T. drosophilae* showed a generally decreasing pattern during the early days of parasitism.

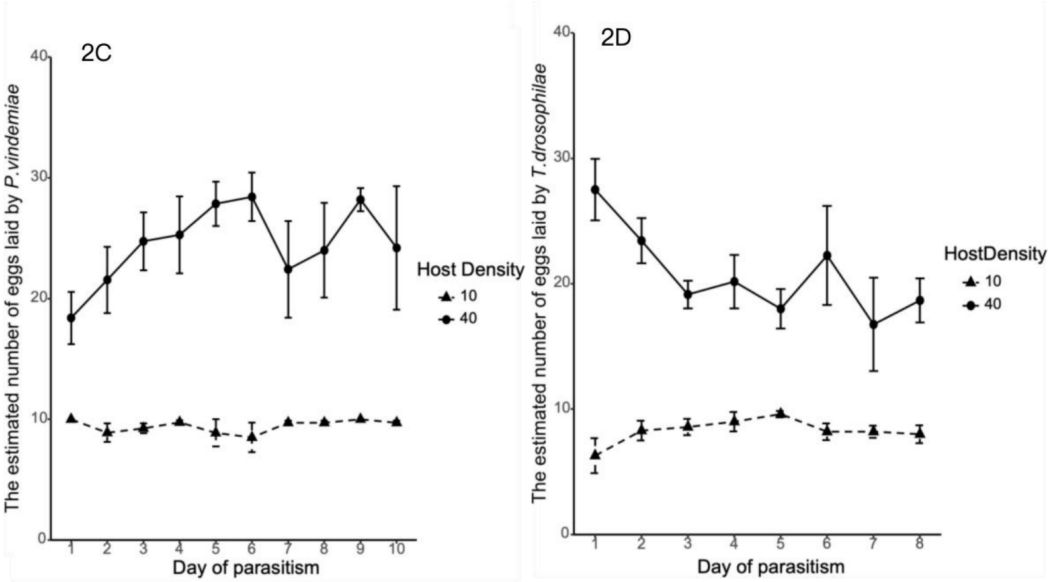


Fig. 2. Estimated egg-laying patterns of unmated *P. vindemmiae* (C) and *T. drosophilae* (D) under low (10 hosts) and high (40 hosts) host-density treatments across five days of parasitism. Bars represent mean ± SEM (n = 9 independent trials).

IV. Discussion

A. Effect of Host Density on Oviposition Latency

The present study demonstrates that host density influences the pre-oviposition behavior of both *P. vindemmiae* and *T. drosophilae*. *P. vindemmiae* exhibited a significantly longer oviposition latency under high host density across all observation days, whereas the response of *T. drosophilae* varied among the observation days. In addition, differences in estimated reproductive output were observed between the two host-density treatments. Both parasitoid species parasitized a greater proportion of the available hosts under the low-density treatment than under the high-density treatment. Such variation is consistent with the broader finding that host density can affect parasitoid attack rates and host exploitation, although the relationship between host density and parasitism is not necessarily linear and can depend on parasitoid characteristics, host characteristics, and the spatial scale at which host density is perceived [26]. These findings suggest that host availability may influence not only the timing of oviposition but also the allocation of reproductive effort, although the two parasitoid species may employ different behavioral strategies in response to host density.

The significantly longer oviposition latency observed in *P. vindemmiae* under the high-host-density treatment suggests that females modify their pre-oviposition behavior in response to host availability. Host density provides information about patch quality and potential reproductive opportunities, and parasitoids can use host-derived cues and previous patch experience when deciding whether to exploit a host [1]. Experimental and theoretical studies have shown that parasitoids can assess host density and alter the oviposition effort accordingly. For example, unmated parasitoid females have adjusted their oviposition decision and effort according to host density and patch encounter rate, indicating that information about host availability can affect foraging decisions [27]. Similarly, models of parasitoids' patch assessment predict that females may establish acceptance thresholds based on the concentration of host-related cues and their recent experience, resulting in different levels of host exploitation among patches of different quality. A high host density provides females with a greater number of potential hosts and consequently increases the range of hosts that may be encountered and assessed before oviposition. Females may therefore spend more time evaluating available hosts or determining which host is most suitable before initiating oviposition. Parasitoids are known to incorporate information concerning host availability and patch quality into foraging and reproductive decisions. Host density may consequently affect how females allocate their time and reproductive effort within a host patch. However, the longer latency observed in the present study should not necessarily be

interpreted as reduced reproductive motivation. Further investigation would be required to determine whether the increased latency primarily reflects host assessment, differences in physiological state, or other behavioral mechanisms.

The mating status of the females may represent an additional factor contributing to the observed variation in oviposition latency. All females used in the present experiment were unmated, and their reproductive status may therefore have influenced their motivation and pattern of oviposition. Under haplodiploid reproduction, unmated females produce haploid male offspring, whereas mated females are capable of producing diploid female offspring [15, 28]. Consequently, the reproductive value of an available host may differ depending on the female's mating status and the sex of the resulting offspring [16, 29]. However, the extent to which mating status influenced the behavioral responses observed in the present study remains uncertain. Experiments comparing mated and unmated females would therefore be necessary to evaluate this explanation.

In contrast to *P. vindemmiae*, *T. drosophilae* exhibited a less consistent response to host density. The pattern observed on Day 1 was opposite to those observed on Days 2, 4, and 5, while no significant difference between host-density treatments was detected on Day 3. This temporal variation indicates that host density alone is unlikely to fully account for changes in oviposition latency in *T. drosophilae*. Parasitoid reproductive strategies can be influenced by several factors, including egg load, female age, nutritional condition, previous oviposition experience, and host availability [30–32]. Therefore, the inconsistent variation may be influenced by additional factors associated with reproductive or physiological state.

One possible explanation is the reproductive strategy of *T. drosophilae*. As a pro-ovigenic species, females emerge with a substantial complement of 40–50 mature eggs [19, 33], potentially enabling them to respond rapidly when suitable hosts are encountered. Under high host density, the increased probability of host encounter may therefore increase the immediate expected reproductive payoff, potentially contributing to the shorter oviposition latency observed under the 40-host treatment on Day 1. Nevertheless, although newly emerged females possess a relatively large number of mature eggs, their physiological and behavioral states may continue to change during the early adult stage. Such temporal changes could contribute to the inconsistent responses observed across observation days. This contrasts with synovigenic parasitoids, which continue to mature eggs during adulthood and may therefore depend more strongly on adult nutritional resources and host-feeding to maintain egg production [31, 34]. In *P. vindemmiae*, for example, host-feeding has been shown to increase the number of mature eggs carried by females, demonstrating a direct connection between adult feeding and reproductive capacity [35].

The contrasting patterns observed between the two species may therefore reflect differences in reproductive biology, host-use strategies, or the mechanisms by which females assess host availability. Although both species utilize *D. melanogaster* pupae as hosts, they may differ in their responses to host density and in the allocation of reproductive effort. Differences in egg maturation, host exploitation, host assessment, or previous oviposition experience may contribute to the species-specific patterns observed in the present study.

B. Host Density and Estimated Reproductive Output

An additional finding of interest is that the longer oviposition latency observed in *P. vindemmiae* under high host density was accompanied by a greater estimated number of parasitized hosts. This result indicates that increased latency did not necessarily correspond to reduced reproductive output. Rather, females exposed to a greater number of hosts may have spent more time before initiating oviposition while subsequently exploiting a larger absolute number of available hosts. The greater host availability in the high-density treatment also provided a substantially larger potential host pool, which should be considered when interpreting differences in estimated reproductive output between treatments. Similar density-dependent patterns are recognized in parasitoid systems, where higher host densities can increase the number of hosts attacked while simultaneously changing the proportion of hosts parasitized [26]. Therefore, comparisons of absolute numbers alone may not fully represent differences in host exploitation.

The hypothesis proposed earlier in this study that females of both species would modify their oviposition behavior in response to host density is partially supported by the results. *P. vindemmiae* exhibited a strong and consistent increase in oviposition latency under high host density, whereas *T. drosophilae* showed significant differences on several observation days but did not exhibit a consistent directional response. The existence of species-specific density responses is consistent with broader evidence that parasitoid responses to host density vary among taxa and depend on both host and parasitoid characteristics [26]. These results suggest that host density influences parasitoid oviposition behavior, but that the magnitude and direction of the response may be species-specific and dependent on the reproductive and physiological state of the female.

C. Limitations

Several limitations should be considered when interpreting the findings of this study. First, only two host-density treatments, consisting of 10 and 40 hosts, were examined. Although differences in oviposition latency were detected between these treatments, the experimental design does not allow us to determine whether the behavioral response changes gradually with host density or whether a particular host-density threshold exists. Density-dependent relationships in parasitoids can vary substantially across spatial scales and host densities, and high host density does not necessarily produce a proportional increase in parasitism [26, 36]. Incorporating a wider range of host

densities would provide a more detailed assessment of the relationship between host availability and oviposition behavior.

Second, only unmated female parasitoids were used. Although this approach controlled for mating status and reduced variation associated with mating, it also limits the generalizability of the findings to mated females. Because mating can influence reproductive state, offspring sex allocation, and potentially oviposition behavior [15, 28], comparisons between mated and unmated females would provide further insight into the mechanisms underlying the observed responses.

D. Future Studies and Conclusion

Future studies could investigate a broader range of host densities to determine whether oviposition latency changes continuously with host availability or responds only after a particular density threshold is reached. Experiments involving both virgin and mated females could further determine whether reproductive state contributes to variation in oviposition behavior. In addition, controlling female age and previous oviposition experience would help distinguish the effects of host density from changes in physiological condition [31, 34]. Direct measurements of parasitism or offspring production would also improve the accuracy of estimates of reproductive output. Furthermore, detailed behavioral observations could clarify whether increased latency results from prolonged host assessment, host selection, or other pre-oviposition activities.

Overall, the results demonstrate that host density can influence parasitoid oviposition behavior, but the nature of this response differs between species. *P. vindemmiae* showed a consistent increase in oviposition latency under high host density, whereas *T. drosophilae* exhibited a more variable response across observation days. The greater estimated absolute number of parasitized hosts under high host density, despite the longer latency observed in *P. vindemmiae*, further indicates that pre-oviposition latency and reproductive output do not necessarily exhibit a simple negative relationship. Instead, parasitoids may adjust the timing of oviposition while simultaneously responding to the number of hosts available within a patch. This interpretation is consistent with broader parasitoid theory in which females integrate information about host density and patch quality into decisions concerning host exploitation [1, 26].

These findings contribute to a broader understanding of how parasitoids adjust their reproductive behavior in response to variation in host availability. They also highlight the importance of considering species-specific reproductive strategies, female physiological state, and host-patch characteristics when investigating parasitoid decision-making and reproductive allocation.

Conflict of Interest

The author declares no conflict of interest.

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