

The combined effect of host and food availability on optimized parasitoid life-history traits based on a three-dimensional trade-off surface

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Abstract

The reproductive success of many insects is considered to be limited by two main factors: the availability of mature eggs to lay (termed egg limitation) and the time to locate suitable hosts (termed time limitation). High host density in the environment is likely to enhance oviposition opportunities, thereby selecting for higher investment in egg supply. In contrast, a shortage of food (e.g. sugar sources) is likely to increase the risk of time limitation, thereby selecting for higher allocation to initial energy reserves. To our knowledge, the combined effect of host and food availability on these optimal life-history allocations has never been investigated. We thus modelled their simultaneous effects on a three-dimensional trade-off between initial investment in energy reserves, egg number and egg size, while focusing on insect parasitoids. The model was based on Monte Carlo simulations coupled with genetic algorithms, in order to identify the optimal life-history traits of a single simulated parasitoid female in an environment in which both hosts and food are present in varying densities. Our results reproduced the simple predictions described above. However, some novel predictions were also obtained, especially when specific interactions between the different factors were examined and their effects on the three-dimensional life-history surface were considered. The work sheds light on long-lasting debates regarding the relative importance of time versus egg limitation in determining insect life-history traits and highlights the complexity of life-history evolution, where several environmental factors act simultaneously on multiple traits.

KEYWORDS

egg load, egg size, food availability, host density, longevity, parasitoid

1 | INTRODUCTION

The study of trade-offs is central to life-history theory. Given that organisms are constrained by the amount of available resources, any investment in one biological or physiological function is likely to

come at the expense of another (Roff, 2002; Stearns, 1992). Being under strong natural selection, life-history traits are considered to represent the optimal resource allocation under certain environmental constraints. Accordingly, many life-history studies have been designed to demonstrate potential trade-offs, either by detecting

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negative correlations between traits or functions (e.g. Clutton-Brock, Guinness, & Albon, 1983; Guisande, Sanchez, Maneiro, & Miranda, 1996; Blomquist, 2009), or by experimentally enhancing investment in a certain function, and detecting a plastic or evolutionary response in another (e.g. Rose, 1984; Sanz & Moreno, 1995; Miyatake, 1997; Hunt et al., 2004). However, although it has long been acknowledged that many functions are likely to compete for the same resource pool (Agrawal, Conner, & Rasmann, 2010; Boggs, 2009; Zera & Harshman, 2001), often only two competing life-history traits are considered at a time. Moreover, although multiple environmental factors are likely to interact in their effects on the optimal resource allocation, often the effect of a single environmental constraint is tested. This may limit our understanding of the complexity of life-history evolution.

Perhaps the most fundamental life-history trade-off that has often been demonstrated is the one between survival and current reproduction (Roff, 2002; Stearns, 1992; Tatar, 2001). A second important trade-off that has also been studied and modelled extensively is between the number and the size of offspring (Messina & Fox, 2001). Notably, these two trade-offs are not likely to act independently as they may compete for the same resource pool (Agrawal et al., 2010; Boggs, 2009). For example, higher investment in survival could potentially come at the expense of either offspring number, offspring size or both. Similarly, a higher investment in offspring number could come at the expense of either parent survival, offspring size or both. Moreover, multiple environmental factors (e.g. oviposition opportunities, food availability, mortality risk and competition) are likely to interact in their effect on the optimal allocation to these competing components (Stearns, 1992). Nonetheless, these combined trade-offs and effects are rarely considered simultaneously.

Insect parasitoids have long been used as models for life-history evolution (Godfray, 1994; Wajnberg, Bernstein, & Alphen, 2008). From an ecological point of view, female parasitoids are generally considered limited either by the number of mature eggs available (termed egg limitation) or by the time to locate and attack suitable hosts (termed host or time limitation). Parasitoid relative investment in egg production is considered to represent the balance between these two limitations: while a high risk of egg limitation is likely to select for an increased investment in egg supply, a high risk of time limitation is likely to select for an increased investment in energy reserves, and thus in overall survival and lifetime duration (Ellers, Sevenster, & Driessen, 2000; Godfray, 1994; Rosenheim, 1996, 1999). Although insect egg size may potentially enhance the initial size, and subsequently the survival of the developing offspring (Fox & Czesak, 2000), and is likely to be highly important in mediating these risks, this has rarely been addressed, experimentally or theoretically, in parasitoids (Ellers et al., 2000; Rosenheim, 1996, 2011).

Several environmental factors are likely to influence the relative risk of time versus egg limitation. Above all, high host density is likely to enhance parasitoid oviposition opportunities and hence the risk of egg depletion, thereby selecting for a higher investment in egg supply. This prediction is supported both theoretically (Ellers et al., 2000; Rosenheim, 1996, 2011; Sevenster, Ellers, & Driessen, 1998)

and by empirical evidence (Kraaijeveld & van Derwel, 1994; Pelosse, Bernstein, & Desouhant, 2007; Segoli & Rosenheim, 2013b). Another factor that could be of importance is food availability. Many parasitoids feed on sugar resources, mostly in the form of flowers or honeydew (Dieckhoff, Theobald, Wackers, & Heimpel, 2014; Jervis & Kidd, 1986; Jervis, Kidd, Fitton, Huddleston, & Dawah, 1993). In addition, sugar supplementation has repeatedly been shown to enhance parasitoid lifespan (e.g. Lee, Heimpel, & Leibee, 2004; Chen & Fadamiro, 2006; Zhu et al., 2013; Wang et al., 2014; Lahiri, Orr, Cardoza, & Sorenson, 2017), whereas it is generally assumed not to contribute significantly to egg production (Jervis, Ellers, & Harvey, 2008; Rivero & Casas, 1999; Visser & Ellers, 2008). This is especially true in pro-ovigenic parasitoids in which females emerge with their full egg supply and do not produce additional eggs during their lifetime (Jervis, Heimpel, Ferns, Harvey, & Kidd, 2001; Rivero & Casas, 1999). Several studies have demonstrated that parasitoids may be limited by sugar availability in the field (Heimpel & Jervis, 2005; Kishinevsky, Cohen, Chiel, Wajnberg, & Keasar, 2018; Segoli & Rosenheim, 2013c). Hence, a shortage of sugar sources is likely to increase the risk of time limitation, thereby selecting for higher allocation to initial energy reserves. Although the combined effect of host and food availability on parasitoid foraging behaviour (e.g. patch time allocation) has previously been examined using both models (Sirot & Bernstein, 1996; Tenhumberg, Siekmann, & Keller, 2006) and experimentation (Lucchetta, Desouhant, Wajnberg, & Bernstein, 2007), to our knowledge, the simultaneous effects of these factors on life-history allocation strategies have never been investigated.

To fill the above knowledge gaps, we modelled the simultaneous effects of host and food availability on the optimal life-history traits of insect parasitoids using a three-dimensional trade-off between female parasitoid initial investment in energy reserves, egg number and egg size, under different environmental situations. For simplicity, our model is based on the life history of a pro-ovigenic parasitoid, hence, the model predicts the optimal allocation pattern upon adult emergence. Based on general theory and on previous knowledge, we predicted that (1) parasitoid investment in egg number will increase with both host and food availability due to the high risk of egg limitation under this scenario; (2) in contrast, investment in energy reserves will increase at low host and low food availability due to the high risk of time limitation; and (3) investment in egg size will increase under conditions of low host and high food availability, where investment in the other two components is less necessary. We used the model to address these basic predictions, whereas we also examined intriguing outputs due to specific interactions between these factors.

2 | MODEL DESCRIPTION

2.1 | General framework

The model developed was based on Monte Carlo simulations in which the behaviour of a single foraging parasitoid individual is simulated (*i.e.* without possible competition between females), following

a discrete time process, in an environment in which both hosts and food are present at varying densities. For simplification, the model assumes a pro-ovigenic parasitoid female without egg maturation, host-feeding or egg resorption capabilities. Finding food (e.g. nectar) can contribute to a longevity increase, and only a single egg is laid in each host encountered. The foraging environment is modelled as a 2D square grid (500 × 500). At each time point, each cell of the grid contains one or no host, or one or no resource item. Hosts attacked and food items eaten disappear, but new hosts and food items randomly reappear somewhere else in the grid to maintain overall constant average resource availabilities. The model thus introduces stochasticity, in both feeding and oviposition opportunities, in a spatially and temporally explicit framework, rather than considering it from a purely statistical point of view (e.g. Rosenheim, 1996; Ellers et al., 2000; Rosenheim, 2011). Adding stochasticity renders the model more realistic, as females often experience stochastic conditions in nature. Notably, the model simulates the foraging process of a parasitoid female that has a perfect (and instantaneous) ability to discriminate between healthy and attacked hosts and between exploited and unexploited potential food sources, in a large continuous environment, where hosts and food items never become depleted. Although these simplifications may potentially reduce the time limitation experienced by foraging females, they were similar across all simulated environments, and hence were not likely to change the results qualitatively.

2.2 | Females' genotype and foraging strategy

Each simulated female has a genotype defining its initial energy reserves, and the number and the size of eggs she can potentially lay. Such a genotype is located on the 3D trade-off surface providing the trade-off between initial investment in energy reserves, the overall number of eggs produced and the size of the eggs. We constrained these three life-history parameters to be within predefined ranges. Longevity was bound to be in the [1; 1,000] energy units, each equivalent to a single time step (i.e. simulated females cannot survive more than 1,000 time steps), egg number in the [1; 100] interval and egg size in the [0; 100] interval. The equation defining the 3D trade-off surface is:

$$\text{egg size} = \frac{\left(100 - \frac{\text{Energy reserves}}{10}\right)}{\text{egg number}} \quad (1)$$

At the beginning of each simulation, the locations of hosts and food items were drawn randomly and independently in the environment, according to different parameters defining their availability (average). The simulated female was then "released" in the middle of the grid and moved to find resource items. If the female found a host, she attacked it (and laid one egg). If she found a food item, she consumed it, in which case her longevity increased by 100 time steps, but without exceeding 1,000 time steps in total. Hence, even if a parasitoid female could find unlimited food

sources, she was simulated to die from other reasons at some point of her life.

In the model, females moved in response to attraction to both available food items and hosts. For this, we considered that the probability of a foraging female to be attracted to a food item should increase as she is getting closer to running out of available time steps. Doing so, and providing that a food item is found, the female will acquire additional survival time and will then be able to forage for additional hosts to increase her fitness. The probability of the foraging female to be attracted to a food item should also increase if a food item is closer to her than a host to attack. We thus defined the probability at each time step for a female to move to the closest food to follow a logistic curve:

$$\frac{He^{-\alpha t}}{F + (H - F)e^{-\alpha t}} \quad (2)$$

in which, H and F are the distances to the closest host or food item, respectively, t is the remaining survival time of the foraging female (i.e. time to death), and α is a shape parameter that was fixed to 0.003 in all computations. Such a decision-making process, which considers both the distance of the foraging animal from the resource items and its physiological state (i.e. time till death), has been theoretically demonstrated to be optimal (Bernstein & Jervis, 2008) and is consistent with some experimental results (Desouhant, Driessen, Amat, & Bernstein, 2005; Sisterson & Averill, 2002). Each simulation stopped when the female's longevity (obtained both from initial energy reserves and from feeding, with a maximal value of 1,000 time steps) was over, or if she laid all her eggs. Since smaller laid eggs should have a lower probability of survival, following Rosenheim (1996), the fitness of the simulated female was then estimated to be the total number of eggs laid, multiplied by

$$1.0 - e^{-(\text{egg size})} \quad (3)$$

For each female genotype, the corresponding fitness was estimated by the average of 10 independent simulation replicates.

2.3 | Optimization procedure

We used a genetic algorithm (Hoffmeister & Wajnberg, 2008; Ruxton & Beauchamp, 2008; Sumida, Houston, Mcnamara, & Hamilton, 1990) to compute the location on the 3D trade-off surface providing the trade-off between initial investment in energy reserves, the number of eggs produced, and the size of the eggs that maximizes the foraging female's fitness. Such a computer-assisted optimization tool has been already used to solve ecological questions (e.g. Sumida et al., 1990; Hoffmeister & Wajnberg, 2008; Ruxton & Beauchamp, 2008; Wajnberg, Coquillard, Vet, & Hoffmeister, 2012; Wajnberg, Hoffmeister, & Coquillard, 2012). In each environmental condition tested, the algorithm was run with 100 chromosomes (each with three loci for the traits being optimized), corresponding to 100

possible female genotypes. At the beginning of the simulation, each female genotype was randomly drawn on the 3D surface providing the trade-off between initial investment in energy reserves, the number of eggs produced and the size of the eggs. In the optimization process, and at each generation, each chromosome could be randomly modified using a mutation rate of 2.5% per gene and a recombination rate of 60%. In all cases, the optimization process was repeated over 1,600 generations (note that “generation” in the context of genetic algorithms refers to model iterations rather than to an organism's generation), leading to a stable evolutionary solution in each of the environmental situations compared. We computed optimized values in all possible environmental situations combining the numbers of food items and hosts available in the environment into the possible set of values [5, 10, 50, 100, 150, 200, 250, 300 and 500], thus in $9 \times 9 = 81$ different environmental situations. Food item and host locations were re-drawn randomly in the grid each time the fitness of a simulated female was evaluated. In all cases, 100 replicates were performed, and average outputs are provided.

3 | RESULTS

Optimal egg number increased with increasing host density and, to a lesser extent, with food availability (Figure 1a). These effects interacted in the sense that host availability had a stronger positive effect on egg number at higher food availability, and food availability had a slightly stronger effect on egg number at higher host availability. In contrast, investment in initial energy reserves was reduced with increasing food availability and, to a lesser extent, with increasing host availability (Figure 1b). These effects also interacted, as the negative effect of host availability on initial energy reserves was only pronounced when food was readily available, and the negative effect of food availability on initial energy reserves was also mainly pronounced when hosts were readily available. Optimal egg size was highest at low host and high food availability, whereas it was the lowest at high host and low food availability (Figure 1c). The probability of a female becoming egg-limited (*i.e.* the actual proportion of females that had zero eggs left at the end of the simulation) followed an opposite trend to egg size. It was lowest at low host and high food availability and highest at high host and very low food availability (Figure 2).

4 | DISCUSSION

In this work, we developed a model, based on a three-dimensional surface representing the life-history trade-off between initial investment in energy reserves, the number of eggs produced and the size of the eggs, to identify the optimized life-history traits in parasitoid wasps foraging simultaneously for food and hosts in their environment. The results we obtained generally agree with our initial predictions. Under conditions of both high host and high food availability, where the risk of egg limitation was likely to be the highest,

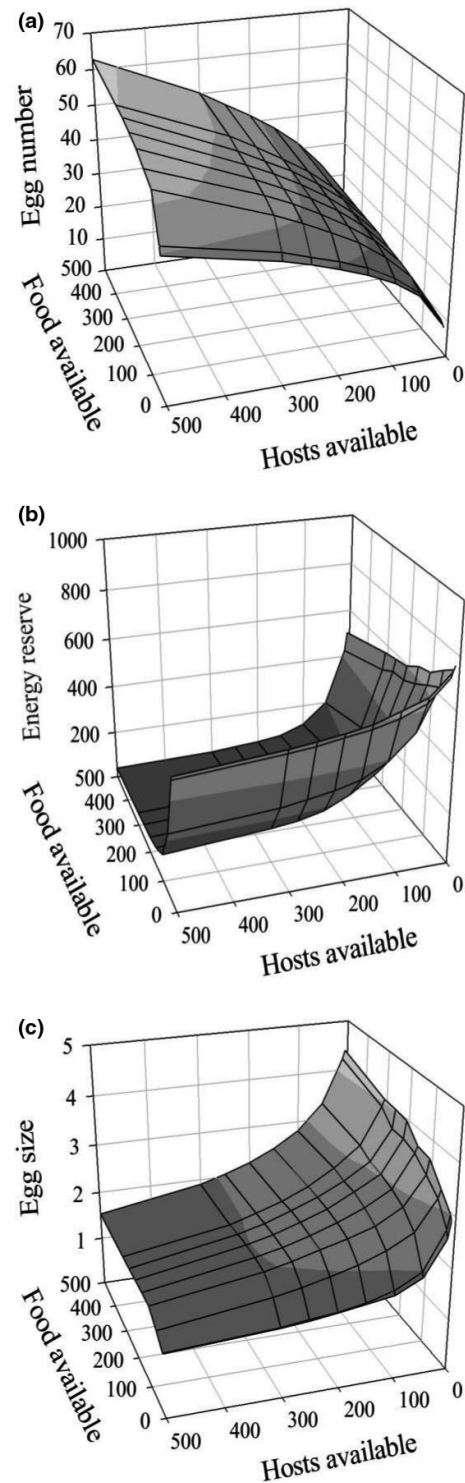


FIGURE 1 Optimized life-history traits, in the 3D trade-off, obtained by the model under different environmental conditions combining the numbers of food items and hosts available in the environment in the possible set of values [5, 10, 50, 100, 150, 200, 250, 300 and 500]. Each point is the average of 100 independent optimization replicates. a: optimized egg numbers; b: optimized energy reserves (in model time steps); and c: optimized egg size

parasitoids optimally invested highly in egg number, at the expense of the other two traits. Reciprocally, under the conditions of both low host and low food availability, where the risk of time limitation

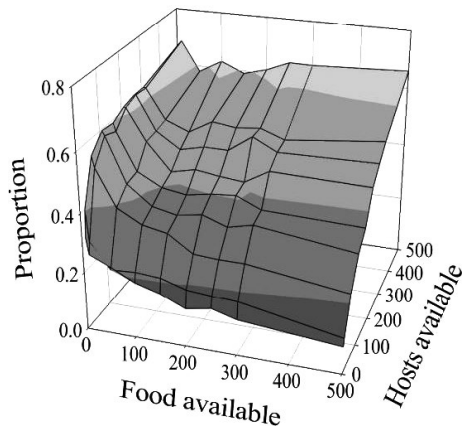


FIGURE 2 Final proportion of optimized females ending their foraging time running out of eggs rather than out of time, under different environmental conditions combining the numbers of food items and hosts available in the environment in the possible set of values [5, 10, 50, 100, 150, 200, 250, 300 and 500]. Note that the axis orientation is different than in Figure 1, to allow a better view of the plot surface

was likely to be the highest, parasitoids invested more heavily in initial energy reserves. Finally, under the conditions of low host and high food availability, where neither of these risks were substantial, parasitoids optimally invested more resources in each egg they produced. In addition to these expected outcomes, however, the results of the model revealed novel insights about the specific interactions between the environmental factors in their effect on the optimal resource allocation of foraging female parasitoids on the three-dimensional trade-off. Below, we discuss the main findings and review supporting evidence from the literature.

A positive evolutionary response in initial egg load to an increase in host density, as shown in our model (see Figure 1a), was predicted by previous models (Ellers et al., 2000; Rosenheim, 1996, 2011; Sevenster et al., 1998) and is supported by several lines of empirical evidence. For example, it has long been suggested that parasitoids attacking hosts of an earlier developmental stage have higher fecundities than those attacking hosts of later stages (Price 1973a,b, 1998). Although this was often explained as a counter-adaptation to the high mortality rate of young hosts, it is also consistent with the interpretation that parasitoids can evolutionarily adjust their egg loads to host availability, as hosts of early developmental stages naturally occur at higher densities in the environment (Godfray, 1994; Mayhew, 2016).

Evidence for adaptations at the population level may include the *Drosophila* parasitoid *Asobara tabida*, where females from southern regions—in which hosts occur at higher densities—were shown to emerge with more eggs than those from northern regions (Kraaijeveld & van Derwel, 1994). Although this species is not strictly pro-ovigenic, these patterns are likely to represent an evolutionary response in egg loads at emergence (Ellers & van Alphen, 1997). Similarly, in another *Drosophila* parasitoid, *Leptopilina boulardi*, females from humid environments—in which host patches are more abundant—were suggested to be locally adapted by investing more in

initial egg loads than females from dry environments (Moiroux et al., 2010). In the flour moth parasitoid *Venturia canescens*, females from grain storage facilities—where hosts tend to aggregate—were shown to emerge with higher egg loads than females from natural habitats (Amat, Alpheni, Kacelnik, Desouhant, & Bernstein, 2017; Pelosse et al., 2007). Finally, in the strictly pro-ovigenic parasitoids *Anagrus erythroneurae* and *A. daanei* that parasitize eggs of grape leafhoppers, females from agricultural vineyards—where host densities are generally higher—were shown to emerge with higher egg loads than those from riparian natural habitats, suggesting a local adaptation in egg loads in response to host densities (Segoli & Rosenheim, 2013a, b).

In our model, optimal investment in egg loads was also positively associated with food availability to the adult parasitoid (see Figure 1a). This is likely because the additional energy sources obtained from feeding allowed adult females to survive longer to lay more eggs during their lifetime. Several studies demonstrated the potential effects of food availability on realized parasitoid longevity (Lee & Heimpel, 2008) or on the number of eggs laid by females in the field (Segoli & Rosenheim, 2013c). However, to our knowledge, evolutionary responses in parasitoid initial egg load to sugar availability have not been demonstrated.

Optimal investment in initial energy reserves showed an opposite response to that of egg load, namely it was higher at low host and low food availability. This is probably because, under these conditions, the risk of time limitation due to the difficulty of finding hosts and food in the environment was higher, promoting investment in initial energy reserves, at the expense of egg number. Although evidence exists for evolutionary trade-offs between investment in survival and reproduction in insects (Tatar, 2001), evidence for such opposite responses in response to host density is limited. For example, in the parasitoid *V. canescens*, the higher number of eggs produced by females from grain storage facilities exhibited a trade-off with the amount of energy reserves (e.g. glycogen) in their bodies (Amat et al., 2017; Pelosse et al., 2007). Similarly, in *L. boulardi*, females from humid environments invested more in early reproduction, but died sooner than females from dry environments (Moiroux et al., 2010). In contrast, no clear evidence for such an opposite response was found in *Anagrus* parasitoids, as females originating from host-rich environments, despite a higher investment in egg number at emergence, did not seem to consistently reduce investment in survival (Segoli, Sun, Nava, & Rosenheim, 2018), but instead produced smaller eggs (Segoli & Rosenheim, 2013b).

These seeming inconsistencies may partially be explained by the interaction between the different environmental factors in their effects on the optimal resource allocation, as demonstrated in our results. For example, optimal longevity in our model was negatively affected by increasing host density, but only when food was readily available (see Figure 1b). This is likely because, under a situation of low food availability, females cannot compromise their initial energy reserves. Instead, under this scenario, female parasitoids are expected to optimally trade-off egg load with egg size (see Figure 1c). This may explain why *Anagrus* females from vineyards—in which host

density is high but sugar availability was shown to be limited (Segoli & Rosenheim, 2013c)—do not seem to compromise their survival, but rather their egg size. Empirical data, thus, appear to be consistent with our model predictions.

Nevertheless, it should be noted that very little is known about either variation in egg size or about the relationship between egg size and larval survival in parasitoids. Moreover, models of parasitoid life history more often considered egg size as a fixed factor, rather than an evolving trait, predicting that as the cost of producing an egg increases, so does the proportion of egg-limited females in the field (Ellers et al., 2000; Rosenheim, 2011). An exception is the classical model by Rosenheim (1996), which explicitly tested evolutionary responses in egg size. Similar to our model, when host density increased, optimal egg size was predicted to decrease, whereas the proportion of egg-limited females in the population was predicted to increase. However, in this model, the response in egg size was tested independently of that of initial energy reserves, and the effect of food availability was not considered. Hence, both the basic assumptions and the subsequent implications of egg size in mediating the relative risks of egg and time limitation in different environments should be further examined.

Our model was based on the biology of pro-ovigenic species, which are common in some parasitoid families, as well as in additional insect groups, for example midges, moths and mayflies (Ellers & Jervis, 2004; Jervis, Boggs, & Ferns, 2005; Rosenheim, Jepsen, Matthews, Smith, & Rosenheim, 2008). However, insights from pro-ovigenic species may often be generalized to synovigenic species, as they are quantitatively similar in their balanced expression of time limitation versus egg limitation (for further discussion see Rosenheim et al., 2008). For example, just like pro-ovigenic females, synovigenic females may exhibit evolutionary responses in their initial egg loads, in relation to variations in oviposition opportunities and other environmental variables (Jervis & Ferns, 2004; Jervis et al., 2001; Kraaijeveld & van Derwel, 1994). In addition, synovigenic females may exhibit plastic responses in their egg production in accordance with host and food availability (Lee & Heimpel, 2008; Papaj, 2000; Wang et al., 2014), consistently with our model predictions.

Although our model focused on host density and food availability in the environment, other factors such as predation risk (Reznick, Butler, & Rodd, 2001), habitat fragmentation (Wajnberg et al., 2012) and environmental stochasticity (Ellers et al., 2000; Rosenheim, 2011) may also interact in their evolutionary effects on various life-history traits in different animal species. Moreover, although our model optimizes three life-history traits that are likely to be interdependent and tightly linked to fitness (Ellers et al., 2000; Rosenheim, 1996, 2011), the simultaneous investment in additional morphological or physiological traits (e.g. mobility, stress tolerance and immune system) may also potentially be considered. Hence, patterns of life-history responses are likely to be even more complex than exemplified here. To elucidate this complexity, the interplay between multiple environmental factors in their effect on multi-dimensional trade-offs should be considered more often in theoretical models

and empirical tests of their predictions. In particular, experiments which detect changes in evolutionary responses to a manipulated environment over many generations are crucial (Kawecki et al., 2012). In the context of the present work, evolutionary experiments in which parasitoids are reared under different combinations of high and low host and food availabilities, and in which changes in their traits are recorded over time, could provide a valuable test of our predictions.

From an applied perspective, our model may have implications for the use of parasitoids for biological control, as it suggests that environmental conditions may have strong evolutionary consequences for parasitoid fitness and life-history traits. For example, parasitoids evolving under conditions of high host and food availability (as is often the case in biological control rearing facilities) may be selected for high fecundities at the expense of longevity and egg size and would thus be less efficient under natural field conditions in which hosts and food are less available. However, such effects, although already suggested several decades ago (Hopper, Roush, & Powell, 1993; Ruberson, Tauber, & Tauber, 1989), are rarely considered when designing biological control programs.

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