The evolution of host utilization strategy: At what timing parasitoids attack and consume their host

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Abstract

In some parasitoid wasp species, larvae consume their host immediately after hatching ("idiobiont"), while in other species, larvae delay the consumption of the host until its maturation ("koinobiont"). The timing at which wasps' larvae start consuming the host after the attack, referred to as Parasitoid Emerging Timing (PET) in this article, is a life-history trait that is correlated to other life history traits (e.g., lifespan and body size). Consequently, the evolution of PET has been studied as an explanation for the diversity of life-history strategies in parasitoid wasps. Using statistical analyses, previous studies have provided support for the association between PET and other life history traits. However, these results lack an adaptive evolutionary explanation necessary to establish PET as a key factor in life-history diversity. In this study, we develop mathematical models to examine the evolutionary associations between PET and other life-history traits. Specifically, we studied the evolutionary dynamics of PET and resulting life history characteristics of host exploitation. Our results show that the reproductive values differ depending on the developmental stage of hosts and determine which stage parasitoids exploit. We discuss some empirical studies support that host density and reproductive value affect PET. Additionally, the evolution of PET can profoundly alter the life-cycles of parasitoid wasps. For example, in species with late PET, wasps attack young hosts that initially have low reproductive value, but only consume them after the hosts mature and their reproductive value increases. These findings suggest that PET may be a driver of the syndrome involving multiple traits related to host utilization in parasitoid wasps. The high diversity of parasitoid wasps provides a rich system for testing hypotheses about life-history syndromes. By linking PET to broader life-history strategies, this study lays a theoretical foundation for understanding life-history syndromes in parasitoid wasps.

1 Introduction

Understanding the evolution of resource exploitation, including its timings and allocation, within a life history is a central research question in evolutionary biology. Parasitoids (wasps) are model systems to study resource-exploiter interactions, producing numerous studies on life history evolution (Wajnberg et al., 2008). The life histories of parasitoid wasps are particularly diverse (Godfray, 1994; Mayhew and Blackburn, 1999; Jervis et al., 2008; Jervis and Ferns, 2011; Quicke, 2014). For example, the order *Hymenoptera* comprises no less than 200,000 species in a conservative estimation (Pennacchio and Strand, 2006), probably each utilizing more or less different host species (mostly arthropods). Taking another example, there are life-history trait variations, by a factor of 18 in body-size (Jervis et al., 2003), more than one hundred in clutch size and lifetime potential fecundity, among wasp species (Jervis et al.,

2008), with these variations presumably resulting from adaptation to host species. Because parasitoid life history traits have significant impacts on the community structure of parasitoid and prey species (Lafferty et al., 2008), pest management (Wang et al., 2019), and coevolution (Amoroso and Antonovics, 2020), improving our understanding of the evolution of parasitoid wasps provide crucial implications for biodiveristy and its applications.

Life-history trait variations are found typically in sequential timings of host exploitation, from attacking, hatching to emerging (Alonzo and Kindsvater, 2008). For example, some parasitoid wasps (e.g., *Apanteles kariyai*) attack only larvae and emerge without the host's further development (to pupae or adult) (Hayakawa, 1991). Meanwhile, others (e.g., *Ichneumon promissorius*) lay eggs on pupae and emerge immediately (Carpenter, 1995). Importantly, such differences in the exploitation timings may influence the phenotype at later life history stages, by changing the degree to which parasitoids acquire resources from younger (and thus smaller) versus older (thus larger) hosts. In other words, the evolution of exploitation timings strongly influences the traits in the entire lifespan.

The duration from the attack to consumption of the host is a key factor in creating diversity in the life history characteristics of parasitoid wasps. (Jervis and Ferns, 2011). For example, paraistoids can be categorized into two groups according to this trait; namely, "idiophytic" species ('idio' means 'own/individual/personal' descending from Greek, indicating that hosts are personalized or monopolized by individual wasps) that consume the host immediately after the attack, and "koinophytic" species ('koino' means 'common', also from Greek, indicating hosts are shared by parasitoids) that allow host to continue to feed and grow after parasitization (Haeselbarth (1978); in this article, we refer to the duration as "Parasitoid Emergence Timing regulator", abbreviated as PET-regulator). By applying this criterion for a wider range of parasitoid wasp species, the major dichotomy is proposed in the larval developmental pattern of parasitoid wasps, namely idiobiont-koinobiont extremes (Askew, 1986). Parasitoid wasps can be therefore divided into two major groups based on PET-regulator (Godfray, 1994; Quicke, 2014; Askew, 1986). For instance, koinobionts typically exhibit a higher larval mortality, higher fecundity and smaller egg size compared to idiobionts (Mayhew and Blackburn, 1999).

To test the dichotomous hypothesis, the relationship between PET and other traits has been examined. Statistical analyses that control for phylogenetic correlations also provide some support for the dichotomy hypothesis, suggesting possible mechanisms for the observed pattern of association between life history traits (Mayhew and Blackburn, 1999). For example, koinobionts exhibit higher larval mortality, greater fecundity, and smaller egg sizes compared to idiobionts (Mayhew and Blackburn, 1999). This study suggests that these traits are explained by both selective pressures and developmental constraints: the higher mortality rate may result from the increased exposure or immaturity of the host, which in turn drives the evolution of higher fecundity. This increase in fecundity is traded-off against smaller egg sizes (Mayhew and Blackburn, 1999). Godfray (1994) predicts the selection pressures on parasitoid wasps based on the dichotomy hypothesis and suggest a diagram depicts chains of selective drivers of the diversity of life history in parasitoid wasps, particularly focusing on idiobionts and koinobionts (Godfray, 1994). However, the conditions under which PET is selected for is poorly understood in the correlations between PET and other traits, which limits our understanding of the variations in life history traits in parasitoid wasps.

In this study, we use mathematical models to explore the adaptive evolution of PET-regulator. We specifically investigate the evolutionary dynamics of both the preference for hosts' developmental stages and that for PET, since parasitoid wasp can attack young hosts due to their ability to live in host body. Using adaptive dynamics theory (Dieckmann and Law, 1996), we determine the directions of natural selection on these traits and the stability of evolutionary outcomes.

2 Method

We investigate the evolution of emergence timing, PET (the timing of emergence from the host), using a mathematical model: we consider a host population with a stage structure consisting of early juvenile hosts, late juvenile hosts, and adult hosts. Either stage of the juvenile hosts, but not adults, may be attacked by the parasitoid wasps and

subsequently transits to the infected stage (Figure 1 for a diagram depicting the patterns of life-cycles). The variables and parameters are summarized in Table 1.

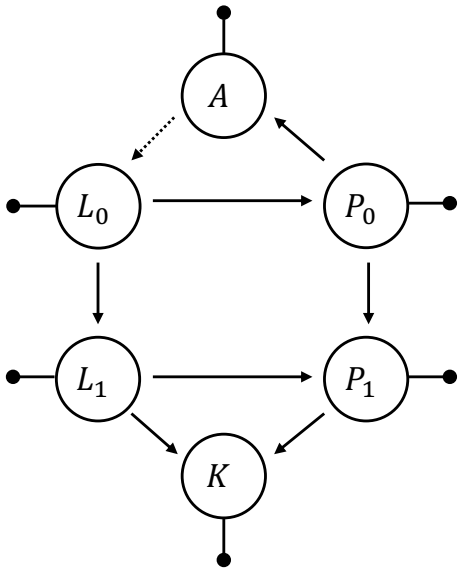

Figure 1: Diagram of host and parasitoid wasps. L represents the density of early juvenile hosts, P represents the density of late juvenile hosts, A represents the density of adult hosts, and K represents the density of parasitoid wasps. We use subscript 0 for uninfected and 1 for infected state, respectively.

We focus on the case where a host population follows exponential growth in the absence of the parasitoid wasps and assume that the attack rate of the parasitoid wasps is proportional to both parasitoid wasps and host densities (i.e., Holling's type-I functional response, Holling (1959); but see Appendix E for the robustness of this assumption against the density-dependent regulation in the parasitoid-free host population). The population dynamics of hosts and parasitoid wasps are described by a set of the following ordinary differential equations:

$$
\begin{aligned}
\dot{L_0} &= \rho d_A A - a_0 L_0 - \lambda \pi L_0 K - \lambda \pi_m L_0 K_m - d_L L_0 \\
\dot{L_1} &= \lambda \pi L_0 K - \epsilon a_1 L_1 - (1-\epsilon)\sigma_L L_1 - (d_L + \upsilon_L) L_1 \\
\dot{P_0} &= a_0 L_0 - \lambda(1-\pi) P_0 K - \lambda(1-\pi_m) P_0 K_m - b_0 P_0 - d_P P_0 \\
\dot{P_1} &= \epsilon a_1 L_1 + \lambda(1-\pi) P_0 K - \sigma_P P_1 - (d_P + \upsilon_P) P_1 \\
\dot{A} &= b_0 P_0 - d_A A \\
\dot{K} &= f_L (1-\epsilon)\sigma_L L_1 + f_P \sigma_P P_1 - d_K K
\end{aligned}
\tag{1}
$$

where we write: dot for the time derivative, r for the ratio of the birth rate of hosts to the mortality rate of adult hosts, a_0 for growth rate of uninfected early juvenile hosts, λ for a searching efficiency of parasitoid wasps, π for the preference for uninfected early juvenile hosts in parasitoid wasps, d_L for mortality rate of uninfected early juvenile hosts, ϵ for preference for late-PET in parasitoid wasps preys on larvae, a_1 for growth rate of infected early juvenile hosts, σ_L for the consumption rate of early juvenile hosts by parasitoid wasps, υ_L for virulence of parasitoid wasps against early juvenile hosts, b_0 for growth rate of uninfected late juvenile hosts, d_P for mortality rate of uninfected late juvenile hosts, σ_P for consumption rate of late juvenile hosts by parasitoid wasps, υ_P for virulence of parasitoid wasps against late juvenile hosts, d_A for mortality rate of adult hosts, f_L for per capita fecundity of parasitoid wasps emerging from early juvenile hosts,f_P for per capita fecundity of parasitoid wasps emerging from late juvenile hosts, and d_K for mortality rate of parasitoid wasps. We consider both preferences, π and ϵ (with $0 \leq \pi \leq 1$ and $0 \leq \epsilon \leq 1$), for host stages and PET as evolutionary traits that evolve independently of each other. For example, the case with $\pi = 1$ and $\epsilon = 0$ is corresponded to the life cycle graph which is depicted as Figure2 (A).

Table 1: Definitions of the parameters

Parameter	Definition
π	Preference for uninfected early juvenile hosts in parasitoid wasps
ϵ	Preference for late-PET in parasitoid wasps preys on larvae
λ	Searching efficiency of parasitoid wasps
ρ	The ratio of the birth rate of hosts to the mortality rate of adult hosts
a_0	Growth rate of uninfected early juvenile hosts
b_0	Growth rate of uninfected late juvenile hosts
a_1	Growth rate of infected early juvenile hosts
d_L	Mortality rate of uninfected early juvenile hosts
d_P	Mortality rate of uninfected late juvenile hosts
d_A	Mortality rate of adult hosts
d_K	Mortality rate of parasitoid wasps
υ_L	Virulence of parasitoid wasps against early juvenile hosts
υ_P	Virulence of parasitoid wasps against late juvenile hosts
σ_L	Consumption rate of early juvenile hosts by parasitoid wasps
σ_P	Consumption rate of late juvenile hosts by parasitoid wasps
f_L	Per capita fecundity of parasitoid wasps emerging from early juvenile hosts
f_P	Per capita fecundity of parasitoid wasps emerging from late juvenile hosts

To investigate the long-term evolutionary dynamics of both traits, we apply the adaptive dynamics theory (Dieckmann and Law, 1996). We first suppose that the resident population dynamics has reached the endemic equilibrium, and introduce a rare mutant of the parasitoid wasp attempting to invade the population. At first, the interior equilibrium is uniquely obtained. We find there is a unique equilibrium of the resident dynamics. To see whether the mutant parasitoid wasp can invade the resident population, we derive the invasion fitness proxy R_m by using the next-generation theorem (Van den Driessche and Watmough, 2002; Hurford et al., 2010):

$$\begin{aligned}
&R_m(\pi_m, \epsilon_m; \pi, \epsilon) \\
&= \underbrace{\frac{\lambda \pi_m L_0^*}{d_K} \cdot \frac{f_L(1-\epsilon_m)\sigma_L}{\epsilon_m a_1 + d_L + \upsilon_L + (1-\epsilon_m)\sigma_L}}_{\text{path (A)}} \\
&+ \underbrace{\frac{\lambda \pi_m L_0^*}{d_K} \cdot \frac{\epsilon_m a_1}{\epsilon_m a_1 + d_L + \upsilon_L + (1-\epsilon_m)\sigma_L} \cdot \frac{f_P \sigma_P}{d_P + \upsilon_P + \sigma_P}}_{\text{path (B)}} \\
&+ \underbrace{\frac{\lambda(1-\pi_m) P_0^*}{d_K} \cdot \frac{f_P \sigma_P}{d_P + \upsilon_P + \sigma_P}}_{\text{path (C)}}.
\end{aligned} \tag{2}$$

where L_0^* and P_0^* represent the density of uninfected early juvenile host and uninfected late juvenile host at the endemic equilibrium, respectively. In Equation (2), we partition the reproductive success of the mutant individual into that through each of the pathways presented in Figure 2. The first, 'path (A)' term represents the reproductive success by attacking and consuming early juvenile hosts (Figure 2A). The path (B) term represents the reproductive success by attacking on early juvenile hosts and consuming late juvenile hosts (Figure 2B). The path (C) term represents the reproductive success by attacking and consuming late juvenile hosts (Figure 2C).

The rare mutant can invade the resident population when $R_m > 1$. By using this criterion, we examine a candidate evolutionary outcome, its evolutionary stability (Smith, 1982) (i.e., no mutants can invade) and also convergence stability (Eshel et al., 1983) (i.e., evolutionary dynamics convergence of the traits).

Although the results in the main text all assume the exponential growth of the parasitoid-free host population (as this assumption immensely simplify the analyses), we also analyze the case where host density follows logistic

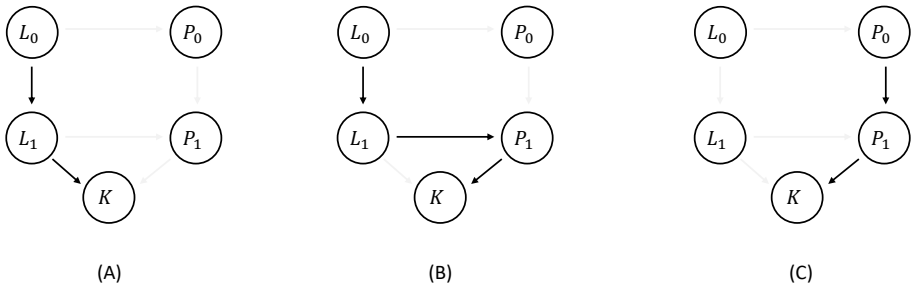

Figure 2: Three pathways involved in the invasion fitness. (A) Parasitoid wasps attack the early juvenile hosts and immediately prey on them. (B) Parasitoid wasps attack the early juvenile hosts and wait until they grow to late juveniles, and then prey on them. (C) Parasitoid wasps attack on the late juvenile host and immediately prey on them.

growth (i.e., density-dependent regulation of of host fecundity). Specifically, we conduct numerical, deterministic simulations, as follows. We first consider 25 strains in the parasitoid population based on the trait values, and construct a mathematical model that represents the population dynamics of these strains. We next numerically solve the population dynamics to determine which strain survives over an extended period. We finally compare the results with host exponential growth with the results with host logistic growth.

3 Results

3.1 Evolution of PET

First, we show the evolution of the preference for late-PET $\epsilon = 1$ (parasitoid emergence timing). Selection gradient (Appendix A) is given by:

$$\left.\frac{\partial R_m(\pi_m, \epsilon_m; \pi, \epsilon)}{\partial \epsilon_m}\right|_{\pi_m=\pi, \epsilon_m=\epsilon} \propto \alpha F_P - F_L. \tag{3}$$

where $\alpha = a_1/(a_1 + d_L + v_L)$ is the growth probability of the infected early juvenile host, $F_P = f_P\sigma_P/(d_P + v_P + \sigma_P)$ or $F_L = f_L\sigma_L/(d_L + v_L + \sigma_L)$ is the expected conversion rate of parasitoid wasps preying on early or late juvenile hosts, respectively. While the selection gradient depends on both of the evolutionary traits π and ϵ, the sign depends only on the parameters such as α and F_P. Thus, the preference evolves monotonically to either 0 or 1 (i.e. early-PET or late-PET) depending on the magnitude relationship between αF_P and F_L. F_L and αF_P corresponds to route (a) (or route (b), respectively) in Figure 2 and represents the expected conversion rate of early juvenile hosts when parasitoid wasps prey on the host immediately (or the conversion rate when parasitoid wasps allow the host to grow after the attack, respectively).

Second, we assess the evolutionary stability that indicates whether the rare mutant can invade a population dominated by the wild type (Smith, 1982). Since the evolutionarily singular point of ϵ is at an edge, it can be shown without taking the second derivative of the fitness function that convergence stability implies evolutionary stability (Appendix C). We summarize the evolutionary consequences with respect to parameters in Figure3.

Equation3 represents the relationship between the reproductive value of infected early juvenile hosts when the parasitoid wasps prey immediately and when wasps wait for their maturation. We can interpret Equation 3 as the evolution of PET such that the hosts' reproductive value is maximized. The preference for late-PET is likely to evolve under the following conditions: (1) the growth probability of the infected early juvenile hosts is high, and (2) the average conversion rate when wasps consume the late juvenile host is higher than that when wasps consume the early juvenile host.

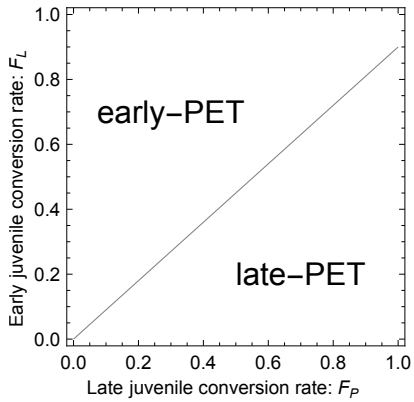

Figure 3: The evolutionary consequences of the preference for late-PET($\alpha = a_1/(a_1 + d_L + \upsilon_L)$: the growth probability of the infected early juvenile host, $F_L = f_L\sigma_L/(d_L + \upsilon_L + \sigma_L)$: the average fecundity rate of parasitoid wasps preying on the early juvenile host and $F_P = f_P\sigma_P/(d_P + \upsilon_P + \sigma_P)$: that on the late juvenile host)

3.2 Evolution of preference for host stages

The selection gradient of the preference for host stages π (Appendix A) is given by:

$$\left.\frac{\partial R_m(\pi_m, \epsilon_m; \pi, \epsilon)}{\partial \pi_m}\right|_{\pi_m=\pi, \epsilon_m=\epsilon} = \frac{\lambda L_0^*}{d_K}\left((p_{L\to P}F_P + p_{L\to K}f_L) - \frac{P_0^*}{L_0^*}(\pi)F_P\right). \tag{4}$$

where $p_{L\to P} = \epsilon a_1/(\epsilon a_1 + d_L + \upsilon_L + (1-\epsilon)\sigma_L$ represents the probability of transition from infected early juvenile hosts to late ones and $p_{L\to K} = (1-\epsilon)\sigma_L/\epsilon a_1 + d_L + \upsilon_L + (1-\epsilon)\sigma_L$ represents the probability of hosts cunsumption by wasps. The sign of Equation 4 is solely determined by ϵ. According to the previous section, ϵ evolves to either 0 or 1. In this section, we will examine the evolution of the preference for early juvenile hosts ((π)) in each scenario involving ϵ.

Since the invasion fitness proxy is linear in π_m, the second derivative is 0. That is,

$$\frac{\partial^2 R_m(\pi_m, \epsilon_m; \pi, \epsilon)}{\partial \pi_m^2} = 0. \tag{5}$$

The point is neutral stable. However, the singular point may be evolutionarily stable which means that mutant individuals cannot invade the resident population. In simulations, the trait values appear to converge to the evolutionary singularity over time and remain stable (Appendix E).

3.2.1 Evolution of preference for host stages when PET is early

The selection gradient on the preference for early juvenile hosts is given by:

$$\left.\frac{\partial R_m(\pi_m, \epsilon_m; \pi, \epsilon)}{\partial \pi_m}\right|_{\pi_m=\pi, \epsilon_m=\epsilon=0} \propto F_L - \frac{P_0^*}{L_0^*}(\pi) F_P. \tag{6}$$

where $F_L = f_L \sigma_L / (d_L + \upsilon_L + \sigma_L)$ is the expected fecundity of parasitoid wasps preying on early juvenile host and $F_P = f_P \sigma_P / (d_P + \upsilon_P + \sigma_P)$ is that on late juvenile host. A unique evolutionarily singular point π^* can be obtained analytically, which is always convergence stable since P_0^*/L_0^* is monotonically increasing function of π^* (Appendix C). Evolutionary consequences of preference for host stages are therefore always continuously stable when parasitoid wasps consume hosts immediately after they attack hosts. When the unique evolutionarily singular point is not between 0 and 1, we carry out case-analyses: the singular value is 0, between 0 and 1, or 1. The evolutionary consequences in each case are shown in Figure 4.

Equation 6 represents the relationship between the class reproductive value of uninfected early juvenile hosts and that of late ones when the parasitoid wasps prey immediately. We can interpret Equation 6 as the evolution of PET such that the hosts' class reproductive value maximizes. When parasitoid wasps consume hosts immediately after they attack hosts, the preference for early juvenile hosts is likely to evolve when the average conversion rate and the density of late juvenile hosts are higher than that of early juvenile hosts. In addition, the lower the growth probability of infected early juvenile hosts, the greater the diversity of host stages can evolve.

3.2.2 Evolution of preference for host stages when PET is late

The selection gradient on the preference for early juvenile hosts is

$$\left.\frac{\partial R_m(\pi_m, \epsilon_m; \pi, \epsilon)}{\partial \pi_m}\right|_{\pi_m=\pi, \epsilon_m=\epsilon=1} \propto \left(\alpha - \frac{P_0^*}{L_0^*}(\pi)\right) F_P. \tag{7}$$

where $\alpha = a_1/(a_1 + d_L + \upsilon_L)$ is the growth probability of infected early juvenile host, $F_P = f_P \sigma_P / (d_P + \upsilon_P + \sigma_P)$ is the expected fecundity rate of parasitoid wasps preying on late juvenile host. A unique evolutionarily singular point π^* can be obtained analytically. The point is always convergence stable because P_0^*/L_0^* is monotonically increasing function of π^*. Evolutionary consequences of the preference for host stages are always continuously stable in the case that parasitoid wasps do not consume hosts immediately after they attack the hosts. As with the previous section, we obtain the evolutionary consequences in three cases (Figure 5).

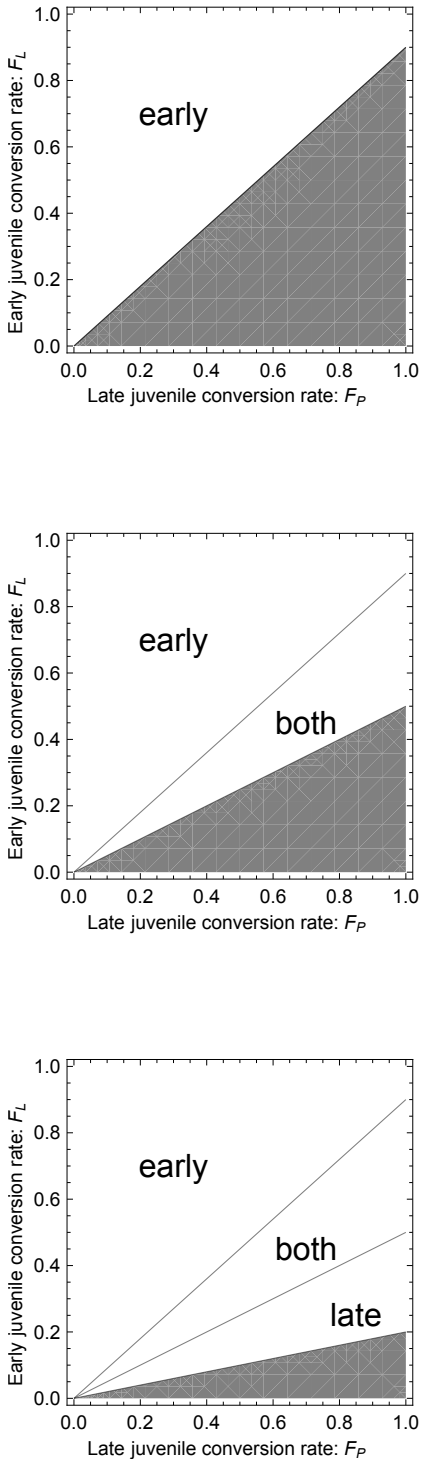

Figure 4: Evolutionary consequences of the preference for host stages when PET is early. Early-PET ($\epsilon = 0$) is convergence stable in the white area, but not in the gray area. Parasitoid wasps attack only early juvenile hosts in the "early" area, attack both of early and late juvenile hosts in the "both" area, and attack late juvenile hosts in the "late" area.

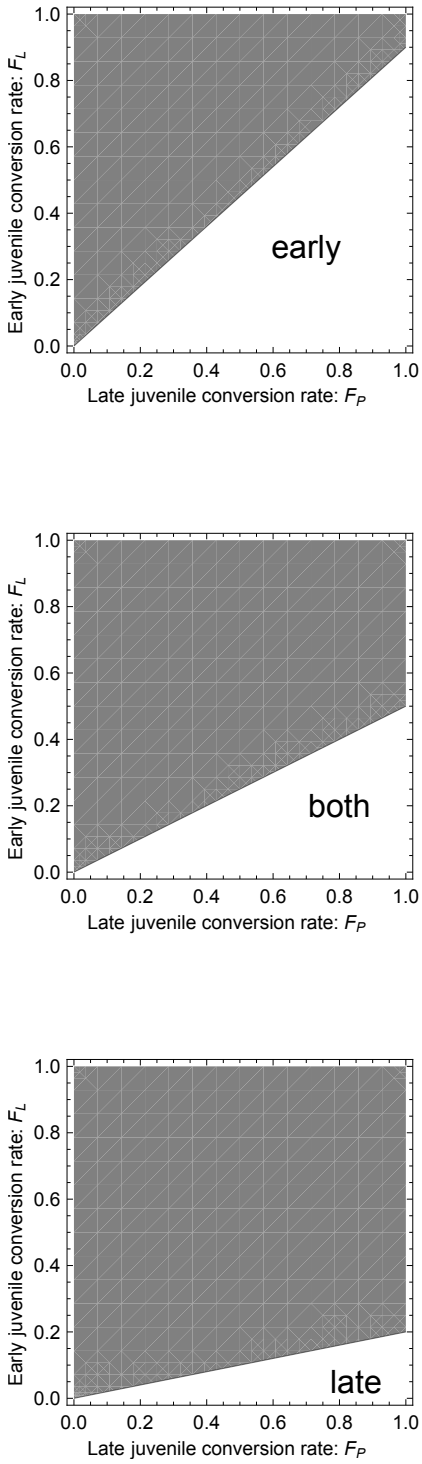

Figure 5: The evolutionary consequences of preference for host stages when PET is late. Late-PET ($\epsilon = 1$) is convergence stable in the white area, but not in the gray area. Parasitoid wasps attack only early juvenile hosts in the "early" area, attack both early and late juvenile hosts in the "both"area, and attack late juvenile hosts in the "late" area.

Equation 7 represents the relationship between the class reproductive value of uninfected early juvenile hosts and that of late ones when wasps wait for their maturation. We can interpret Equation 7 as the evolution of PET such that the hosts' class reproductive value maximizes. Therefore, in the case that parasitoid wasps do not consume hosts immediately after they attack the hosts, the preference for the uninfected early juvenile host is likely to evolve under

two conditions: (1) the growth probability of the infected early juvenile host is high, and (2) the density of the late juvenile host is lower than that of early juvenile hosts.

3.3 Evolution of idiobiont and koinobiont

We show the combined results of the two traits to interpret the results according to the dichotomy hypothesis (Figure 6). Here, we consider the parasitic strategy that the parasitoid wasps to attack uninfected late juvenile hosts and prey on the host immediately as idiobiont. We consider the parasitic strategy that the parasitoid wasps attack an uninfected early juvenile host and prey on the host after the host grows up to the late juvenile stage as koinobiont.

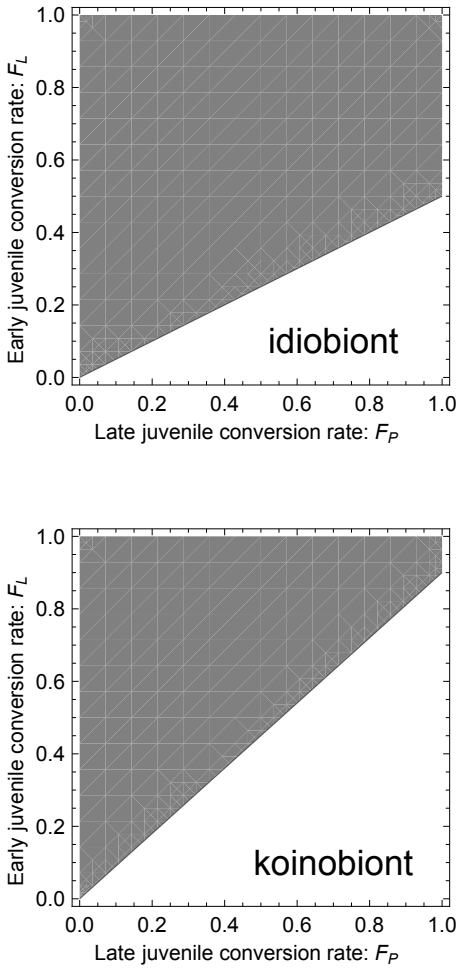

Figure 6: Evolutionary consequences of idiobiont and koinobiont: They are evolutionary consequences in each white area, respectively

The necessary condition for which idiobionts or koinobionts are the evolutionary outocmes is that F_P is greater than F_L, meaning that the average conversion rate of late juvenile hosts exceeds that of early juvenile hosts. The evolution of idiobionts is more likely when the growth probability of infected early juvenile hosts is low, and the density of late juvenile hosts is higher than that of early juvenile hosts. Conversely, koinobionts are more likely to evolve when the growth probability of infected early juvenile hosts is high, and the density of late juvenile hosts is lower than that of early juvenile hosts.

Lastly, we compare our analytical results based on the exponential growth of the host population and the numerical simulations for the cases where the host population exhibits logistic growth. We find consistent results between the two scenarios, confirming the robustness of our results against the logistic growth case.

4 Discussion

We have studied the evolution of parasitoids' emergence timing ('PET') as a life history strategy. Our first key prediction is that the reproductive values of parasitoids determine the evolutionary consequences of the timing of emergence from the host (Fisher, 1930). Specifically, if the host's developmental growth does not increase the expected conversion efficiency (a measure of nutritional quality), the wasps are then selected to emerge from the host immediately. Otherwise, there occurs a variation in the timing of emergence, either early or late. In this case, the early emergence is selected for when the reproductive value of the host for wasps emerging early is higher than that for those waiting for host growth. These results can be understood as cost-benefit balance in delayed emergence (increased mortality versus increased resource quality). Overall, the results suggest that natural selection can shape the patterns of PET in parasitoid wasps, and such patterns are determined by the relative resource quality.

Our second key insight is that the variation in the timing of emergence shapes the diversity in the life cycle (Figure 2). The emergence timing-differences results in the differences in the attack-timing (or target, larvae or pupae). Since parasitoid wasps consume their hosts at the time of emergence, the timing of emergence, but not that of attack, determines their fitness. We considered two developmental stages of hosts available for the parasitoid wasps. In the model, infected early juvenile hosts are allowed to grow to a later developmental stage. As a result, the host utilization strategies of parasitoid wasps exhibit three distinct patterns as follows: attacking young hosts and hatching immediately (Figure 2-(A)), attacking young hosts with prolonged emergence (Figure 2-(B)), and attacking older host and consuming immediately (Figure 2-(C)). This line of results suggests that the variation in the emergence timing produces diversity in the life cycle of parasitoid wasps.

In our analysis, we found that the density ratio of late juvenile hosts to early ones affects the evolution of wasps' preference for hosts' developmental stages. For example, the greater the density ratio, the more the parasite evolves to attack late juvenile hosts. Intuitively, the relative resource quantity matters to the evolution of parasitoid wasps' exploitation strategy. Finding examples of the density ratio between two developmental stages of hosts can be difficult as the stage structures are more complex in nature. Nonetheless, some information is available about host-mortality, which significantly influences the density ratio. Idiobiont hosts are considered to have lower natural mortality than koinobiont hosts, presumably because idiobionts tend to attack hosts that have not been exposed to predation risk, as the host is immobile (Mayhew and Blackburn, 1999; Quicke, 2014). In contrast, koinobionts can parasitize hosts that are exposed to predation because they do not paralize the hosts (Quicke, 2014). Consequently, the density ratio of late juvenile hosts to early juvenile hosts is suggested to be higher for koinobionts than for idiobionts, consistent with observed findings, although we should note that density ratios depend also on differences in fecundity and growth rates. Our finding provides a qualitative prediction for the effect of the relative availability of resource on the diversification of the parasitoid wasps' exploitation strategies.

In addition to the quantity, resource quality plays a role in the evolution of idiobiont and koinobiont strategies. Specifically, the host quality must increase with host growth for natural selection to favour idiobiont and koinobiont strategies. Several empirical studies support this finding. In *Trissolcus mitsukurii* (egg parasitoid) and *Sclerodermus harmandi* (larval parasitoid), for example, host size positively correlates with parasitoids' body size and fecundity (Arakawa et al., 2004; Liu et al., 2011); female parasitoids emerging from larger hosts tend to have higher fertility in *Lysiphlebia mirzai* (nymphal parasitoid) and *Dirhinus giffardii* (pupal parasitoid) (Pandey and Singh, 1999; Wang and Messing, 2004). However, the relationship between host size and fecundity is not straightforward. For example, in *Campoplex dubitator* (larval parasitoid), while larger and more fertile females emerge from larger hosts, their developmental periods are also longer (Jenner and Kuhlmann, 2006). Despite these complexities, it could be hypothesized that developmental stages reflect resource qualities that determine the adaptive evolution of exploitation strategies of parasitoid wasps. Future empirical studies may test the hypothesis and carry out comparative analysis to examine the predicted patterns in this study.

We theoretically studied the life history evolution in parasitoid wasps based on the idiobiont and koinobiont dichotomy. Previous studies have used comparisons and meta-analyses of various traits associated with this dichotomy,

suggesting correlations between the occurrence of specific traits. However, these correlations do not constitute a theory of life history evolution (Mayhew and Blackburn, 1999), as these studies do not disentangle the causal effects of some trait's evolution on others. By focusing on the evolution of PET regulators, the present study formulated the relationship between PET regulator which is a dichotomous driver and other life history traits (e.g. fecundity and virulence). Therefore, our study helps fill the knowledge gap in the correlated selection in life history strategies.

The present study predicted the occurrence of "PET-regulator-syndrome" in parasitoid wasps. When convergent evolution involves the simultaneous appearance of multiple traits, it is referred to as "syndrome", defined as multiple traits evolving concurrently in response to common environmental pressures (Sinnott-Armstrong et al., 2022). For example, parasitoid wasps of the family Ichneumonidae that exploit wood-boring hosts are associated with six traits, such as teeth on the ovipositor and a long terebra (Legrand et al., 2016). In general, mechanisms for the simultaneous evolution of multiple traits include supergenes arising from chromosomal inversions that involve multiple genetic functions, as well as the multifaceted effects of single genes (or pleiotropy; (Raia et al., 2010; Thompson and Jiggins, 2014)). Highly diverse taxa, such as parasitoid wasps, may provide a suitable system for examining convergent evolution and syndromes (Dal Pos and Sharanowski, 2024). Because parasitoid wasps fully rely on their hosts to complete their life cycle (Dal Pos and Sharanowski, 2024), natural selection favors various morphological traits associated with locating a host, laying eggs, developing on the host, and ultimately exiting the host (Quicke, 2014). Historically, the concept of syndrome has been considered to arise from adaptation to a single selective factor (e.g., primary pollinator, preferred habitat) (Sinnott-Armstrong et al., 2022). The idiobiont-koinobiont dichotomy can be therefore interpreted as a syndrome driven by PET-regulator. In particular, our analytical calculations of the evolutionary dynamics can allow for incorporating other factors (e.g. competition among wasps and non-linear searching efficiency of wasps). Thus, our study can analyze the relationship of selection pressure between various life history characteristics and PET-regulator.

To simplify the analysis, multiple parasitisms are omitted from the model, despite their occurrences in nature. Because multiple parasitisms are assocaited with competition, such interactions may cause temporal niche differentiation in host developmental stages and promote the evolution of the PET regulator. Future studies may incorporate the effects of such competition into a model, which may provide testable predictions for the evolution of life history variations in parasitoid wasps.

In summary, our results show that host density and fecundity have a significant impact on PET- regulator evolution and that PET- regulator can alter the structure of the life-cycle graph. These results are supported, in part, by empirical studies. Our approach reveals a relationship between the PET-regulator and other traits in evolution that could not be explained by empirical studies. This study provides a theoretical basis to interpret the idiobiont-koinobiont dichotomy as a life history syndrome of parasitioid wasps generated by the PET-regulator. Future studies could reveal the mechanism that produces the polarized traits of idiobiont and koinobiont by incorporating the effects of resource competition.

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Appendix

A Next generation matrix and invasion fitness proxy

To study life-history evolution, we assess the invasion possibility of a rare mutant into the resident population assuming that the ecological dynamics has reached an equilibrium. The population dynamics of the rare mutant is given by:

$$\frac{\mathrm{d}\mathbf{X_m}}{\mathrm{d}t} = (\mathbf{F_m} - \mathbf{V_m})\mathbf{X_m} \tag{A-1}$$

where

$$\begin{aligned}
\mathbf{X_m} &= \begin{pmatrix} L_{1m} \\ P_{1m} \\ K_m \end{pmatrix} \\
\mathbf{F_m} - \mathbf{V_m} &= \begin{pmatrix} -(\epsilon_m a_1 + d_L + \upsilon_L + (1-\epsilon_m)\sigma_L) & 0 & \lambda\pi_m L_0^* \\ \epsilon a_1 & -(d_P + \upsilon_P + \sigma_P) & \lambda(1-\pi_m)P_0^* \\ (1-\epsilon_m)f_L\sigma_L & f_P\sigma_P & -d_K \end{pmatrix} \\
\mathbf{F_m} &= \begin{pmatrix} 0 & 0 & \lambda\pi_m L_0^* \\ 0 & 0 & \lambda(1-\pi_m)P_0^* \\ (1-\epsilon_m)f_L\sigma_L & f_P\sigma_P & 0 \end{pmatrix} \\
\mathbf{V_m} &= \begin{pmatrix} \epsilon_m a_1 + d_L + \upsilon_L + (1-\epsilon_m)\sigma_L & 0 & 0 \\ -\epsilon_m a_1 & d_P + \upsilon_P + \sigma_P & 0 \\ 0 & 0 & d_K \end{pmatrix}
\end{aligned} \tag{A-2}$$

The Next-Generation Theorem (Van den Driessche and Watmough, 2002) states that if the dominant eigenvalue of the next-generation matrix $\mathbf{G_m} = \mathbf{F_m} \cdot \mathbf{V_m^{-1}}$ exceeds 1, then the mutant can invade and drive the resident individuals extinct. The squared, dominant eigenvalue $\rho(\mathbf{G_m})$ is given by:

$$\begin{aligned}
(\rho(\mathbf{G_m}))^2 =& \frac{\lambda\pi_m L_0^*}{d_K} \cdot \frac{\epsilon_m a_1}{\epsilon_m a_1 + d_L + \upsilon_L + (1-\epsilon_m)\sigma_L} F_P \\
&+ \frac{\lambda\pi_m L_0^*}{d_K} \cdot \frac{f_L(1-\epsilon_m)\sigma_L}{\epsilon_m a_1 + d_L + \upsilon_L + (1-\epsilon_m)\sigma_L} \\
&+ \frac{\lambda(1-\pi_m)P_0^*}{d_K} F_P
\end{aligned} \tag{A-3}$$

where

$$\begin{aligned}
\mathbf{G_m} &= \begin{pmatrix} 0 & 0 & \frac{\lambda\pi_m L_0^*}{d_K} \\ 0 & 0 & \frac{\lambda(1-\pi_m)P_0^*}{d_K} \\ p_{m,L\to P}F_P + p_{m,L\to K}f_L & F_P & 0 \end{pmatrix} \\
p_{m,L\to P} &= \frac{\epsilon_m a_1}{\epsilon_m a_1 + d_L + \upsilon_L + (1-\epsilon_m)\sigma_L} \\
p_{m,L\to K} &= \frac{(1-\epsilon_m)\sigma_L}{(\epsilon_m a_1 + d_L + \upsilon_L + (1-\epsilon_m)\sigma_L}
\end{aligned} \tag{A-4}$$

where $p_{m,L\to P}$ represents the probability that mutant wasps' larvae can transit from infected early juvenile hosts to late ones and $p_{L\to K}$ represents the probability that mutant wasps' larvae consume the host. Since $\rho^2 \gtrless 1$ is equivalent to $\rho \gtrless 1$, we use ρ^2 for the invasion proxy.

B Selection gradient

In this section, we derive the stable class distribution, reproductive values and selection gradient using the next-generation matrix.

B.1 Stable class distribution

The right eigenvector associated with the dominant eigenvalue of the next-generation matrix gives the stable class distribution (Taylor, 1990; Otto and Day, 2011), which represents the asymptotic distribution of mutant alleles. It is given by:

$$\mathbf{G}\vec{u} = \rho(\mathbf{G})\vec{u}, \tag{A-5}$$

where

$$\vec{u} = \begin{pmatrix} \dfrac{\lambda\pi L_0^*}{d_K} \\ \dfrac{\lambda(1-\pi)P_0^*}{d_K} \\ \rho(\mathbf{G}) \end{pmatrix} \tag{A-6}$$

represents the stable distribution of the mutant allele.

B.2 Reproductive value of each class

The left eigenvector associated with the dominant eigenvalue of the next-generation matrix gives the reproductive values of each of these classes (Fisher, 1930; Otto and Day, 2011). The reproductive values represent the contributions of individuals in each class to future reproduction after sufficiently long generations, given by:

$$\vec{v}^\top \mathbf{G} = \rho(\mathbf{G})\vec{v}^\top \tag{A-7}$$

where

$$\begin{aligned} \vec{v}^\top &= \begin{pmatrix} p_{L\to P}F_P + p_{L\to K}f_L \\ F_P \\ \rho(\mathbf{G}) \end{pmatrix} \\ p_{L\to P} &= \frac{\epsilon a_1}{\epsilon a_1 + d_L + \upsilon_L + (1-\epsilon)\sigma_L} \\ p_{L\to K} &= \frac{(1-\epsilon)\sigma_L}{\epsilon a_1 + d_L + \upsilon_L + (1-\epsilon)\sigma_L} \end{aligned} \tag{A-8}$$

$p_{L\to P}$ represents the probability that wasps' larvae can transit from infected early juvenile hosts to late ones and $p_{L\to K}$ represents the probability that mutant wasps' larvae consume the host.

B.3 selection gradient of π

From the calculations above, we have $\vec{u}\vec{v} = 2\rho^2(\mathbf{G}) = 2$. Let $c_i = u_i v_i$ be class reproductive value of class i; the selection gradient of π is given by:

$$\begin{aligned}
\frac{\partial}{\partial \pi_m}\left(\frac{\vec{v}\mathbf{G_m}\vec{u}}{\vec{v}\vec{u}}\right)\Bigg|_{\pi_m=\pi} =& \frac{1}{2}c_1\left(\frac{\partial g_{11}}{\partial \pi_m} + \frac{v_2}{v_1}\cdot\frac{\partial g_{21}}{\partial \pi_m} + \frac{v_3}{v_1}\cdot\frac{\partial g_{31}}{\partial \pi_m}\right)\\
&+\frac{1}{2}c_2\left(\frac{v_1}{v_2}\cdot\frac{\partial g_{12}}{\partial \pi_m} + \frac{\partial g_{22}}{\partial \pi_m} + \frac{v_3}{v_2}\cdot\frac{\partial g_{32}}{\partial \pi_m}\right)\\
&+\frac{1}{2}c_3\left(\frac{v_1}{v_3}\cdot\frac{\partial g_{13}}{\partial \pi_m} + \frac{v_2}{v_3}\cdot\frac{\partial g_{23}}{\partial \pi_m} + \frac{\partial g_{33}}{\partial \pi_m}\right)\\
=& \frac{1}{2}c_3\left(\frac{v_1}{v_3}\cdot\frac{\partial g_{13}}{\partial \pi_m} + \frac{v_2}{v_3}\cdot\frac{\partial g_{23}}{\partial \pi_m}\right)
\end{aligned} \tag{A-9}$$

where

$$\begin{aligned}
\frac{\partial \mathbf{G_m}}{\partial \pi_m}\Bigg|_{\pi_m=\pi} &= \begin{pmatrix} \frac{\partial g_{11}}{\partial \pi_m} & \frac{\partial g_{12}}{\partial \pi_m} & \frac{\partial g_{13}}{\partial \pi_m} \\ \frac{\partial g_{21}}{\partial \pi_m} & \frac{\partial g_{22}}{\partial \pi_m} & \frac{\partial g_{23}}{\partial \pi_m} \\ \frac{\partial g_{31}}{\partial \pi_m} & \frac{\partial g_{32}}{\partial \pi_m} & \frac{\partial g_{33}}{\partial \pi_m} \end{pmatrix}\Bigg|_{\pi_m=\pi}\\
&= \begin{pmatrix} 0 & 0 & \frac{\lambda L_0^*}{d_K} \\ 0 & 0 & -\frac{\lambda P_0^*}{d_K} \\ 0 & 0 & 0 \end{pmatrix}\\
c_3 &= \rho^2(\mathbf{G}) = 1\\
v_1 &= p_{L\to P}F_P + p_{L\to K}f_L\\
v_2 &= F_P\\
v_3 &= \rho(\mathbf{G}) = 1
\end{aligned} \tag{A-10}$$

B.4 selection gradient of ϵ

Selection gradient of ϵ is given by:

$$\begin{aligned}
\frac{1}{2}\vec{v}\,\frac{\partial \mathbf{G_m}}{\partial \epsilon_m}\Bigg|_{\epsilon_m=\epsilon}\vec{u} =& \frac{1}{2}c_1\left(\frac{\partial g_{11}}{\partial \epsilon_m} + \frac{v_2}{v_1}\cdot\frac{\partial g_{21}}{\partial \epsilon_m} + \frac{v_3}{v_1}\cdot\frac{\partial g_{31}}{\partial \epsilon_m}\right)\\
&+\frac{1}{2}c_2\left(\frac{v_1}{v_2}\cdot\frac{\partial g_{12}}{\partial \epsilon_m} + \frac{\partial g_{22}}{\partial \epsilon_m} + \frac{v_3}{v_2}\cdot\frac{\partial g_{32}}{\partial \epsilon_m}\right)\\
&+\frac{1}{2}c_3\left(\frac{v_1}{v_3}\cdot\frac{\partial g_{13}}{\partial \epsilon_m} + \frac{v_2}{v_3}\cdot\frac{\partial g_{23}}{\partial \epsilon_m} + \frac{\partial g_{33}}{\partial \epsilon_m}\right)\\
=& \frac{1}{2}c_1\frac{v_3}{v_1}\cdot\frac{\partial g_{31}}{\partial \epsilon_m}
\end{aligned} \tag{A-11}$$

where

$$
\begin{aligned}
\left.\frac{\partial \mathbf{G_m}}{\partial \epsilon_m}\right|_{\epsilon_m=\epsilon} &= \left.\begin{pmatrix} \frac{\partial g_{11}}{\partial \epsilon_m} & \frac{\partial g_{12}}{\partial \epsilon_m} & \frac{\partial g_{13}}{\partial \epsilon_m} \\ \frac{\partial g_{21}}{\partial \epsilon_m} & \frac{\partial g_{22}}{\partial \epsilon_m} & \frac{\partial g_{23}}{\partial \epsilon_m} \\ \frac{\partial g_{31}}{\partial \epsilon_m} & \frac{\partial g_{32}}{\partial \epsilon_m} & \frac{\partial g_{33}}{\partial \epsilon_m} \end{pmatrix}\right|_{\epsilon_m=\epsilon} \\
&= \begin{pmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ \frac{a_1(d_L+v_L+\sigma_L)}{(\epsilon a_1+d_L+v_L+(1-\epsilon)\sigma_L)^2)}F_P - \frac{f_L\sigma_L(a_1+d_L+v_L)}{(\epsilon a_1+d_L+v_L+(1-\epsilon)\sigma_L)^2} & 0 & 0 \end{pmatrix} \qquad \text{(A-12)} \\
c_1 &= \frac{\lambda\pi L_0^*}{d_K}\left(p_{L\to P}F_P + p_{L\to K}f_L\right) \\
v_1 &= p_{L\to P}F_P + p_{L\to K}f_L \\
v_3 &= \rho(\mathbf{G}) = 1
\end{aligned}
$$

C Evolutionary stability

By examining the sign of the second derivative given that the evolutionarily singular point is in the interior of the phenotypic space (which is the square rectangle), we assess the evolutionary stability of π using the adaptive dynamics theory.

The second derivative with respect to π_m is given by:

$$
\left.\frac{\partial^2 R_m(\pi_m,\epsilon_m;\pi,\epsilon)}{\partial \pi_m^2}\right|_{\pi_m=\pi=\pi^*,\epsilon_m=\epsilon} = 0. \qquad \text{(A-13)}
$$

On the other hand, the evolutionarily singular point of ϵ is located on the boundary of the phenotypic space. We here examine whether the convergence stability implies the evolutionary stability without taking the second derivative of the fitness function.

When $\epsilon = 0$ is convergence stable and the evolutionarily singular point of π has an interior solution π^*, the selection gradient is given by:

$$
\left.\frac{\partial R_m(\pi_m,\epsilon_m;\pi,\epsilon)}{\partial \epsilon_m}\right|_{\pi_m=\pi,\epsilon_m=\epsilon} \propto \alpha F_P - F_L < 0. \qquad \text{(A-14)}
$$

which always holds (i.e., never positive, implying that selection pushes the phenotype (preference for late-PET) towards zero). Substituting this equation into the Taylor expansion of the fitness function around $\epsilon = 0 (0 < \delta << 1)$, we obtain

$$
\begin{aligned}
R_m(\pi^*,\delta;\pi^*,0) &= R_m(\pi^*,0;\pi^*,0) + \delta \left.\frac{\partial R_m(\pi^*,\epsilon_m;\pi^*,0)}{\partial \epsilon_m}\right|_{\epsilon_m=0} \qquad \text{(A-15)} \\
&< R_m(\pi^*,0;\pi^*,0). \qquad \text{(A-16)}
\end{aligned}
$$

Thus, $\epsilon^* = 0$ is evolutionarily stable because it attains a local maximum. When the singular point has an interior solution, the selection gradient is 0, i.e., the second term of the Taylor expansion vanishes. Thus it is necessary to take the second derivative to evaluate the sign of the third term. We can apply a similar argument to the case where $\epsilon^* = 1$, and find that $\epsilon^* = 1$ is also evolutionarily stable because it attains a local maximum.

D The density proportion of pupae to larvae

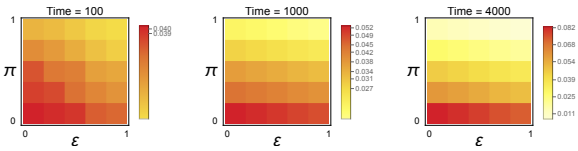
We can obtain the density ratio of P_0^* to L_0^* as follows:

$$\frac{P_0^*}{L_0^*}(\pi) = \frac{-d_A(b_0+d_P)\pi + d_A(a_0+d_L)(1-\pi) + \sqrt{\left(d_A(b_0+d_P)\pi + d_A(a_0+d_L)(1-\pi)\right)^2 + 4rd_Aa_0b_0\pi(1-\pi)}}{2rb_0(1-\pi)} \tag{A-17}$$

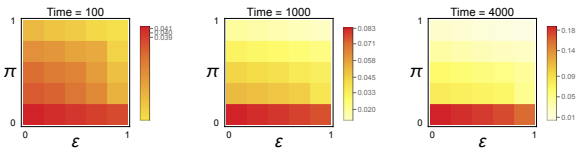
which is a monotone increasing function of π.

E Simulation

We conduct deterministic evolutionary simulations and then compare the results of exponential growth with those of logistic growth. First, we divide the parasitoid wasps population into multiple strains based on the evolutionary traits and construct a mathematical model that represents the population dynamics of these strains. Second, we numerically solve the population dynamics to determine which strain survives over an extended period. Finally, we compare the outcomes of evolutionary simulations of the case where the host has logistic growth with that of the case where the host has exponential growth. We show that our analytical results are robust against this modified assumption.

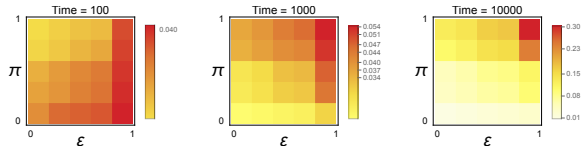


(a)Time variation of frequency of each strain

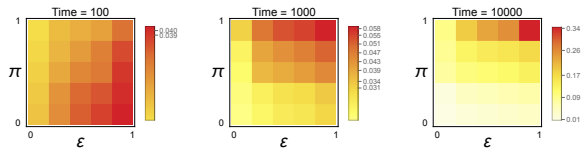


(b)Time variation of frequency of each strain

Figure 7: Evolutionary simulations: (a) The host density follows linear growth. (b) The host density follows logistic growth (carrying capacity $c = 100$). Both represent the case where wasps evolve to idiobiont. Wasps attack late juvenile hosts when $\pi = 0$, so the preference for late-PET ϵ is neutral. ($\lambda = 1$, $r = 4$, $a_0 = 1.5$, $b_0 = 0.5$, $d_L = 1$, $d_P = 1$, $d_A = 0.5$, $d_K = 0.5$, $\upsilon_L = 0.5$, $\upsilon_P = 0.5$, $\sigma_L = 0.5$, $\sigma_P = 1$, $f_L = 0.5$,$f_P = 0.6$)



(c)Time variation of frequency of each strain



(d)Time variation of frequency of each strain

Figure 8: Evolutionary simulation:(a)The host density follows linear growth. (b)The host density follows logistic growth(The carrying capacity c=100). Both of them represent the case that wasps evolve to koinobiont($\lambda = 0.1$, $r = 0.5$, $a_0 = 0.16$, $b_0 = 0.2$, $d_L = 0.1$, $d_P = 0.1$, $d_A = 0.1$, $d_K = 0.1$, $\upsilon_L = 0.1$, $\upsilon_P = 0.1$, $\sigma_L = 1$, $\sigma_P = 1$, $f_L = 1$,$f_P = 2$).

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