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# Host kairomone learning and foraging success in an egg parasitoid: a simulation model

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**Abstract.** 1. *Trissolcus basalis* (Wollaston) (Hymenoptera: Scelionidae) is an egg parasitoid that recognises chemical residues left by its host the green stink bug *Nezara viridula* (L.) (Heteroptera: Pentatomidae) as kairomone signals, enabling it to find egg masses in which to lay eggs.

2. Kairomones are usually present as patches deposited by *N. viridula* females, and recent results (Peri *et al.*, *Journal of Experimental Biology*, **209**, 3629–3635, 2006) indicated that females of *T. basalis* are able to learn the features of their foraging environment and to adjust accordingly the amount of time spent on the patches of kairomones they are visiting, depending on whether or not host eggs are found.

3. In order to assess the impact of this learning ability, a Monte Carlo, spatially explicit and individual-based simulation model was built to quantify the foraging efficiency of *T. basalis* females in environments with different levels of host abundance and distribution. In all cases, the present study compared the foraging efficiency of simulated *T. basalis* females having the ability to learn with those lacking this ability.

4. Learning females always visited a higher number of kairomone patches and attacked a higher number of hosts than non-learning females, especially when there was a high density of kairomone patches in the environment.

5. Learning ability globally appears to allow the maintenance of efficient foraging success, especially when there is a low probability for the kairomone patches to contain discoverable hosts.

6. The increase in foraging efficiency for learning females appears to depend on the characteristics of the habitat in which they are foraging. Results thus suggest that significant variation in learning ability is likely to occur in natural wasp populations facing different environments with different host spatial distributions.

**Key words.** Kairomone, learning, Monte Carlo simulation, patch, *Trissolcus basalis*.

## Introduction

The efficiency with which insect parasitoids locate and attack their hosts is known to be influenced by the ability of females to modify their behaviour through experience, during the host location process (Turlings *et al.*, 1993; Vet *et al.*, 1995; Vinson, 1998; Takasu & Lewis, 2003). Behavioural modification based on past experience has been defined as learning and, during the last decade, it has been demonstrated that parasitoid females can indeed learn to associate visual and olfactory stimuli with successful host location, and use such stimuli in making foraging decisions (Turlings *et al.*, 1993; Vet *et al.*, 1995; Vinson, 1998). Learning occurs at every phase of the host selection process and can even occur during larval development in particular hosts or host environments. However, learning mechanisms more commonly affect the adult stage during foraging (Vet *et al.*, 2003). Consequently, parasitoids have evolved the ability to learn specific stimuli that they encounter, which can enhance the probability of finding suitable hosts (Turlings *et al.*, 1990; Vet *et al.*, 1995).

Behavioural modifications induced by a given stimulus, which can either be associated with a reward or an adverse

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experience, are termed associative learning (Lewis & Tumlinson, 1988). Evidence shows that female wasps can either: (1) improve a weak pre-existing response to innate cues (a mechanism called $\alpha$-conditioning), or (2) learn to respond to novel cues when they are associated with innate cues (a process called $\beta$-conditioning) (Vinson, 1998). For example, in Trichogrammatidae (egg parasitoids), host habitat location is clearly influenced by $\alpha$-conditioning, as in the case of *Trichogramma brassicae* Bezdenko in which females previously experienced with tomato plants, search longer on tomato plants than naive females (Bjorksten & Hoffmann, 1998). In females of *Trichogramma evanescens* Westwood, the usual weak attraction to (*Z*,*E*)-9, 12-tetra-decadenyl acetate, the main component of the host sex pheromone, is greatly increased by oviposition experience in the presence of this chemical (Scholler & Prozell, 2002).

*Trissolcus basalis* (Wollaston) (Hymenoptera: Scelionidae) is a parasitoid that attacks the eggs of several pentatomid bugs. It is native to the Palearctic/Ethiopian regions (Caltagirone, 1981), but now has a cosmopolitan distribution as a result of its use in biological control programmes against *Nezara viridula* (L.) (Heteroptera: Pentatomidae), a serious pest of many economically important crops (Todd, 1989). Earlier reports on the host selection process by *T. basalis*, stated the important role played by chemical cues in allowing foraging females to find and select suitable host eggs. Host-derived pheromone and feeding- and ovipositional-induced plant synomones are volatile chemical cues that allow foraging female *T. basalis* to locate a suitable host habitat (Mattiacci *et al.*, 1993; Colazza *et al.*, 1999, 2004). On the other hand, host adult footprints and host egg contact kairomones are low-volatile cues that induce arrestment and antennation by *T. basalis* females, and probing with their ovipositor, respectively (Bin *et al.*, 1993; Colazza *et al.*, 1999; Peri *et al.*, 2006).

Associative learning is one of the main factors responsible for behavioural variability in parasitoid females. The associative learning ability of *T. basalis* females related to indirect host-related cues has been recently investigated by Peri *et al.* (2006). Host searching behaviour of *T. basalis* females is affected by contact with chemical residues left by both nymphs and adults of *N. viridula* (Colazza *et al.*, 1999; Peri *et al.*, 2006). These signals are used by the wasps to find the egg masses laid by *N. viridula*. Such chemicals elicit arrestment and motivated searching, leading *T. basalis* females to spend a longer period of time searching around the areas where signals have been deposited. The females' arrestment response has been taken to be adaptive since it could enhance the wasps' chances of locating host eggs, as a result of prolonged intense searching behaviour characterised by variation in orthokinetic and klinotactic locomotion, and increased turning frequency (Colazza *et al.*, 1999; Peri *et al.*, 2006).

*Trissolcus basalis* females do not always respond with the same intensity to chemical residues left by *N. viridula*. Indeed, naive female wasps show a significantly stronger arrestment response when in contact with areas contaminated with traces left by adult host females in pre-ovipositional condition, than with traces left by either nymphs or adult host males (Colazza *et al.*, 1999). The adaptive significance of such behaviour, has been explained in terms of higher probability for host eggs to be found and attacked near traces left by host females that are ready to lay eggs (Colazza *et al.*, 1999). Motivated searching induced by chemical residues left on a substrate by true bugs while moving, has been observed on several other species of *Trissolcus* and with *Telenomus posidi* (Colazza *et al.*, 1999; Borges *et al.*, 2003; Conti *et al.*, 2003, 2004; Salerno *et al.*, 2006). However, *T. basalis* females that respond to host female chemical residues and are unsuccessful in locating host eggs during a certain amount of time, gradually lose their arrestment responsiveness (i.e. habituation) and progressively return to more general host-searching behaviour (Colazza *et al.*, 1999). Oviposition experience makes *T. basalis* more responsive to host female chemical residues (α-conditioning) (Peri *et al.*, 2006).

Taken together, these learning and forgetting mechanisms are regarded as having an adaptive meaning, since they are most likely leading foraging parasitoid females in finding their hosts and in attacking them in a more efficient way. However, this interpretation has never been quantitatively tested. In particular, no account has so far been taken of the spatial characteristics of the environment in which female wasps forage for hosts. Thus, the present study aimed to develop a spatially explicit Monte Carlo simulation and specifically parameterised it to simulate the behaviour of *T. basalis* females foraging for their hosts (i.e. the egg masses of *N. viridula*). More accurately, the specific objectives were to: (1) accurately determine the conditions under which it should be advantageous for parasitoid females to learn the information associated with host footprints, and (2) using different parameter values, to determine what are the best foraging strategies females should adopt under different conditions.

## Material and methods

An individual-based and spatially explicit model was developed in order to simulate the behaviour and the effect of learning on the host finding success of female parasitoids. Since the wasp is capable of analysing its immediate environment and making elementary decisions, the software can be roughly considered as a simple agent-simulator model. The model is discrete in space and time, and integrates both stochastic and deterministic processes. The main characteristics of the simulator are described below.

### *Design of environment*

In the model, the space in which *T. basalis* moves is a square grid, of modifiable size, in which cells are analogous to surface units of 0.428 × 0.428 cm. 0.428 cm was retained as the minimum distance that *T. basalis* can run in 1 s during an extensive exploration phase in laboratory experiments (Colazza *et al.*, 1999). Across this space are spread numerous patches contaminated by chemical residues, supposedly deposited by ovipositing *N. viridula* females. Patches consisted of circular surfaces of 14 cells (i.e. approximately 6 cm) diameter, which corresponds to the size used in empirical studies (Colazza *et al.*, 1999). A percentage (fixed by the user) of these kairomone patches include, in their centre and at the beginning of the simulation, a host egg mass occupying four cells covering approximately 0.73 $\text{cm}^2$, i.e. containing 80–120 eggs (Waterhouse, 1998). The entire space with patches of kairomones defines the environment in which each female wasp forages for hosts. Some examples are provided in Fig. 1.

The following algorithm was used to generate the aggregative distribution of kairomone patches over the simulated surfaces:

**1** Let $P$ be the overall number of kairomone patches.

**2** Let $P_p$ be the number of primary patches, i.e. the number of aggregates of kairomone patches. In other words, if the number of primary patches equals $P$, there is no aggregation and the distribution of kairomone patches is random.

**3** The location of the $P_p$ patches is then drawn randomly over the space grid.

**4** $P_s$ $(=P - P_p)$ secondary patches are then equally spread around the primary patches at a distance drawn from a normal distribution having an average value of 30.0 and a standard deviation of 5.0 (values are expressed in cell numbers and have been chosen in order to reduce the probability of patches overlaps). No superposition among patches, even partial ones, is allowed.

**5** Host egg masses, if any, are then spread randomly over all the $P$ kairomone patches.

In order to avoid bias in the results due to edge effects that could modify the insect trajectories, workers have sometimes used a folded 2D grid, i.e. closing the surface on itself so that it forms a torus with a pseudo-infinite surface (Coquillard & Hill, 1997). Despite the elegance and attractiveness of such a scenario, the resulting unclosed surface is unrealistic. Therefore, for simplicity's sake, it was decided that kairomone patches could not be located on a 100-cell-wide border strip in the four edges of the square space (see Fig. 1).

### *Walking behaviours*

Experiments conducted in the laboratory revealed that, in a first approximation, *T. basalis* females adopt two kinds of walking behaviour (Colazza *et al.*, 1999; Peri *et al.*, 2006): (1) in the absence of kairomone traces, wasps followed a rather straight trajectory, a so-called extensive walking path, with an average (±SD) linear velocity of $1.46 \pm 0.37\ \text{cm s}^{-1}$; (2) when a patch contaminated by host female chemical residues was encountered, the insect walking pattern changed drastically, showing a lower average linear velocity ($0.28 \pm 0.02\ \text{cm s}^{-1}$) and many changes in direction. Consequently, the insect switched from an extensive to a so-called intensive walking behaviour.

Roitberg (1985) and Bruins *et al.* (1994) defined the reactive distance as the minimal distance from which the insect can detect the presence of any resource item (or chemical compound). The algorithm thus includes the ability of the insect to laterally detect, during its walking behaviour, the presence of kairomones (or eggs) within a distance of one cell (i.e. 0.428 cm).

To simulate the extensive walking behaviour, a method was used that consists, at each time step, of drawing randomly the direction and linear velocity of the wasp. To this effect, normal distributions of average 3.41 and SD of 0.86 cell $\text{s}^{-1}$ for the linear velocity and average of 0.00 and SD of 15.80° for the angles were used. These values gave walking tracks similar to those obtained on real *T. basalis* females (Colazza *et al.*, 1999). Concerning intensive walking behaviour, it was discovered that using the same values as those used for the extensive walking path gave acceptable and realistic results when combined with a specific algorithm when females encountered a patch edge. In brief, instead of a simple bounce on the patch edge, we considered that the insect was able to leave, during one time step, the patch it was exploring. At this point, if the period of time the female should remain on the kairomone patch has not elapsed, the insect begins returning to the patch. Thus, its trajectory follows an Archimedes' spiral until it re-encounters the patch border (Bell, 1991). Such behaviour has already been described for the desert isopod *Hemilepistus reaumuri* (Audouin & Savigny) (Crustacea, Isopoda, Oniscidae) (Hoffmann, 1983). An example of resulting trajectories can be seen in Fig. 2. The simulated walking patch showed some realistic patterns in comparison with those obtained on real *T. basalis* females (see Colazza *et al.*, 1999).

### *Learning*

In the model, it is assumed that females have a constant motivation for attacking hosts and that the number of eggs they can lay is unlimited (i.e. very high lifetime potential fecundity).

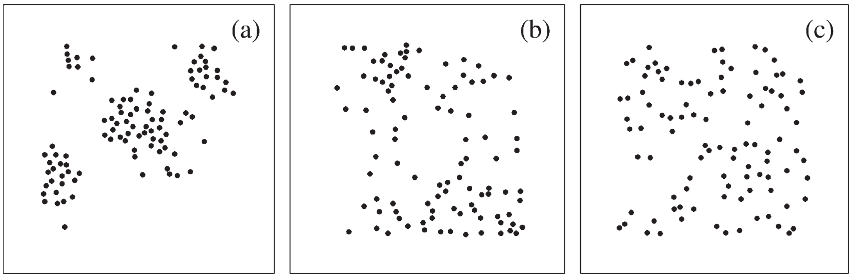

**Fig. 1.** Examples of three different simulated environments containing patches contaminated by host footprints (black dots) in which a single *Trissolcus basalis* female is foraging. Grid edge length = 580 cells, number of patches = 99. Average (SD) distance between primary patches and secondary patches = 30 (5) cells. Five, 15, and 99 primary patches were used for Fig. 1a–c, respectively. See text for a detailed explanation of the parameters used.

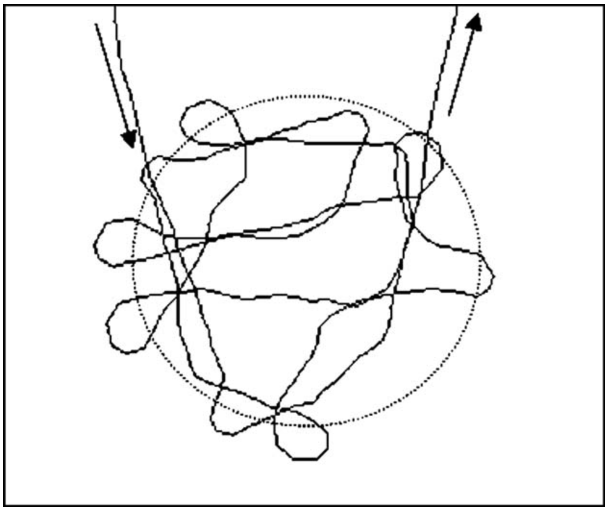

**Fig. 2.** Example of a simulated trajectory of a wasp exploring a kairomone patch of 6 cm diameter (dotted line) that does not contain a host egg mass. The arrows indicate the orientation of the walking behaviour. The wasp uses the Archimedes' spiral (see text) to re-enter the patch after it has left during the exploration time. Values of the parameters used in this simulation are those indicated in the text and the total time the wasp has to stay before leaving the kairomone patch was set to 220 s.

However, Peri *et al.* (2006) demonstrated that *T. basalis* has some learning–forgetting capacities as far as the response to host footprints is concerned. Unfortunately, available data on learning–forgetting in time spent by foraging *T. basalis* females on kairomone patches are still incomplete. Peri *et al.* (2006) showed that only one repetition of the experience is enough for the wasp to learn. In brief, experiments showed that if a naive wasp is entering a kairomone patch having (or not) a host egg mass, it will explore it for a period of 220 s (initial residence time). Subsequently: (1) either the patch was host-free or hosts were present but not discovered, in which case the amount of time the wasp will devote to exploring the next patch will be 90 s only, or (2) hosts were present and discovered, in which case the amount of time the wasp will devote to foraging in the next patch will remain at 220 s. These results can be interpreted as learning of the probability of finding host eggs. A first unsuccessful experience on a kairomone patch indicates to the foraging wasp that the probability of finding host eggs is small, and it would be more advantageous to spend less time patch exploring in order to explore more patches in the future. Experiences repeated 1 h after the first contact with a patch where hosts were discovered, showed that the wasp has not yet forgotten the previous experience. Nevertheless, these interesting results are insufficient to feed into a regression programme and to estimate, quantitatively and accurately, the learning–forgetting parameters of the standard theoretical models available in the literature (see Jaber & Bonney, 1997; Jaber & Kher, 2004 for details). Hence, we retained the following qualitative model in which the learning is instantaneous. Suppose the wasp explores an empty patch, it will explore the next one taking 90 s to do so, this period being independent of the time it spent on the first one. Then, the forgetting process obeys the logistic model. The persistence time of learning is estimated to be 1 h. After this delay, the exploration time of the next patch progressively returns to 220 s, following the logistic model:

$$T = \frac{K}{1 + a.e^{-\alpha.t}} + c \quad (1)$$

where $T$ (seconds) is the exploration time on the next patch; $t$ is the amount of time elapsed since the wasp left the previous visited patch; $c$ is the minimum residence time on patches (90 s); $K$ is the difference between the maximum and the minimum residence time on patches ($220 - 90 = 130$ s); $\alpha$ is the forgetting coefficient; and $a$ is the amount of time needed for total forgetting. Values for these last two parameters were computed by assuming that Equation (1) was passing through point {3 600; 91} corresponding to the minimal persistent time of learning, and point {18 000; 130} corresponding to the inflexion point appearing 4 h afterwards, i.e. roughly after half of the total simulation time has passed ($a = 434.75$; $\alpha = 3.3749 \times 10^{-4}$).

The choice of the logistic model was guided by three considerations: (1) it is a very general model widely used in biological modelling, providing a symmetric profile of the response, (2) it is a simple equation, the response depending on few parameters only, and (3) it easily integrates the persistence time of learning and returns progressively to the initial exploring time. In spite of these advantages, the model constitutes an oversimplification of the phenomenon and it must be viewed as a provisional solution only.

Females that were not able to learn were also simulated. These females stayed 220 s on all kairomone patches they visited, without modifying such a residence time, according to their ability to discover host egg masses or not.

Finally, the values used for parameters in such a learning–forgetting process, originated from experimental data as indicated above. In order to check the quantitative importance of the values of such parameters, simulations were also run in which females forgot four times faster. Results obtained were qualitatively equivalent. It was thus decided to present the results obtained with the values of the parameters originating from experimental data only.

### *Simulations and experimental design*

Various environments were generated in order to simulate different situations in which parasitoid females should forage for hosts. All environments contained 99 patches and the grid edge side was a cell length of either 420, 470, 580, 740, or 1400, leading to kairomone patches that covered approximately 8.31, 6.63, 4.33, 2.67, and 0.75% of the total grid surface, respectively. As the amount of time spent by the wasp between two patch visits can modify its forgetting level, we thought that patch density and aggregation could play a major role in the success of the foraging females to find hosts to attack. Thus, in each case, we tested different initial numbers of primary kairomone patches ($P_p$): 10, 15, 20 or 99. Modifying both the grid size and the number of primary kairomone patches allowed us to obtain variation both in patch densities and in patch aggregation levels at constant densities. Similarly, we also assumed that the percent of kairomone patches that included a host egg mass could influence the final results, because the time spent on a patch is dependent on the success or failure of finding hosts in the previous

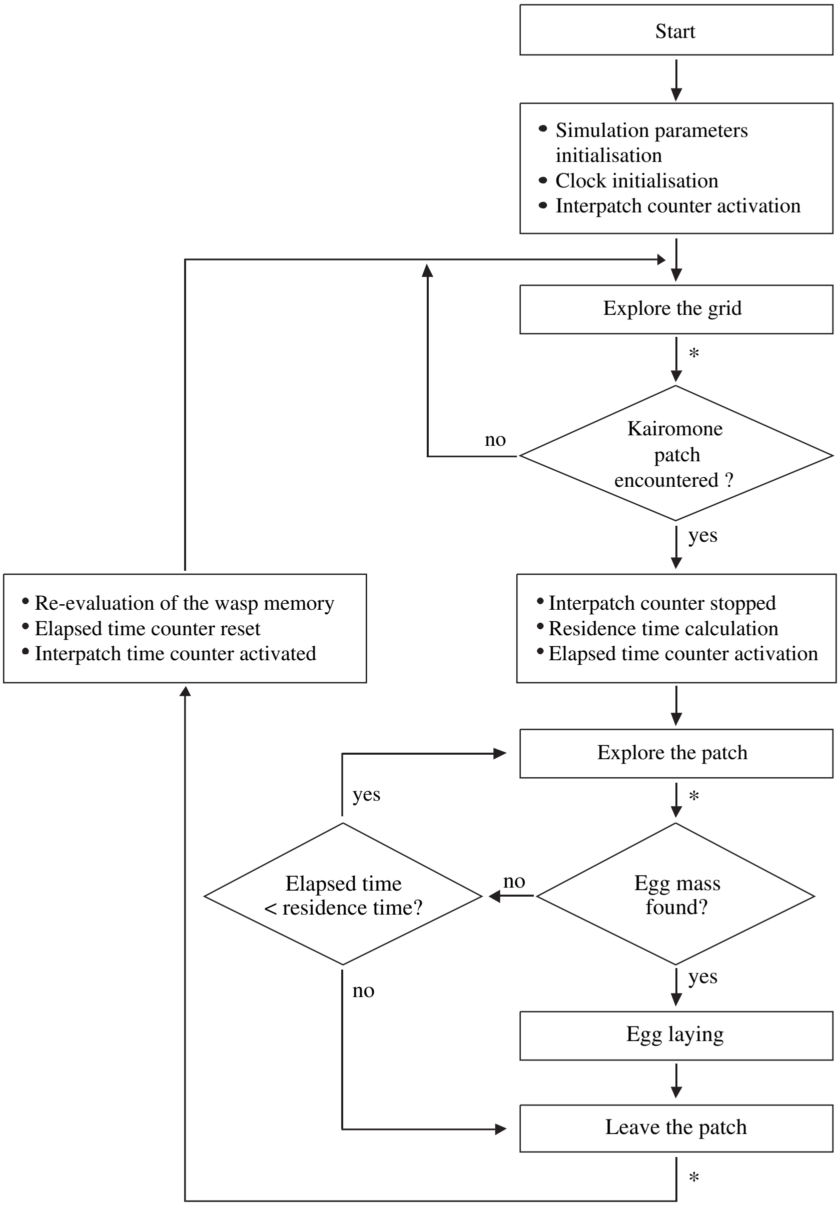

**Fig. 3.** Simplified chart showing the different steps used by the simulator. The asterisk (*) indicates a test to show whether the total elapsed time is over and if the simulation replicate should be ended. Runs are constituted of 100 replicates of simulations using identical values of the parameters (see details in text).

explored patch. Therefore, in each situation, we also tested different percentages of kairomone patches including a host egg mass: either of 25, 50, 75, or 100%.

Due to the intrinsic stochasticity of the walking process, several replicates of simulations, running with identical initial conditions, were performed in order to obtain accurate estimates of average results. Figure 3 gives the different steps of the simulation process used. Preliminary simulations showed that 100 replicates of each combination of initial parameters were necessary to obtain simultaneously accurate estimates. Consequently, the experimental design consisted of $5 \times 4 \times 4 = 80$ runs of 100 replicates each. Finally, we compared, under each of these conditions, the two cases of learning and non-learning. Altogether, this represented a total of $80 \times 2 = 160$ runs of 100 replicates each. In each run, the wasp entered the environment at the same location, i.e. in the centre. Simulations were performed over 30 000 time-steps (equivalent to 30 000 s – 8 h and 20 min in the real system). The highly reliable pseudo-random generator number of L'Ecuyer shuffled with the congruential generator of Bays-Durham was used (Press *et al.*, 1992) instead of the built-in generator of the compiler.

For each parameter combination, average values of the three following descriptive parameters were computed over the

100 replicates at the end of simulation time: (1) the total number of patch explorations, (2) the number of different patches visited, and (3) the average number of host egg masses discovered and attacked. Since these three parameters are counts that likely follow a Poisson distribution, the results were analysed using a log–linear model, a generalised linear model using a log link function (McCullagh & Nelder, 1989), with: (1) the ability of the female to learn or not, (2) the grid size, (3) the number of primary patches, and (4) the percent of patches with hosts, as main effects. Interactions between the ability to learn and the three other effects were added to the model to test whether the effect of learning changes in different environments. Finally, the interaction between the grid size and the number of primary kairomone patches was also tested to understand the effect of aggregation levels of patches at constant densities. All average results are expressed with their SE.

Besides describing the output of the model at the end of simulation time, the dynamics of the number of host egg masses discovered during female foraging time was also examined. This appeared to be important in order to accurately understand the effects of changes in environmental conditions, and the difference observed between learning and non-learning females. Results look like simple exponential saturation models (see examples on Fig. 7) that can be efficiently described by the following equation (Gause, 1934):

$$y = y_{\max}(1 - \mathrm{e}^{-kt}) \qquad (2)$$

where $y_{\max}$ is the total number of egg masses present in the environment; and $k$, expressed in time$^{-1}$, is the speed at which the resource is acquired by the simulated females. This equation was fitted using a standard least-square, non-linear procedure to the simulation results obtained, using different values for the parameters. This led to an estimation of each time parameter $k$, which was then compared among different situations using standard analyses of variance.

## Results

Table 1 shows the results of the statistical comparisons made on the three descriptive outputted parameters computed at the end of simulation time, while Figs 4–6 provide graphical representations of average changes in these three parameters, with different values of the features describing the environment. First of all, some obvious results are obtained, an indication that the simulation model developed was not leading to aberrant outputs. More accurately, the bigger the grid size, the lower the number of kairomone patches simulated that animals are able to discover (see Fig. 4). Such a result is clearly due to a ‘dilution’ effect, the parasitoids having a lower chance of discovering kairomone patches when the patches are present at a lower density. Also, the higher the percent of kairomone patch with an egg mass, the larger the number of egg masses actually discovered (see Fig. 6). An increase in the percent of kairomone patches containing an egg mass also led to a slight, significant increase in the number of kairomone patches visited (see Fig. 6). Actually, the higher the percent of kairomone patches with an egg mass, the lower the average time the animal will spend on each patch, since patches are left immediately after a host egg mass is found (see Fig. 3). This provided the foraging parasitoid female with more time to explore her environment, leading her to visit a higher average number of patches during the simulation time.

Although the effect of the number of primary kairomone patches $P_p$ (i.e. level of patches aggregation) appears to be weak on Fig. 5, it shows a strong effect on the three average parameters computed (see Table 1). The higher the level of patches aggregation, the higher the foraging efficiency of the simulated females. More interestingly, there is also an obvious significant interaction between the effect of grid size and the aggregation level of kairomone patches. On a smaller grid, aggregation is blurred, and results obtained then progressively appear like those obtained with a random distribution of kairomone patches.

Globally, the three average parameters computed vary in the same direction, and they all indicate significant influences of changes in the characteristics of the environment, in which simulated parasitoid females were foraging for hosts. Furthermore, in all results, females with the ability to learn the features of their environment, are concomitantly able to visit more patches and then discover more hosts to attack, likely leading to higher lifetime reproductive success. Actually, females having the ability to learn remained on empty patches and on patches containing an egg mass of 133.58 ± 4.11 s and 52.35 ± 4.24 s, respectively (mean ± SE), while females lacking this ability remained on

**Table 1.** Results of the log–linear model used to test the effect of the different parameters (and their interactions), describing the environment in which simulated parasitoid females were foraging for hosts, on: (1) the total number of patches visited, (2) the number of different patches visited, and (3) the number of egg masses discovered.

| | Total number of patches visited | | Number of different patches visited | | Number of egg masses discovered | |
|---|---|---|---|---|---|---|
| Source of variation | $\chi^2$ (d.f.) | *P*-value | $\chi^2$ (d.f.) | *P*-value | $\chi^2$ (d.f.) | *P*-value |
| Ability to learn (1) | 85 992.20 (1) | <0.0001 | 15 010.50 (1) | <0.0001 | 3 659.80 (1) | <0.0001 |
| Grid size (2) | 33 7581.00 (4) | <0.0001 | 79 734.60 (4) | <0.0001 | 41 901.70 (4) | <0.0001 |
| Number of primary patches (3) | 52.91 (3) | <0.0001 | 58.76 (3) | <0.0001 | 50.73 (3) | <0.0001 |
| Percent patches with hosts (4) | 12 384.30 (3) | <0.0001 | 2 585.97 (3) | <0.0001 | 289 462.00 (3) | <0.0001 |
| Interaction (1) × (2) | 8 495.31 (4) | <0.0001 | 766.95 (4) | <0.0001 | 523.86 (4) | <0.0001 |
| Interaction (1) × (3) | 3.13 (3) | 0.3719 | 0.77 (3) | 0.8563 | 0.69 (3) | 0.8756 |
| Interaction (1) × (4) | 6 232.00 (3) | <0.0001 | 1 545.89 (3) | <0.0001 | 364.06 (3) | <0.0001 |
| Interaction (2) × (3) | 43.45 (12) | <0.0001 | 37.90 (12) | 0.0002 | 643.19 (12) | <0.0001 |

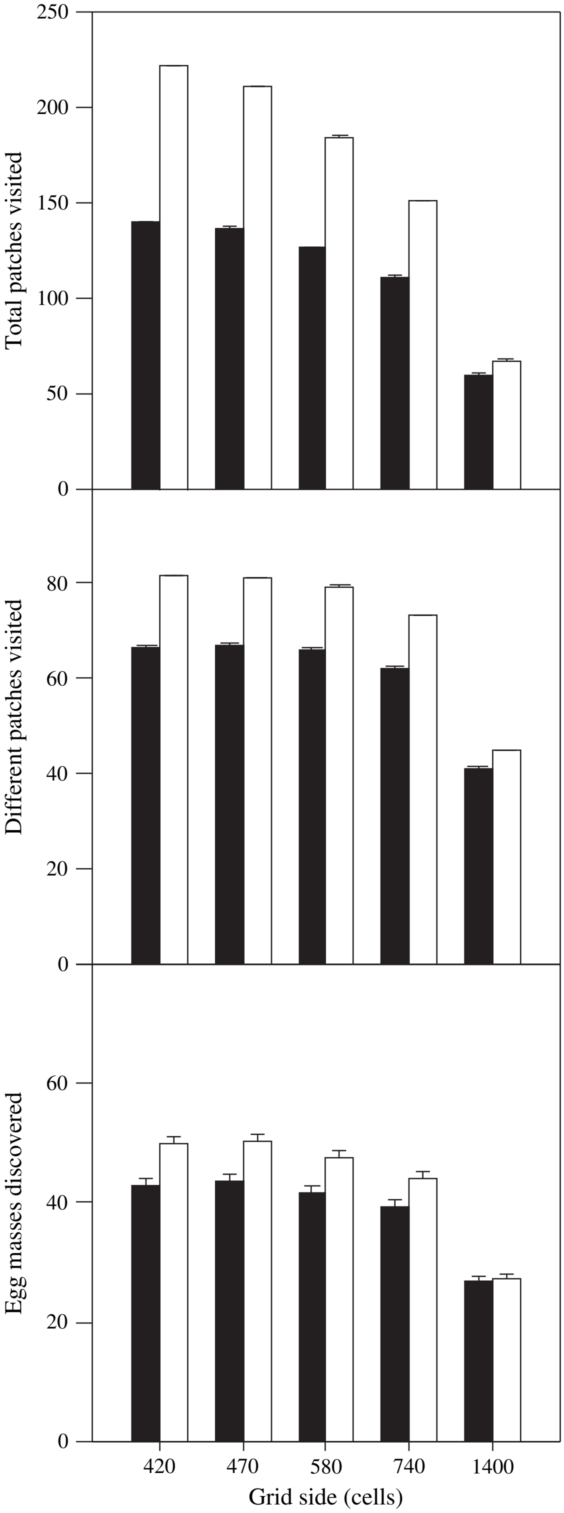

**Fig. 4.** Effect of a change in the grid edge size (in terms of number of cells) on the average (+SE) total number of patches visited, different patches visited, and number of egg masses discovered by simulated foraging parasitoid females, that were able (white bars) or not able (black bars) to learn the features of their environment.

these two types of patches on average 168.94 ± 1.89 s and 71.77 ± 5.09 s, respectively. Thus, since learning females remained on average a shorter time on the kairomone patches they visited, they missed the host egg masses to be discovered more frequently (41.76 ± 4.01% vs. 32.68 ± 3.79%). Despite this, since they consequently have more time to explore their environment, they were generally able to exploit the available hosts more efficiently than non-learning females. Finally, significant interactions between learning ability and the different features of the environment indicated that, except for the level of kairomone patch aggregation, an increase in foraging efficiency for learning females can be modulated by the characteristics of their environment.

Looking at the dynamics of host exploitation during foraging time, gives additional complementary information, and Fig. 7 provides a couple of examples showing the effect of variation in the characteristics of the environment (here the effect of grid size) on the cumulative number of egg masses discovered by simulated females. More accurately, Fig. 8 shows changes in the speed at which the resource is acquired during simulation time by learning and non-learning females in different environments.

As noted above, in most of these cases, learning females show a higher foraging efficiency, acquiring their resources more rapidly than non-learning females [on Fig. 7, on a grid with an edge size of 420 cells, learning females discovered statistically more egg masses than non-learning females from the 64th minute onwards ($P < 0.05$); on Figs 8a–c, global comparisons of $k$-values between learning and non-learning females all lead to $P < 0.001$]. However, here again, such an increase in foraging efficiency appears to depend on the features of the environment in which females are foraging for hosts.

## Discussion

Learning ability in insect parasitoids is now widely recognised as being adaptive, but such a hypothesis has never been analysed quantitatively, especially with regards to the spatial characteristics of the environment where potential hosts have to be discovered and exploited. Based on recent laboratory experimental data on the association between *N. viridula* and *T. basalis*, showing that females of this parasitoid species were indeed able to adjust their foraging strategy according to past experience (Peri *et al.*, 2006), a Monte Carlo, spatially explicit individual-based simulation model specifically parameterised for this host–parasitoid association was developed (see DeAngelis & Mooij, 2005 for a general recent consideration about the use of individual-based simulation models in ecology). The results of the present study clearly indicate an overall greater foraging success for female wasps that are able to learn the characteristics of their habitat, compared to females that are not able to learn. Females able to learn are globally exploiting a higher number of resource items, and are also acquiring resources more rapidly than non-learning females. However, such an increase in foraging efficiency when females are able to learn, appears to be more or less pronounced under different environmental conditions. Differences in foraging efficiency between learning and non-learning females seem to progressively vanish

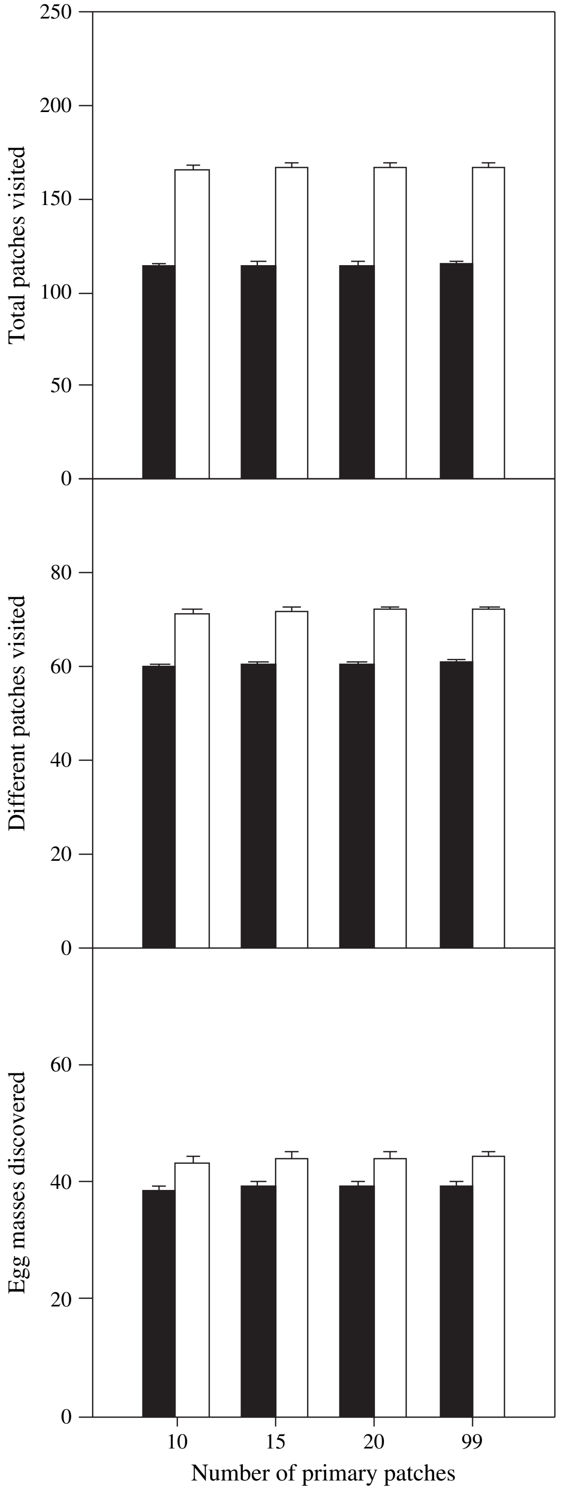

**Fig. 5.** Effect of a change in the number of primary kairomone patches on the average (+SE) total number of patches visited, different patches visited, and number of egg masses discovered by simulated foraging parasitoid females that were able (white bars) or not able (black bars) to learn the features of their environment. The lower the number of primary patches, the higher the patch aggregation level in the environment.

when the environment increases in size (see Fig. 4 and the significant interaction between learning ability and grid size in Table 1; see also Fig. 8a). Since all simulations were performed with a constant number of kairomone patches (i.e. 99), an increase in grid size led to a decrease in patch density. In such a case, learning females are spending an increasing time travelling between patches and are thus forgetting more frequently, at least partially, what they learned, leading them to progressively forage as efficiently as non-learning females. Also, the advantage of learning seems to vanish progressively with an increase in the percentage of kairomone patches containing a host egg mass (see Fig. 6 and the significant interaction between learning ability and the percentage of patches with hosts in Table 1; see also Fig. 8c). An increase in the proportion of kairomone patches containing hosts, corresponds to an increase in habitat richness, and it is thus not surprising that in such cases, even non-learning females can be efficient. The fitness advantage of learning, thus appears to be the ability to maintain efficient foraging even when the habitat is not particularly rich in hosts.

The results of the present study also indicate that an increase in foraging efficiency when females are able to learn remains the same, whatever the level of kairomone patch aggregation (see Fig. 5 and the non-significant interaction between learning ability and the number of primary kairomone patches in Table 1; see also Fig. 8b). A likely explanation of such a result, is that with a high aggregation level, learning females are sometimes spending a significant amount of travel time between aggregates of kairomone patches and are then, in these cases, forgetting most of what they learned. On the other hand, when the aggregation level is low, learning females are forced to repeat smaller travel times between patches, and are then progressively accumulating smaller forgetting events. Consequently, these two opposing mechanisms, including all intermediate situations, likely compensate for each other, leading to similar results. The average inter-patch travelling time when kairomone patches are aggregated, is most likely greater than when kairomone patches are distributed randomly in the habitat, causing the average foraging efficiency to slightly, but significantly increase, with an increase in the number of primary kairomone patches (see Fig. 5 and Table 1).

The model developed in the present study is simulating the foraging behaviour of female wasps having an infinite number of eggs to lay. However, *T. basalis* females are known to be limited to a total of approximately 200 eggs in their entire life (Mattiacci *et al.*, 1991), most likely allowing females to exploit less than about 10 host egg masses in their life, less than what the results of the model presented here suggest. However, our analysis of the dynamics of host exploitation during simulated foraging time (see, e.g. Fig. 7) indicate that, in some cases, differences between the foraging efficiency of learning and non-learning females appear early in the simulation, at a moment when females are not yet egg limited (e.g. on a grid with an edge size of 420 cells, a significant difference appears before 10 host egg masses are discovered).

Peri *et al.* (2006) indicated that *T. basalis* females were able to learn the characteristics of their environment, by adjusting their foraging time to patches of chemical residues deposited by females of their host *N. viridula*. The simulation in the present study indicates that such a learning ability can lead the females to a higher foraging efficiency. Under the same foraging time, and compared to non-learning females, learning females visited more

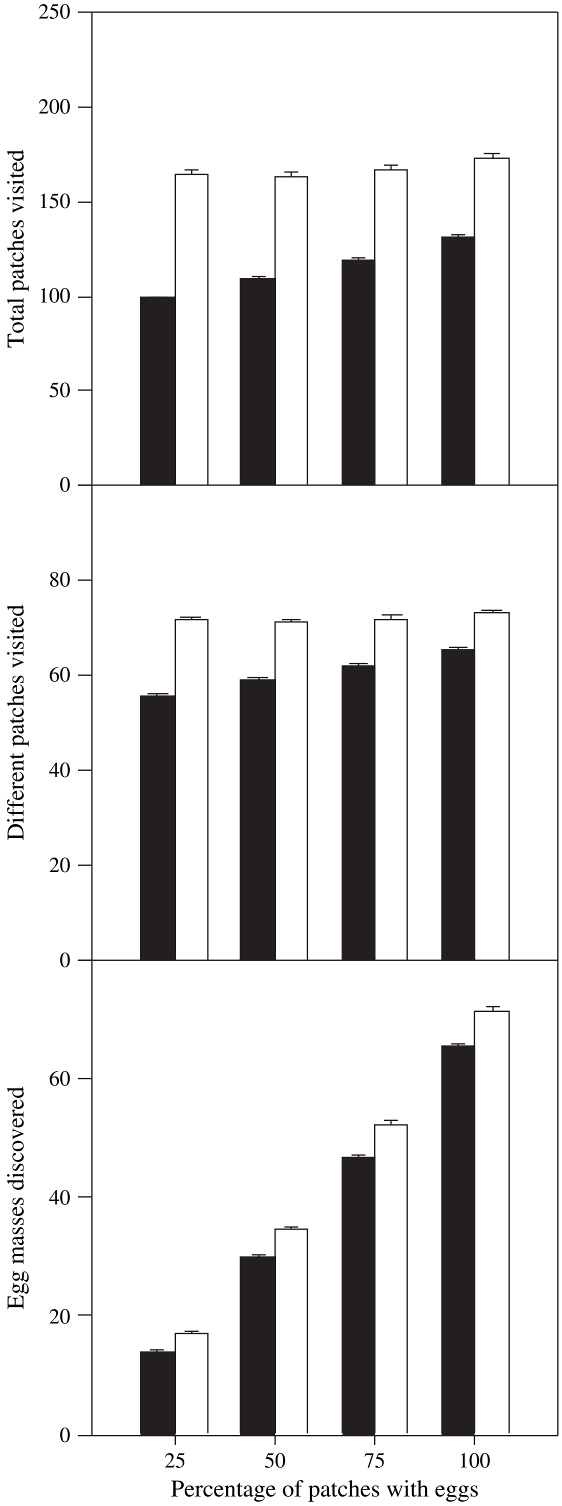

**Fig. 6.** Effect of a change in the percentage of kairomone patches that included a host egg mass on the average (+SE) total number of patches visited, different patches visited, and number of egg masses discovered by simulated foraging parasitoid females that were able (white bars) or not able (black bars) to learn the features of their environment.

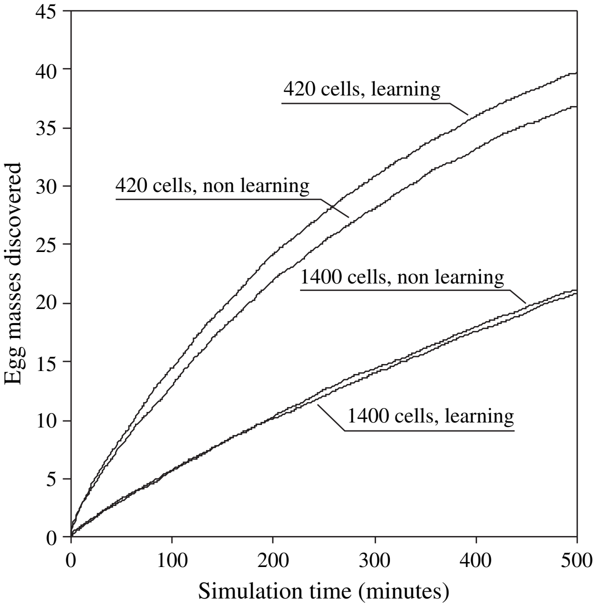

**Fig. 7.** Average cumulative number of egg masses discovered by learning and non-learning simulated females during simulation time on a grid with an edge size of 420 or 1400 cells. In all cases, 50% of kairomone patches contained a host egg mass and 20 primary kairomone patches were used to generate the kairomone patches' spatial distribution. Results shown are an average of 100 replicates of the simulation.

kairomone patches and discovered more hosts to attack. They were also globally able to acquire their resources more rapidly. The ecological meaning of such results lies in the fact that chemical residues left by *N. viridula* cannot guarantee the presence of hosts or provide directional information. It only represents 'promising host cues' (Peri *et al.*, 2006). In such a case, it is adaptive for foraging females to give up and leave the area if host eggs are not found after a certain amount of time. The results of the present study, which are based on real observations, suggest that adding a learning ability to such foraging mechanisms, should enable the females to respond dynamically to changes in probability of the presence of hosts associated with kairomone residue, leading them to a global increase in their host finding success.

Learning ability in insects is known to be generally associated with some fitness cost (see e.g. Mery & Kawecki, 2003, 2004, 2005). Such cost was not taken into account in the simulation model presented here. However, the timescales over which the cost of learning can be observed is usually far longer (i.e. 1 day and even sometimes more) than the duration of the simulation time in this work. Thus, the cost of learning, if any, should remain very low, and adding it in the model should not lead to drastic changes in the results obtained.

It should be noted that an increase in foraging efficiency for learning females appears to depend on the characteristics of the habitat in which they are foraging. Female wasps, and especially those of *T. basalis*, have to cope regularly with different environments having different host spatial distributions (Austin *et al.*, 2005). The results of the present study thus suggest that significant inter- and intra-population variation in learning

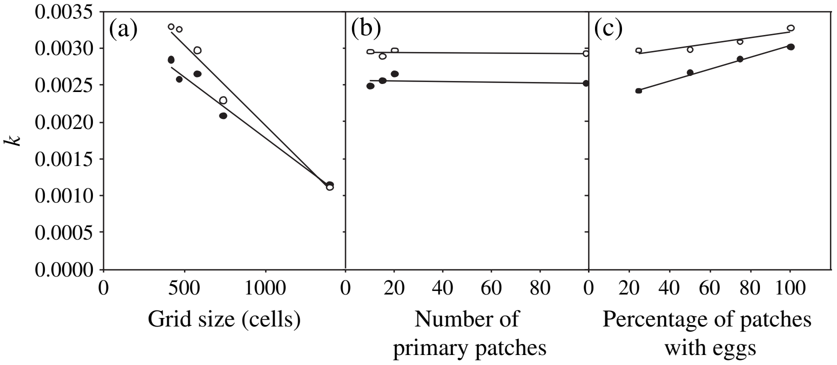

**Fig. 8.** Changes in estimates of the value of *k*, expressed in time$^{-1}$, representing the speed at which the resource is acquired by learning (open circles) and non-learning (filled circles) simulated females in relation to the grid edge size (a), the number of primary kairomone patches (b), or the percentage of kairomone patches that included a host egg mass (c). Linear regression lines are plotted in each case. In (a), simulations were carried out with 20 primary kairomone patches and 50% of kairomone patches contained a host egg mass. In (b), simulations were carried out with a grid edge size of 580 and 50% of kairomone patches contained a host egg mass. In (c), simulations were carried out with a grid edge size of 580 and with 20 primary kairomone patches.

ability is likely to occur in natural wasp populations. Such variation can even be genetically determined (Wajnberg, 2004) and experiments will soon be undertaken to search for such genetic variation in different *T. basalis* populations.

Even if some variation is observed, the results of the simulation model clearly indicate that an ability to learn leads to an overall higher foraging efficiency. Such results can most probably be generalised to all parasitoid species using kairomone patches as a cue to locate and attack their hosts. In the simulation model presented here, and following results of Colazza *et al.* (1999) and Peri *et al.* (2006), some parameters were specifically chosen to describe the actual behaviour of *T. basalis* females foraging for host eggs on kairomone patches of *N. viridula* (i.e. features of the walking behaviour, from the learning–forgetting curve). Generalising these results to other species, would simply involve both the quantitative and qualitative changes in the values of the parameters used in the model, specifically describing the behaviour of the simulated wasp females.

A sound modelling approach should lead to identifying more accurate points that need to be analysed further, in order to better understand the biological system under study (Jørgensen, 1994; Hill & Coquillard, 2007). Accordingly, additional experimental and theoretical works should now be carried out on *T. basalis* foraging behaviour, allowing collection of relevant information that is still missing. In particular, the real speed of learning and forgetting of *T. basalis* females is not completely understood, and laboratory experiments need to be run in order to more accurately estimate these important features of *T. basalis* foraging activity. Furthermore, the simulation model used here is based on obvious over-simplifications of real situations. For example, it assumes that the egg-laying motivation of the wasp females remains constant throughout their foraging time and is not influenced by the presence of previously attacked hosts in the habitat. This is most likely not the case, and experiments are also planned to test whether the learning ability of foraging females actually changes over the course of their foraging time, and/or when they are offered previously parasitised hosts. Results of these experiments will then be used to modify the simulation model accordingly. Finally, several *T. basalis* females foraging simultaneously on a host patch are known to compete, sometimes by means of intense fighting behaviours (Wajnberg *et al.*, 2004). Such strong interference between parasitoid females will likely modify the situations in which learning females have a higher foraging efficiency than non-learning ones. The behavioural mechanisms of interference competition are now added to the simulation models and the results obtained with several females foraging simultaneously in the environment, will likely provide important, general information about foraging efficiency of *T. basalis* females in more realistic situations.

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