



# Why do predators attack parasitized prey? Insights from a probabilistic model and a literature survey

Michal Segoli<sup>a,\*</sup>, Yves Papegay<sup>b</sup>, Tamir Rozenberg<sup>a</sup>, Eric Wajnberg<sup>b,c,d</sup>

<sup>a</sup> Marco and Louise Mitrani Department of Desert Ecology, SIDEER, BIDR, Ben-Gurion University of the Negev, Midreshet Ben-Gurion 8499000, Israel

<sup>b</sup> INRIA, Sophia Antipolis, Projet Hephaistos, 2004 Route des Lucioles, BP 93, 06902 Sophia Antipolis Cedex, France

<sup>c</sup> INRAE, 400 Route des Chappes, 06903 Sophia Antipolis Cedex, France

<sup>d</sup> USP/ESALQ, Departamento de Entomologia e Acarologia, Piracicaba, Brazil

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## ABSTRACT

Predators and parasitoids often encounter parasitized prey or hosts during foraging. While the outcomes of such encounters have been extensively studied for insect parasitoids, the consequences of a predator encountering parasitized prey have received less attention. One extreme example involves the potter wasp *Delta dimidiatipenne* that frequently provision their nest with parasitized caterpillars, despite the low suitability of this prey for consumption by their offspring. This raises two main questions: (1) why do female potter wasps continue collecting parasitized caterpillars? and (2) is this an exceptional example, or do predatory insects often suffer from fitness costs due to encounters with parasitized prey? We addressed the first question using a probabilistic mathematical model predicting the value of discrimination between parasitized and unparasitized prey for the potter wasp, and the second question by surveying the literature for examples in which the parasitism status of prey affected prey susceptibility, suitability, or prey choice by a predator. The model demonstrates that only under certain conditions is discrimination against parasitized prey beneficial in terms of the potter wasp's lifetime reproductive success. The literature survey suggests that the occurrence of encounters and consumption of parasitized prey is common, but the overall consequences of such interactions have rarely been quantified. We conclude that the profitability and ability of a predator to discriminate against parasitized prey under natural conditions may be limited and call for additional studies quantifying the outcome of such interactions.

## 1. Introduction

Predators and parasitoids often encounter previously parasitized prey or hosts while foraging. Since parasitism status may affect the behavior, physiology, and nutritional content of a prey individual, such encounters may have major consequences for the foraging animal (van Alphen and Visser, 1990; Rosenheim et al., 1995; Brodeur and Boivin, 2004). For parasitoids (mostly wasps), the likelihood and consequences of such encounters and the potential associated adaptive strategies have been extensively studied (Godfray, 1994; Wajnberg et al., 2008). These may include: (1) the rejection of an already parasitized host (Weisser and Houston, 1993); (2) host marking to reduce the chances of later parasitism events (Nufio and Papaj, 2001); (3) ovidice — the killing of progeny from a previous clutch laid in or on the host (Takasu et al., 1997); and (4) superparasitism — the oviposition of one or more additional eggs in an already attacked host—which often reduces the

survival prospects and resource availability for the developing parasitoid offspring, but could still be adaptive when alternatives are limited (van Alphen and Visser, 1990).

In contrast, the causes and consequences of a predator encountering previously parasitized prey have received less attention. One reason could be that predators are often assumed to be more generalist than parasitoids, feeding on whatever prey they may be able to capture (Snyder and Ives, 2001; Krey et al., 2020). Hence, the parasitism status of their prey may be considered less important to them. In addition, a predator normally feeds on many prey items, while a parasitoid, by definition, develops on or in a single host, or even sometimes on or in a single developmental stage of its host (Godfray, 1994; Poulin, 2011). This can be another reason why the parasitism status of any single prey item encountered may be considered to have lower significance for the overall predator's fitness. Finally, predators often fully consume and thereby remove prey items from the environment, while parasitized

\* Corresponding author.

E-mail address: [msegoli@bgu.ac.il](mailto:msegoli@bgu.ac.il) (M. Segoli).

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hosts may still be available for subsequent parasitism, leading to a wide range of outcomes and adaptive strategies, as described above.

Despite these common assumptions, the parasitism status of prey could be important for predator-prey interactions, as it may potentially affect the susceptibility, attractiveness, and suitability of the prey to the predator (Brodeur and Boivin, 2004; Brodeur and Rosenheim, 2000; Hasik et al., 2023). For example, parasitized caterpillars of the cabbage butterfly are more likely to be predated by ants, possibly due to their reduced ability to defend themselves (Jones, 1987). The predatory bug *Nesidiocoris tenuis* shows preference for unparasitized moth eggs, especially when the parasitoid within it is at an advanced stage of development (Cabello et al., 2015). Similarly, parasitized mummified aphids appear to be inferior prey for the larvae of the coccinellid beetle, *Coccinella undecimpunctata*, probably due to their lower nutritional value (Bilu and Coll, 2009).

The consequences of attacking low-quality prey may be especially strong for mass-provisioning predatory insects (mainly wasps) where each offspring is provided with a fixed amount of food in a sealed chamber (Field et al., 2020). This is because, in such cases, the progeny consuming parasitized prey items cannot compensate for associated dietary deficiencies by acquiring more food at a later stage of development. Therefore, mass-provisioning females are expected to discriminate against parasitized prey if they are of lower quality for their offspring. Despite this, evidences exist that mass-provisioning insects may provide parasitized prey in their nests, which is not always consumed by the offspring (Bohart et al., 1982; Jennings and Houseweart, 1984; Tscharnkte et al., 1998; Buschini and Buss, 2010; Segoli et al., 2020), suggesting that either provisioning females have limited discrimination ability, or that, under certain conditions, discrimination against parasitized prey may not be profitable.

One extreme case with strong consequences for offspring survival is highlighted in two recent studies of the potter wasp, *Delta dimidiatipenne* (Hymenoptera, Vespidae, Eumeninae) (Segoli et al., 2020; Leduc et al., 2022). Females of this species frequently provision their nest with caterpillars parasitized by the endoparasitoid *Copidosoma primulum* (Hymenoptera, Chalcidoidea, Encyrtidae), to provide food for their progeny. When provisioned with parasitized caterpillars, *D. dimidiatipenne* larvae feed less efficiently, have reduced developmental success and reduced final weight (Leduc et al., 2022). *C. primulum* parasitoids also do not benefit from this interaction, as they apparently cannot break out of the chambers composing the potter wasp nest, leading to their death. Despite these high costs for all interacting species, the collection of parasitized caterpillars by *D. dimidiatipenne* foraging females seems to be frequent in the field. For example, evidence for parasitized caterpillars (mummies) was found in ~85% of the sampled field sites in the Negev Desert, Israel, and in ~70–80% of newly constructed nest cells. Also, the presence of parasitized prey in a brood cell reduced developmental success and the final body size of the developing potter wasps (Segoli et al., 2020). This raises two main questions: (1) Why do potter wasps continue collecting parasitized caterpillars despite their low suitability for consumption by their offspring; and (2) Is this an exceptional example, or do predatory insects often suffer from such high fitness costs due to the collection of parasitized prey?

We addressed the first question by developing a probabilistic mathematical model predicting the fitness of potter wasps under different values of discrimination between parasitized and unparasitized prey, and under different environmental conditions. For the second question, we surveyed the literature for examples in which the parasitism status of a prey affected prey susceptibility, suitability, or prey choice by a predator. The model demonstrates that only under certain conditions is discrimination against parasitized prey beneficial in terms of the potter wasp's lifetime reproductive success. The literature survey suggests that the occurrence of encounters and consumption of parasitized prey is common, but the overall consequences of such interactions have rarely been quantified.

## 2. Methods

### 2.1. Probabilistic model

The model developed, based on a probabilistic approach, computes the overall fitness output of a potter wasp female, estimated by the total number of surviving progeny she produces during her entire life. Each progeny is assumed to survive if it has been enclosed in a cell with a sufficient amount of food (provided by the caterpillars brought back by its mother to the cell) to enable its complete development. Otherwise, the progeny is assumed to have a lower probability of survival.

To estimate the total number of progeny produced, we considered that the potter wasp female has a total lifetime duration  $tLife$ , which is used to produce progeny only. This includes, for each female, the time needed to build the cell  $tCellBuilding$ , and the time to find and bring each caterpillar back  $tFindCaterpillar$  to it.

$$nbProgeny (tCellBuilding + nbCaterpillar tFindCaterpillar) = tLife \quad (1)$$

where  $nbProgeny$  is the total number of progeny produced, and, for each one of them,  $nbCaterpillar$  is the total number of caterpillars brought back to the cell. The time to find each caterpillar is the sum of the time required to look for it  $tLookingForCaterpillar$  plus the discrimination time  $TimeDiscrimination$  needed to identify it as being either unparasitized or parasitized, plus the time  $taHandlingCaterpillar$  needed to paralyze and bring back a caterpillar, if the female decides to do so:

$$tFindCaterpillar = tLookingForCaterpillar + TimeDiscrimination + taHandlingCaterpillar \quad (2)$$

The time needed for discrimination is assumed to be linearly and positively related with the discrimination ability by the wasp  $pDiscrimination$ , which represents the probability for the wasp to correctly recognize whether the caterpillar is parasitized or not. This is based on personal observations that potter wasps often have difficulties holding on to an attacked caterpillar, and, hence, examining the caterpillar is likely to be difficult and time-consuming, and such a cost is likely to be higher for the potter wasp to achieve a higher discrimination ability. Hence, the time needed for discrimination was given by the following equation:

$$TimeDiscrimination = tCaterpillarDiscrimination \times (2 \times pDiscrimination - 1) \quad (3)$$

with  $tCaterpillarDiscrimination$  corresponding to the time the wasp must invest in discrimination when  $pDiscrimination$  is maximal (i.e., equal to 1.0).

The way  $taHandlingCaterpillar$  is computed is explained below. In order to compute how many caterpillars a female must bring back to the cell, we considered the minimal amount of food  $mTargetFood$  needed to enable the survival of each progeny, and the average mass of food provided by each caterpillar brought back to the nest  $maWaspCaterpillar$ , as it is perceived by the female wasp. Since parasitized caterpillars are less palatable (Leduc et al., 2022) they are assumed to provide a lower mass of food for consumption by the potter wasp offspring. Also, since a female cannot bring back a fraction of a caterpillar, the number of caterpillars the female must bring back to each cell is:

$$nbCaterpillar = ceiling\left(\frac{mTargetFood}{maWaspCaterpillar}\right) \quad (4)$$

in which the function  $ceiling()$  returns the smallest integer not less than the argued value.

The average mass of food provided by a caterpillar, as it is perceived by the female, is computed using the known proportion of parasitized caterpillars in the environment  $pParasitized$ , and the probability of the female being able to recognize an unparasitized or a parasitized caterpillar,  $pDiscrimination$ . We assumed that caterpillars identified as

parasitized are never brought back to the nest due to their low nutritional value. Hence, although the model is probabilistic, this part remains deterministic. Using this notation, the weighted average mass of food provided by each caterpillar, as it is perceived by the female wasp, can be computed using the decision tree shown in Fig. 1. Using such a decision tree, the weighted average mass of food provided by a caterpillar in the environment, as it is perceived by the female wasps, can be computed from the mass of food provided by an unparasitized caterpillar  $mHealthyCaterpillar$  using the following equation:

$$\begin{aligned}
 maWaspCaterpillar &= mHealthyCaterpillar \times [(1 - pParasitized) \\
 &\times pDiscrimination + pParasitized \\
 &\times (1 - pDiscrimination)] \quad (5)
 \end{aligned}$$

If we call  $mParasitizedCaterpillar$  the mass of food provided by a parasitized caterpillar, the real average mass of food  $maCaterpillar$  provided by all caterpillars brought back to the nest can be computed using the equation:

$$\begin{aligned}
 maCaterpillar &= mHealthyCaterpillar \times (1 - pParasitized) \\
 &\times pDiscrimination + mParasitizedCaterpillar \\
 &\times pParasitized \times (1 - pDiscrimination) \quad (6)
 \end{aligned}$$

In the same way, using the same decision tree (Fig. 1), the average overall handling time  $taHandlingCaterpillar$  for paralyzing and bringing back a caterpillar to the nest can also be computed. It depends on the fixed time  $tHandlingCaterpillar$  that the wasp will take for each caterpillar, if it decides to bring it back to the nest:

$$\begin{aligned}
 taHandlingCaterpillar &= tHandlingCaterpillar \times [(1 - pParasitized) \\
 &\times pDiscrimination + pParasitized \\
 &\times (1 - pDiscrimination)] \quad (7)
 \end{aligned}$$

Finally, the overall survival of each progeny is defined as the ratio of the real average caterpillar mass in the environment to the average mass of food provided by a caterpillar as perceived by the female ( $maCaterpillar/maWaspCaterpillar$ ). Since this is a survival probability, this ratio is bounded to be between 0 and 1.

The total fitness of each wasp is considered to be the number of progeny produced multiplied by their survival probability. Hence, combining all these equations, the total fitness of a potter wasp female

can be calculated using the following equation:

$$\begin{aligned}
 fitness &= \left( tLife / \left( tCellBuilding + (tLookingForCaterpillar \right. \right. \\
 &+ tCaterpillarDiscrimination \times (2 \times pDiscrimination - 1) \\
 &+ taHandlingCaterpillar) \times ceiling \left( \frac{mTargetFood}{maWaspCaterpillar} \right) \left. \right) \\
 &\times \min \left( 1; \frac{maCaterpillar}{maWaspCaterpillar} \right) \quad (8)
 \end{aligned}$$

Table 1 gives the list of all parameter with their default value. The R code to compute the probabilistic model is provided as a [supplementary information](#).

### 2.2. Literature survey

We searched the Web of Science Core Collection using the following keywords: “predator”, “predation”, “parasitoid”, “parasitism”, “interaction”, “intraguild predation”, and their combinations within titles and

**Table 1**  
Definition of all parameters of the model with the default values used.

Parameter name	Meaning	Default value
$tLife$	Total lifespan of the female	100
$tCellBuilding$	Time needed to build each cell	2
$tLookingForCaterpillar$	Time needed to find each caterpillar	[0, 0.5, 2]
$tCaterpillarDiscrimination$	Time needed to distinguish between parasitized and unparasitized caterpillar when $pDiscrimination$ is equal to 1.0.	[0, 0.5, 2]
$tHandlingCaterpillar$	Time needed to paralyze and bring back a caterpillar if the female is willing to do so	3
$pParasitized$	Proportion of parasitized caterpillar in the environment	[0.0; 1.0]
$pDiscrimination$	Probability to correctly recognize a unparasitized caterpillar	[0.5; 1.0]
$mTargetFood$	Amount of food needed for a progeny to survive	5
$mParasitizedCaterpillar$	Food supplied by a parasitized caterpillar	0.2
$mHealthyCaterpillar$	Food supplied by a unparasitized caterpillar	0.8

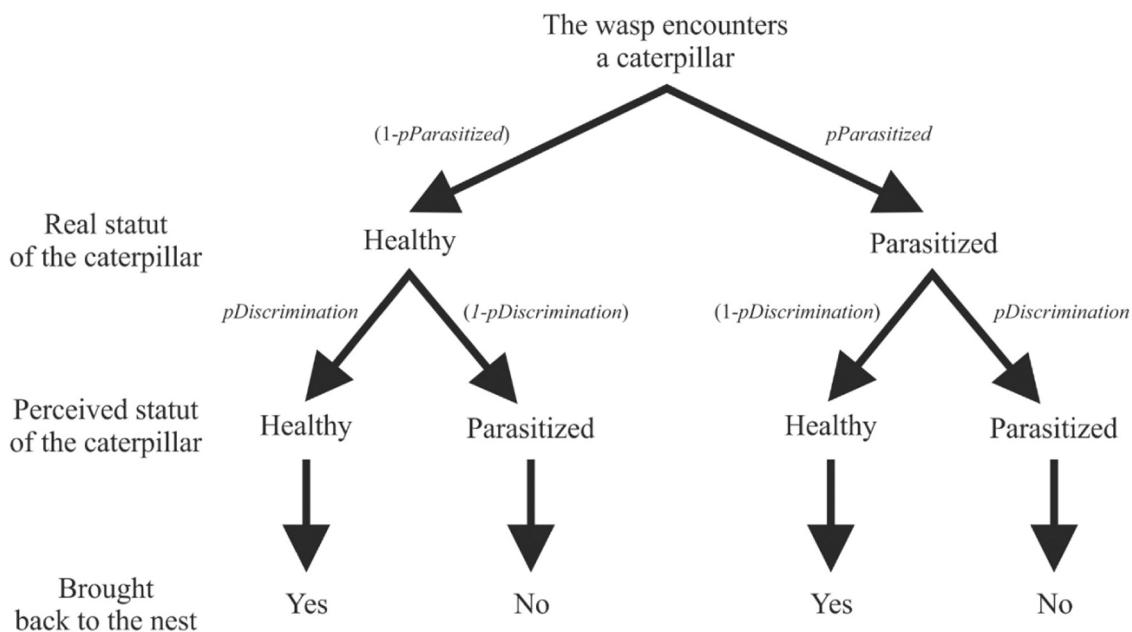


Fig. 1. Decision tree showing the different possible steps leading a potter wasp female to bring back, or not, a caterpillar to the nest.

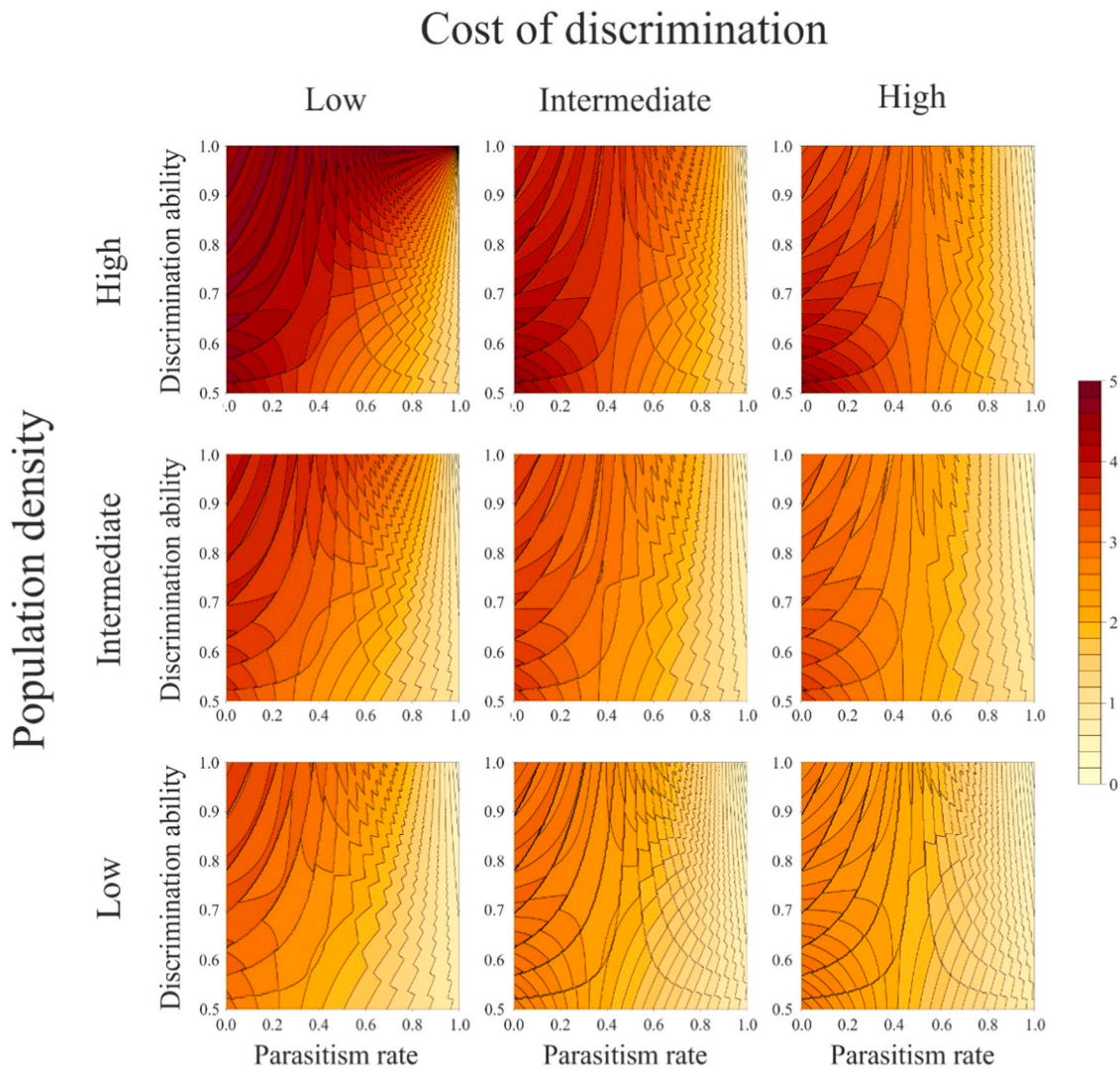
abstracts. In addition, we searched the reference list of three review papers addressing interactions between parasitism and predation (Brodeur and Boivin, 2004; Hasik et al., 2023; Rosenheim et al., 1995). We considered studies that have tested for differential responses of a predator to parasitized vs. unparasitized prey, focusing on parasitism by insect parasitoids. These were further divided into studies testing for: (1) differential susceptibility, *i.e.*, differential attack or consumption rates of prey by a predator in the field, regardless of the underlying mechanism; (2) differential preference for parasitized vs. unparasitized prey by a predator, as indicated by controlled choice experiments; and (3) differential quality, *i.e.*, differences in the performance or fitness measures of predators consuming parasitized vs. unparasitized prey. For each study, we recorded the outcome as higher/lower/similar susceptibility, preference, or quality of parasitized vs. unparasitized prey. Studies in which the results depended on the species or sex of one of the players were considered as mixed evidence.

### 3. Results

#### 3.1. Probabilistic model

The results of the model for a range of parameter values are

presented in Fig. 2. The results indicate that, under no cost of discrimination (left column), wasp fitness increases as the investment, and correspondingly the ability to discriminate, increases. In other words, when the cost is negligible, being discriminative to avoid bringing parasitized caterpillars to the nest is always beneficial. In contrast, when the cost of discrimination is high (right column), fitness is always reduced with discrimination. This reduction in fitness was most pronounced at low parasitism rate, likely because discrimination provides almost no benefits (only costs) when parasitized caterpillars are rare. The most interesting outcome occurs when the cost of discrimination is intermediate (middle columns). In this case, fitness is reduced with discrimination at low (<0.4) or high (>0.8) parasitism rates but increases with discrimination at intermediate parasitism rates (~0.4 – 0.8). In other words, discrimination is only profitable when parasitism rate is intermediate. The time to find a caterpillar (which may be interpreted as population density) does not qualitatively change the effect. However, it does change its magnitude. When the time to find a caterpillar is very low (high population density; upper line), discrimination ability has a large effect on the wasp fitness, while, when finding a caterpillar takes time (low population density; lower line), the magnitude of the effect is reduced.



**Fig. 2.** Potter wasp fitness produced by a probabilistic theoretical model in relation to parasitism rate (x-axis) and ability to discriminate (y-axis), under low ( $t_{CaterpillarDiscrimination}=0$ ), intermediate ( $t_{CaterpillarDiscrimination}=0.5$ ) and high ( $t_{CaterpillarDiscrimination}=2$ ) cost of discrimination, and under high ( $t_{LookingForCaterpillar}=0$ ), intermediate ( $t_{LookingForCaterpillar}=0.5$ ), 2, and low ( $t_{LookingForCaterpillar}=2$ ) population density.

### 3.2. Literature survey

We found 74 papers reporting 84 cases in which differential susceptibility ( $N = 12$ ), preference ( $N = 57$ ), or quality ( $N = 15$ ) of parasitized vs. unparasitized prey have been tested (for details see Table S1 in the supplementary material). Most of the studies testing for differential susceptibility (67%), found evidence for higher predation rates on parasitized over unparasitized prey, while the remaining (33%) found lower predation rates on parasitized prey (Fig. 3). In contrast, most of the studies testing for differential preference (58%) found evidence for higher preference for unparasitized over parasitized prey (especially when the parasitoid was at later stages of development, *i.e.*, close to, or at the pupal stage, Table S1), while only 11% found evidence for preference for parasitized prey. The remaining studies found no evidence for differential preference (20%) or mixed results (11%). Finally, the majority of studies (86%) testing for differential quality, found evidence for inferior quality of parasitized vs. unparasitized prey for the predator, while the rest showed no (7%) or a mixed (7%) effect. The survey was highly taxonomically biased with most studies focusing on coleopteran (mainly coccinellid beetles) or hemipteran (mainly true bug) predators, and on hemipteran (mainly aphids) and lepidopteran (mainly moth egg or larvae) prey (Table S1). Parasitoids were mainly wasps and a few fly species.

## 4. Discussion

We examined the occurrence and consequences of a predator attacking previously parasitized prey using a probabilistic model based on the ecology and behavior of the potter wasp *Delta dimidiatipenne* and via a literature survey aimed at understanding the commonality of this phenomenon. The results of our model suggest that potter wasps are actually likely to bring parasitized prey into their nest under a wide range of environmental conditions and that discrimination is mainly beneficial at intermediate parasitism rates of the prey and when discrimination is not too costly. The literature survey indicates that the occurrence of predators attacking previously parasitized prey is widespread in nature, although the consequences for the predator have rarely been fully quantified. Below we summarize the main insights from both the model and the literature survey and relate them to broader aspects of the ecology of predator-prey interactions.

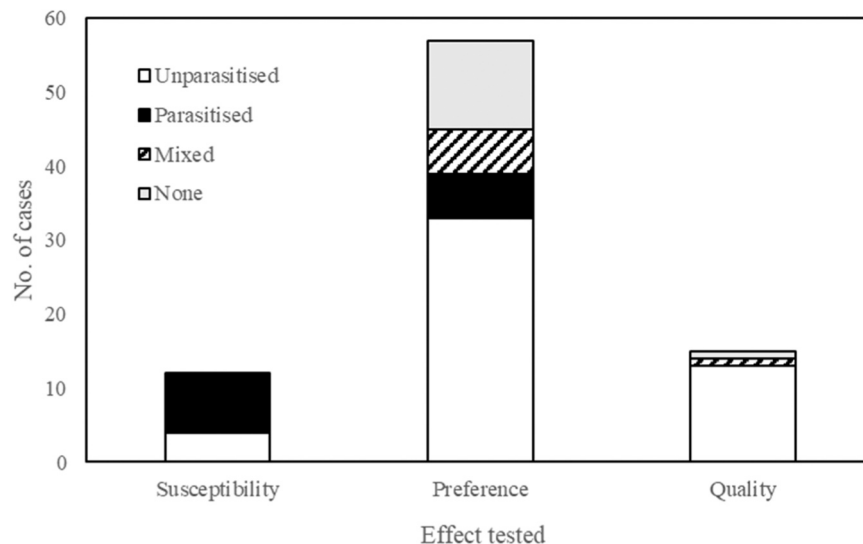
### 4.1. Probabilistic model

The results of our model indicate that when the cost of discrimination is negligible, it is worth being choosy to avoid bringing poor-quality parasitized prey to the nest. This result is consistent with evidence from studies showing that predators often avoid parasitized (low-quality) prey when they are similarly accessible and easily distinguishable from unparasitized (high-quality) prey items (see examples from the literature survey, Table S1).

When the cost of discrimination is intermediate, discrimination becomes profitable, but only at intermediate levels of parasitism in the prey population. This is most likely because, at lower parasitism rates, the probability of encountering a parasitized caterpillar is very low, while at very high parasitism rates, most caterpillars are parasitized anyway. Hence, discrimination will rarely make a difference in these situations, while the cost will remain. The results are consistent with classical models and empirical studies of optimal diet, demonstrating that the relative frequency of low- and high-quality food resources in the environment may affect the benefit of being discriminative (Stephens and Krebs, 1986; van Alphen and Visser, 1990; Weisser and Houston, 1993; Sih and Christensen, 2001; Schuldiner-Harpaz et al., 2022).

In contrast, when the cost of discrimination was high, fitness always decreased with discrimination. This is most likely because, in this case, the cost of discrimination outweighs the benefit of avoiding bringing parasitized prey to the nest. The difference is most pronounced at low parasitism rates, likely because the risk of mistakenly rejecting an unparasitized caterpillar increases when parasitized caterpillars are rare. Indeed, the cost of discrimination and erroneous identification are known to affect animal decisions in other contexts (Sherman et al., 1997). For example, birds may restrain from rejecting cuckoo eggs when discrimination is difficult, in order to avoid mistakenly evicting their own eggs from the nest (Lotem et al., 1995), and parasitoid larvae may tolerate competitors inside the body of their host if their kin-discrimination ability is limited (Segoli et al., 2009).

The time for the wasp to find caterpillars in their environment, which may be linked to population density, did not change the direction of the abovementioned effects. However, it changed their magnitude. When very little time is required for the potter wasp to find a caterpillar, discrimination ability has a large effect on the wasp's fitness. In contrast, at low caterpillar density, especially combined with a high parasitism rate, the magnitude of the effect is lower, as maximal fitness remains generally low.



**Fig. 3.** Number of studies testing for differential susceptibility, preference, or quality of parasitized vs. unparasitized prey. Black sections of the bar represent higher susceptibility, preference, or quality of parasitized prey. White sections represent higher susceptibility, preference, or quality of unparasitized prey. Grey sections represent studies where no difference was found, and striped section represents studies with mixed results (depending on species, sex, etc.).

Our model makes several assumptions that may not be entirely realistic. First, the number of prey items that can be placed into a cell is assumed to be unlimited, while provisioning females may often be restricted by a lack of space in their brood cell. This is likely to be the case in many nest-provisioning insects that construct the brood cell prior to prey provisioning (e.g., potter wasps), but perhaps less in others, where the size or the brood cell may be determined at a later stage (Field, 1992; Field et al., 2020). The occurrence of space shortage in a brood cell might make discrimination more profitable as the female cannot easily compensate for the collection of low-quality prey. However, the net benefit is still likely to depend on the cost of discrimination and on parasitism rate.

Second, our model does not consider other potential risks experienced by the potter wasps while foraging for caterpillars. These may include predation risk on the foraging potter wasp itself (e.g., by birds), theft of prey from the nest, and brood parasitism (e.g., by cuckoo wasps) (West-Eberhard et al., 1995; Auko et al., 2014; Field et al., 2020). Although there is no direct evidence of predation on adult *D. dimidiatipenne* in the field, on a few occasions females did not return to their nest despite being in the process of provisioning a brood cell, and the cell reminded unsealed (M. Segoli, T. Rosenberg, personal observations), suggesting that they were predated upon or died from another cause while searching for caterpillars. In addition, the presence of brood parasites in and around *D. dimidiatipenne* nests has been documented (Leduc et al., 2022). The occurrence of such risks is likely to further restrict the set of conditions under which discrimination is profitable, as rejecting low-quality prey to search for high-quality one will increase the time a female is required to spend foraging away from the nest.

Third, our model assumes that the potter wasps are time- rather than egg-limited, while in reality, insects do experience egg limitation in the field (Heimpel and Rosenheim, 1998; Rosenheim et al., 2008; Segoli and Rosenheim, 2013). The risk of egg depletion is likely to make females choosier (Iwasa et al., 1984; Mangel, 1989), and, hence, in the current case, might make discrimination against parasitized caterpillars more profitable. Although the risk of egg limitation has not been estimated in *D. dimidiatipenne*, in a few cases we found no mature eggs in the reproductive tract of mature females that were captured in the field, suggesting that egg depletion may actually occur under field conditions (M. Segoli, A. D. Johnson, personal observations).

Fourth, we assumed that parasitized and unparasitized caterpillars are similarly accessible and susceptible to predation while evidences suggest that parasitized prey may be either more, or less, susceptible to predation (see 'Literature review' below). Specifically, parasitized caterpillars of the species *Heliothis nubigera* — the most common prey collected by *Delta dimidiatipenne* in the Negev desert — are less active in their response to a simulated predator attack, which might make them more susceptible to predation by the potter wasp (Leduc et al., 2022). Such asymmetries might slightly shift the profitability of discrimination. However, again, this is not likely to change the main insights from the model.

#### 4.2. Literature survey

In our survey, we found several examples of differential predation on unparasitized compared to parasitized prey in various taxa. Cases where the prey was an agricultural pest (mainly aphids or moths) and both the predator (mainly coccinellid beetles and predatory bugs) and the parasitoid were biological control agents used against this pest, were prevalent, possibly causing some biases. For example, mummified aphids were often shown to be inferior, less preferred prey (e.g., Kindlmann and Ruzicka, 1992; Colfer and Rosenheim, 2001; Almoahamad et al., 2008; Bilu and Coll, 2009; Aparicio et al., 2020; Liu et al., 2020). Most examples were related to differential preference, while fewer studies have tested for differential susceptibility, or quality of parasitized prey to the predator (Fig. 3 and Table S1). Hence, the actual frequency and consequences of encounters with parasitized prey in the field are in most cases unknown.

Several studies demonstrated higher susceptibility of previously parasitized prey to predation in the field, as observed for *D. dimidiatipenne* potter wasps (Leduc et al., 2022). Suggested mechanisms included the parasitized prey being more exposed to predation at the periphery of the colony (Tostowaryk, 1971), exposed for longer durations (Roland, 1988, 1990; Roland and Embree, 1995), or being less defended against the predator compared to an unparasitized prey (Jones, 1987; Snyder and Ives, 2001; Paull et al., 2012; Leduc et al., 2022). In most cases, such effects were considered as non-adaptive, indirect behavioral changes related to the prey being parasitized (Brodeur and Boivin, 2004). In a few cases, it was suggested that parasitized aphids expose themselves to predation as an 'adaptive suicide' strategy, thereby reducing the population of their parasitoid to benefit their kin (McAllister and Roitberg, 1987; Brodeur and Boivin, 2004; Perier et al., 2022). This interpretation, however, is still under debate (Humphreys and Ruxton, 2019).

In contrast, several studies showed lower susceptibility of parasitized prey to predation, either due to their tendency to be less mobile and hence less exposed to predation (Chen et al., 2017), to move to a more protected location (Brodeur and McNeil, 1992), or even to bury themselves in the soil (Muller, 1994). Such responses are often interpreted as manipulations imposed by the developing parasitoid to increase its own survival, although support for such interpretation is probably stronger in cases where the parasitized prey actively change their location or exhibit complex behavioral responses (Moore, 2002; Thomas et al., 2005; Poulin and Maure, 2015).

The majority of studies testing for differential preference by a predator found a lower preference for parasitized prey (Fig. 3 and Table S1), as was also demonstrated for *D. dimidiatipenne* larvae, though yet to be tested for adult females (Leduc et al., 2022). In many cases, this preference was only exhibited or was more pronounced when the parasitoid was at an advanced developmental stage (e.g., Zang and Liu, 2008; Kutuk et al., 2011; Chailleux et al., 2013; Mustu and Kilincer, 2014; Cabello et al., 2015; Fu et al., 2017; Mottaghinia et al., 2018; Leduc et al., 2022). This is often explained by the parasitized prey being less nutritious, less palatable, or less penetrable when the parasitoid within it is close to pupation or already pupated (Brodeur and Boivin, 2004). As evidence, in one case it was demonstrated that parasitized mummified aphids were protected from predation by ladybird larvae, but the larvae were able to feed on the mummies when the cuticle was experimentally broken. Nevertheless, the performance of larvae feeding on such parasitized prey was lower than that of those developing on unparasitized prey, suggesting lower nutritional value of these prey items (Bilu and Coll, 2009).

All additional studies comparing the performance (e.g., survival, developmental time, final mass) of a predator when feeding on parasitized vs. unparasitized prey, indicated higher quality of unparasitized over parasitized prey for the predator (e.g., Takizawa et al., 2000; Mullins et al., 2013; Toosi et al., 2019; Liu et al., 2020; Mohammadpour et al., 2020; Yu et al., 2020; Leduc et al., 2022). This may indicate the generality of parasitized prey being of a lower nutritional quality, although additional examples from more diverse taxa are required.

#### 4.3. Integration of the model and literature survey

While the literature survey addressed a slightly different question than the model (see Introduction), it does demonstrate several related aspects. First, it confirms one of the model's assumptions that, in general, parasitized prey are often of a lower nutritional value. Second, the survey clearly demonstrates that despite this difference, predators often still attack and consume parasitized prey. This could partially be related to the insights from the model, that, under certain circumstances, e.g., high cost of discrimination, certain population densities, or certain parasitism rates in the environment (factors that have not been quantified in most of the reviewed studies), discrimination against parasitized prey is not profitable. Further work is required to address the

model's predictions more directly, in a variety of predatory organisms. This can be done, for example, by examining predators' response to varying densities of parasitized and unparasitized prey, or by manipulating the physiological condition of the predator making discrimination more, or less, costly.

#### 4.4. The case of the potter wasp

Although our literature survey suggests that there are multiple examples of differential responses of predators to parasitized vs. unparasitized prey, the case of the potter wasp *D. dimidiatipenne* can still be considered a unique case (more likely due to lack of research than due to its uniqueness in nature). First, it is one of the few studied cases considering a hymenopteran predator, and the only one considering a predatory wasp (rather than ants). Moreover, it is the only studied example where the prey is being attacked by the adult female but consumed by her offspring (as typical for mass-provisioning insects), rather than both attack and consumption being executed by the same individual. Hence discrimination against parasitized prey can be exhibited both by the mother while foraging, and by the offspring in the brood cell. In another example, larvae of the ground-nesting wasp, *Odynerus dilectus*, were observed to ignore parasitized prey that was brought to the nest by their mother, possibly due to their lower quality (Bohart et al., 1982). However, this was not examined via controlled choice experiments and hence was not included in our survey. Finally, to our knowledge, the case of the potter wasp *D. dimidiatipenne* is the only one where evidence for differential susceptibility, preference, and quality of prey to a predator were all demonstrated in a single system. Findings suggest higher susceptibility of parasitized caterpillars (probably due to their lower responsiveness), discrimination against parasitized caterpillars by the potter wasp larvae (especially at later stages of parasitoid development), and lower performance (*i.e.*, survival and final size) when provided with parasitized prey (Leduc et al., 2022). The only aspect that was not directly tested is discrimination by the adult females. However, our model suggests that only under certain environmental conditions discrimination by a foraging female is likely to be beneficial. At the same time, the case of the potter wasp *D. dimidiatipenne* may be considered a representative example. This is because the pattern of higher susceptibility for parasitized prey, despite its lower attractiveness and suitability, mirrors the overall results of our survey (Fig. 3). Whether such pattern is consistent over a wider taxonomical and environmental context should be further explored, but if indeed common, this may have important implications for predator-parasitoid-prey interactions, as it may result in increased likelihood of intraguild predation, and at the same time, high fitness costs for predators.

#### CRedit authorship contribution statement

**Wajnberg Eric:** Conceptualization, Data curation, Formal analysis, Investigation, Visualization, Writing – review & editing. **Rosenberg Tamir:** Data curation, Formal analysis, Writing – review & editing. **Papegay Yves:** Data curation, Formal analysis, Software, Visualization, Writing – review & editing. **Segoli Michal:** Conceptualization, Data curation, Investigation, Methodology, Project administration, Writing – original draft.

#### Data Availability

data is provided as supplementary materials.

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#### Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.beproc.2024.105002.

#### References

- Almohamad, R., Verheggen, F.J., Francis, F., Hance, T., Haubruge, E., 2008. Discrimination of parasitized aphids by a hoverfly predator: effects on larval performance, foraging, and oviposition behavior. *Entomol. Exp. et. Appl.* 128, 73–80.
- van Alphen, J.J.M., Visser, M.E., 1990. Superparasitism as an adaptive strategy for insect parasitoids. *Annu. Rev. Entomol.* 35, 59–79.
- Aparicio, Y., Gabarra, R., Arno, J., 2020. Interactions among *Myzus persicae*, predators and parasitoids may hamper biological control in Mediterranean peach orchards. *Entomol. Gen.* 40, 217–228.
- Auko, T.H., Trad, B.M., Silvestre, R., 2014. Five new associations of parasitoids in potter wasps (Vespidae, Eumeninae). *Rev. Bras. de Entomol.* 58, 376–378.
- Bilu, E., Coll, M., 2009. Parasitized aphids are inferior prey for a coccinellid predator: Implications for intraguild predation. *Environ. Entomol.* 38, 153–158.
- Bohart, G.E., Parker, F.D., Tepedino, V.J., 1982. Notes on the biology of *Odynerus dilectus* (Hym, Eumenidae), a predator of the alfalfa weevil, *Hypera postica* (Col. Curculionidae). *Entomophaga* 27, 23–31.
- Brodeur, J., Boivin, G., 2004. Functional ecology of immature parasitoids. *Annu. Rev. Entomol.* 49, 27–49.
- Brodeur, J., Mcneil, J.N., 1992. Host behavior-modification by the endoparasitoid *Aphidius nigripes* - a strategy to reduce hyperparasitism. *Ecol. Entomol.* 17, 97–104.
- Brodeur, J., Rosenheim, J.A., 2000. Intraguild interactions in aphid parasitoids. *Entomol. Exp. et. Appl.* 97, 93–108.
- Buschini, M.L.T., Buss, C.E., 2010. Biologic aspects of different species of *Pachodynerus* (Hymenoptera; Vespidae; Eumeninae). *Braz. J. Biol.* 70, 623–629.
- Cabello, T., Bonfil, F., Gallego, J.R., Fernandez, F.J., Gamez, M., Garay, J., 2015. Can interactions between an omnivorous hemipteran and an egg parasitoid limit the level of biological control for the tomato pinworm? *Environ. Entomol.* 44, 12–26.
- Chailleux, A., Bearez, P., Pizzol, J., Amiens-Desneux, E., Ramirez-Romero, R., Desneux, N., 2013. Potential for combined use of parasitoids and generalist predators for biological control of the key invasive tomato pest *Tuta absoluta*. *J. Pest Sci.* 86, 533–541.
- Chen, W.B., Vasseur, L., You, M.S., Li, J.Y., Wang, C.X., Meng, R.X., Gurr, G.M., 2017. Parasitised caterpillars suffer reduced predation: potential implications for intraguild predation. *Sci. Rep.* 7, 42636.
- Colfer, R.G., Rosenheim, J.A., 2001. Predation on immature parasitoids and its impact on aphid suppression. *Oecologia* 126, 292–304.
- Field, J., 1992. Patterns of nest provisioning and parental investment in the solitary digger wasp *Ammophila sabulosa*. *Ecol. Entomol.* 17, 43–51.
- Field, J., Gonzalez-Voyer, A., Boulton, R.A., 2020. The evolution of parental care strategies in subsocial wasps. *Behav. Ecol. Sociobiol.* 74, 1–12.
- Fu, W.Y., Yu, X.L., Ahmed, N., Zhang, S.Z., Liu, T.X., 2017. Intraguild predation on the aphid parasitoid *Aphelinus asychis* by the ladybird *Harmonia axyridis*. *BioControl* 62, 61–70.
- Godfray, H.C.J., 1994. Parasitoids: Behavioral and Evolutionary Ecology. Princeton University Press.
- Hasik, A.Z., de Angeli Dutra, D., Doherty, J.-F., Duffy, M.A., Poulin, R., Siepielski, A.M., 2023. Resetting our expectations for parasites and their effects on species interactions: a meta-analysis. *Ecol. Lett.* 26, 184–199.
- Heimpel, G.E., Rosenheim, J.A., 1998. Egg limitation in parasitoids: a review of the evidence and a case study. *Biol. Control* 11, 160–168.
- Humphreys, R.K., Ruxton, G.D., 2019. Adaptive suicide: is a kin-selected driver of fatal behaviours likely? *Biol. Lett.* 15, 20180823.
- Iwasa, Y., Suzuki, Y., Matsuda, H., 1984. Theory of oviposition strategy of parasitoids. 1. Effect of mortality and limited egg number. *Theor. Popul. Biol.* 26, 205–227.
- Jennings, D.T., Houseweart, M.W., 1984. Predation by eumenid wasps (Hymenoptera, Eumenidae) on spruce budworm (Lepidoptera, Tortricidae) and other lepidopterous larvae in spruce-fir forests of maine. *Ann. Entomol. Soc. Am.* 77, 39–45.
- Jones, R.E., 1987. Ants, parasitoids, and the cabbage butterfly *Pieris rapae*. *J. Anim. Ecol.* 56, 739–749.
- Kindlmann, P., Ruzicka, Z., 1992. Possible consequences of a specific interaction between predators and parasites of aphids. *Ecol. Model.* 61, 253–265.
- Krey, K.L., Cooper, W.R., Renkema, J.M., 2020. Revealing the diet of generalist insect predators in strawberry fields: Not only pests, but other predators beware. *Environ. Entomol.* 49, 1300–1306.
- Kutuk, H., Yigit, A., Alaoglu, O., 2011. Intraguild predation of *Serangium parcesetosum* (Coleoptera: Coccinellidae), on whitefly *Bemisia tabaci* (Homoptera: Aleyrodidae) parasitized by *Eretmocerus mundus* (Hymenoptera: Aphelinidae). *Biocontrol Sci. Technol.* 21, 985–989.

- Leduc, S., Rosenberg, T., Johnson, A.D., Segoli, M., 2022. Nest provisioning with parasitized caterpillars by female potter wasps: costs and potential mechanisms. *Anim. Behav.* 188, 99–109.
- Liu, J.F., Wang, X.Q., Beggs, J.R., Ou, H.D., Yu, X.F., Shen, X.X., Yang, M.F., 2020. Consuming parasitized aphids alters the life history and decreases predation rate of aphid predator. *Insects* 11, 889.
- Lotem, A., Nakamura, H., Zahavi, A., 1995. Constraints on egg discrimination and cuckoo-host co-evolution. *Anim. Behav.* 49, 1185–1209.
- Mangel, M., 1989. Evolution of host selection in parasitoids - does the state of the parasitoid matter. *Am. Nat.* 133, 688–705.
- Mcallister, M.K., Roitberg, B.D., 1987. Adaptive suicidal-behavior in pea aphids. *Nature* 328, 797–799.
- Mohammadpour, M., Hosseini, M., Michaud, J.P., Karimi, J., Hosseinaveh, V., 2020. The life history of *Nabis pseudoferus* feeding on *Tuta absoluta* eggs is mediated by egg age and parasitism status. *Biol. Control* 151, 104401.
- Moore, J., 2002. Parasites and the Behavior of Animals. Oxford University Press, Oxford.
- Mottaghinia, L., Hassanpour, M., Razmjou, J., Chamani, E., Hosseini, M., 2018. Intraguild predation on the parasitoid wasp *Aphidius colemani* by the predator *Aphidoletes aphidimyza*: Effect of host plant cultivars. *J. Agric. Sci. Technol.* 20, 533–542.
- Muller, C.B., 1994. Parasitoid induced digging behavior in bumblebee workers. *Anim. Behav.* 48, 961–966.
- Mullins, C.B., Giles, K.L., Royer, T.A., 2013. Impact of *Lysiphlebus testaceipes* stage of development within greenbug hosts on survival and development of late-stage *Hippodamia convergens* larvae. *Southwest. Entomol.* 38, 549–559.
- Mustu, M., Kilincer, N., 2014. Intraguild predation of *Planococcus ficus* parasitoids *Anagrus pseudococci* and *Leptomastix dactylopii* by *Nephus kreissli*. *Biocontrol Sci. Technol.* 24, 257–269.
- Nufio, C.R., Papaj, D.R., 2001. Host marking behavior in phytophagous insects and parasitoids. *Entomol. Exp. et Appl.* 99, 273–293.
- Paull, C.A., Schellhorn, N.A., HilleRisLambers, R., Austin, A.D., 2012. Escape from parasitoids leave larvae vulnerable to predators and has unexpected outcomes for pest suppression. *Basic Appl. Ecol.* 13, 542–550.
- Perier, J.D., Haseeb, M., Kanga, L.H.B., Meagher, R.L., Legaspi, J.C., 2022. Intraguild interactions of three biological control agents of the fall armyworm *Spodoptera frugiperda* (JE Smith) in Florida. *Insects* 13, 815.
- Poulin, R., 2011. The many roads to parasitism: a tale of convergence. *Adv. Parasitol.* 74, 1–40.
- Poulin, R., Maure, F., 2015. Host manipulation by parasites: A look back before moving forward. *Trends Parasitol.* 31, 563–570.
- Roland, J., 1988. Decline in winter moth populations in north-America - Direct versus indirect effect of introduced parasites. *J. Anim. Ecol.* 57, 523–531.
- Roland, J., 1990. Interaction of parasitism and predation in the decline of winter moth in Canada. In: Watt, A.D., Leather, S.R., Hunter, M.D., C. K.N.A. (Eds.), *Population Dynamics of Forest Insects*. Intercept, Andover, UK, pp. 289–302.
- Roland, J., Embree, D.G., 1995. Biological-control of the winter moth. *Annu. Rev. Entomol.* 40, 475–492.
- Rosenheim, J.A., Kaya, H.K., Ehler, L.E., Marois, J.J., Jaffee, B.A., 1995. Intraguild predation among biological-control agents - Theory and evidence. *Biol. Control* 5, 303–335.
- Rosenheim, J.A., Jepsen, S.J., Matthews, C.E., Smith, D.S., Rosenheim, M.R., 2008. Time limitation, egg limitation, the cost of oviposition, and lifetime reproduction by an insect in nature. *Am. Nat.* 172, 486–496.
- Schuldiner-Harpaz, T., Coll, M., Wajnberg, E., 2022. Optimal foraging strategy to balance mixed diet by generalist consumers: a simulation model. *Behaviour* 159, 1263–1284.
- Segoli, M., Rosenheim, J.A., 2013. Limits to the reproductive success of two insect parasitoid species in the field. *Ecology* 94, 2498–2504.
- Segoli, M., Keasar, T., Harari, A.R., Bouskila, A., 2009. Limited kin discrimination abilities mediate tolerance toward relatives in polyembryonic parasitoid wasps. *Behav. Ecol.* 20, 1262–1267.
- Segoli, M., Leduc, S., Meng, F.Q., Hoffmann, I., Kishinevsky, M., Rozenberg, T., 2020. Frequency and consequences of the collection of already parasitized caterpillars by a potter wasp. *Sci. Rep.* 10, 8655.
- Sherman, P.W., Reeve, H.K., Pfennig, D.W., 1997. Recognition systems. In: Krebs, J.R., Davies, N.B. (Eds.), *Behavioural Ecology: an Evolutionary Approach*. Blackwell Scientific, Oxford, pp. 69–96.
- Sih, A., Christensen, B., 2001. Optimal diet theory: when does it work, and when and why does it fail? *Anim. Behav.* 61, 379–390.
- Snyder, W.E., Ives, A.R., 2001. Generalist predators disrupt biological control by a specialist parasitoid. *Ecology* 82, 705–716.
- Stephens, D.W., Krebs, J.R., 1986. *Foraging Theory*. Princeton University Press, Princeton, N.J.
- Takasu, K., Ode, P.J., Antolin, M.F., Strand, M.R., 1997. Environmental and genetic determinants of ovicide in the parasitic wasp *Bracon hebetor*. *Behav. Ecol.* 8, 647–654.
- Takizawa, T., Yasuda, H., Agarwala, B.K., 2000. Effects of parasitized aphids (Homoptera: Aphididae) as food on larval performance of three predatory ladybirds (Coleoptera: Coccinellidae). *Appl. Entomol. Zool.* 35, 467–472.
- Thomas, F., Adamo, S., Moore, J., 2005. Parasitic manipulation: where are we and where should we go? *Behav. Process.* 68, 185–199.
- Toosi, M., Rasekh, A., Osawa, N., 2019. Effects of intraguild predation on the life history traits and progeny of the ladybird beetle *Hippodamia variegata*. *Bull. Insect* 72, 161–168.
- Tostowaryk, W., 1971. Relationship between parasitism and predation of diprionid sawflies. *Ann. Entomol. Soc. Am.* 64, 1424–1427.
- Tscharntke, T., Gathmann, A., Steffan-Dewenter, I., 1998. Bioindication using trap-nesting bees and wasps and their natural enemies: community structure and interactions. *J. Appl. Ecol.* 35, 708–719.
- Wajnberg, E., Bernstein, C., van Alphen, J. (Eds.), 2008. *Behavioral Ecology of Insect Parasitoids: From Theoretical Approaches to Field Applications*. Blackwell, Malden MA.
- Weisser, W.W., Houston, A.I., 1993. Host discrimination in parasitic wasps - when is it advantageous? *Funct. Ecol.* 7, 27–39.
- West-Eberhard, M.J., Carpenter, J.M., Hanson, P.E., 1995. The vespid wasps (Vespidae). In: Hanson, P.E., Gauld, I.D. (Eds.), *The Hymenoptera of Costa Rica*. Oxford Science Publications, (NY), pp. 561–587.
- Yu, X.L., Feng, Y., Feng, Z.J., Chana, P., Zhu, G.X., Xia, P.L., Liu, T.X., 2020. Effects of mummy consumption on fitness and oviposition site selection on *Harmonia axyridis*. *Insect Sci.* 27, 1101–1110.
- Zang, L.S., Liu, T.X., 2008. Intraguild interactions between *Bemisia tabaci* predator, *Delphastus catalinae*, and parasitoid, *Encarsia sophia*, and their impacts on whitefly suppression. *J. Insect Sci.* 8, 53–53.