

Patch leaving decision rules and the Marginal Value Theorem: an experimental analysis and a simulation model

Eric Wajnberg,^a Xavier Fauvergue,^a and Odile Pons^b

^aINRA, Ecologie des Parasitoïdes, 37 Boulevard du Cap, 06600 Antibes, France, ^bINRA, Biométrie, Domaine de Vilvert, 78352 Jouy-en-Josas Cedex, France

The patch exploitation strategy of females of the insect parasitoid *Trichogramma brassicae* was studied on patches containing different proportions of hosts that were previously attacked by conspecific females. On average, *T. brassicae* females spent more time on patches of higher quality, and all patches were reduced to the same level of profitability before being left. This appeared to be in accordance to the optimal predictions of the Charnov Marginal Value Theorem. The proximate leaving mechanisms involved were analyzed by means of a Cox proportional hazards model. Each oviposition in a healthy host appeared to have an incremental influence on the patch residence time, whereas each rejection of a healthy host or of a host that was previously attacked by the same female (i.e., self-superparasitism) had a decremental effect. These patch leaving mechanisms did not change according to the quality of the patch the females were exploiting. A Monte Carlo simulation was developed around the results of the Cox regression model. The results suggest that this set of patch leaving rules seems to provide the females with a sufficient way to reach the predictions of the Charnov model. Among the different mechanisms involved, the incremental effect associated with each oviposition in a healthy host appeared to play the most important role. The relationship between the proximate mechanistic rules adopted by the females and the ultimate prediction of the Charnov model is discussed. *Key words*: patch leaving rules, Marginal Value Theorem, Cox regression model, parasitoids, *Trichogramma*, Monte Carlo simulation. [*Behav Ecol* 11:577–586 (2000)]

Foraging behavior in insect parasitoids has long been a favored subject in behavioral ecology. Among the different behaviors studied, the time allocated to patches of hosts of different profitability is likely the one that has received most of the interest in the last few decades, particularly in the context of optimal foraging theory (see Stephens and Krebs, 1986, for a review). Hosts of most of the parasitoid species occur in discrete patches in the environment (Godfray, 1994) and, in order to maximize their reproductive success, female wasps have to adjust accurately their foraging time in each of the patches they encounter. A number of theoretical models have been proposed in order to predict the optimal residence time a female should allocate to each visited patch. The Marginal Value Theorem (MVT) developed by Charnov (1976) is based on the assumption that females, foraging on depleting patches of hosts, should experience diminishing returns. In such a condition, this model predicts that each patch should be exploited until the rate of fitness gain within the patch has decreased to a marginal value. This is the mean rate of fitness gain that can be achieved in all the available patches in the environment. Factors having an influence on the rate of fitness gain on the patch under exploitation should lead to a change in the optimal time a female should remain on the patch. Consequently, three main predictions can be drawn from the MVT: (1) Females should spend more time on each patch when travel time between patches is high (Charnov, 1976; Godfray, 1994); (2) females should remain a longer time on patches of higher quality (Bonser et al., 1998; McNair, 1982); and (3) patches of different quality should be reduced

to the same level of profitability before leaving (Bell, 1991; Cook and Hubbard, 1977). The last two predictions have been frequently verified experimentally on different host-parasitoid systems (e.g., Hassell, 1978; Hubbard and Cook, 1978; Waage, 1979).

These predictions are based on the implicit assumptions that foraging females have a perfect knowledge of the spatial distribution and quality of all the patches in the habitat (Iwasa et al., 1981; McNair, 1982; van Alphen and Vet, 1986; Waage, 1979). For this, foragers are supposed to visit sequentially a relatively large number of patches and to assess quickly their profitability (Galis and van Alphen, 1981; Godfray, 1994; Krebs et al., 1974). Such assumptions are not realistic, especially in a stochastic, unpredictable environment (Green, 1980; McNamara, 1982). Thus, there is a need to link the functional, optimality predictions with the actual proximate mechanisms used by the foragers (van Alphen, 1993; van Alphen and Vet, 1986; Vos et al., 1998). These mechanisms should be relatively simple, leading the females to adopt an optimal behavior without having to know the spatial distribution and quality of all the patches in the habitat (Iwasa et al., 1981; Shaltiel and Ayal, 1998).

Despite the fact that they are usually considered to be difficult to analyze (van Alphen, 1993), several patch leaving mechanisms have been proposed. They are all built on the assumption that the females, while foraging on a patch, are likely to sample their environment in order to collect the information needed to trigger the patch leaving decision (Green, 1984; Li et al., 1993; Yamada, 1988). Among the possible mechanisms, the rule suggested by Waage (1979) is probably the most well known one attempting to relate a proximate, rule-based to an ultimate, goal-based model. In his mechanistic approach, Waage (1978, 1979) supposed that a female enters a patch with an initial level of responsiveness (i.e., an initial tendency to remain on the patch) that is related to the number of hosts available. Then, this responsive-

Address correspondence to E. Wajnberg. E-mail: wajnberg@antibes.inra.fr.

Received 2 February 1999; revised 14 September 1999; accepted 23 January 2000.

© 2000 International Society for Behavioral Ecology

ness decreases with the time spent on the patch, until a critical threshold value is reached whereby the patch is abandoned. Each oviposition in a host has an incremental influence on the responsiveness, thereby increasing the total residence time. Such an incremental effect has been observed in several parasitoid species. However, it has been shown more recently that in some cases, each oviposition may have a decremental effect on the responsiveness to the patch, thereby decreasing patch residence time. This decremental effect, called a "count-down" mechanism (Driessen et al., 1995), has been observed with several other wasp species (see Driessen and Bernstein, 1999; Wajnberg et al., 1999, for recent reviews). Incremental mechanisms are supposed to be adaptive when there is a large heterogeneity in patch quality in the environment. On the other hand, a count-down mechanism is generally thought to perform better when the patches contain an uniform number of hosts (Iwasa et al., 1981; Vos et al., 1998).

Using a simple simulation procedure, Waage (1979) showed that his incremental mechanistic model could generate patch exploitation strategies that are in accordance with some of the predictions of the MVT. Using such a proximate rule, (1) females would stay longer on patches of higher quality, and (2) the rate of oviposition in the last few min before leaving the patch would be similar for a range of patch qualities. This suggested that all patches would be reduced to the same level of profitability before being left. As far as we know, this is the only study, based on experimental data, trying to relate patch leaving mechanisms to the ultimate predictions of the MVT. Therefore, there is a need for a more detailed analysis aiming to relate accurately the patch leaving rules adopted by the females to theoretical predictions.

This was the aim of the present study. Females of the egg parasitoid *Trichogramma brassicae* Bezdenko (Hym.; Trichogrammatidae) were offered patches of one of their hosts, the eggs of the Mediterranean flour moth *Ephesia kuehniella* Zeller (Lep.; Pyralidae). Patches of different quality were compared and the females' patch exploitation strategy was analyzed in the light of the predictions of the MVT. Besides this, the experimental data were also analyzed by means of a Cox (1972) proportional hazards model, a specific statistical method whose features seem to be particularly appropriate when analyzing data on time allocation (see Hemerik et al., 1993; van Roermund et al., 1994; van Steenis et al., 1996; Vos et al., 1998; Wajnberg et al., 1999). In turn, the results of the Cox model were used to build a Monte Carlo model simulating the exploitation of a patch by a *T. brassicae* female. The results indicate that the females' behavior was in accordance with some of the predictions of the MVT, and their patch leaving mechanisms, revealed by the Cox model, seem to provide them with a simple and efficient proximate way to achieve this ultimate goal.

MATERIAL AND METHODS

Insects and experimental set-up

T. brassicae is a polyphagous parasitic wasp that attacks the eggs of several moth species. It is one of the most intensively produced insects over the world for inundative biological control programs (Wajnberg and Hassan, 1994). Like all *Trichogramma* species, *T. brassicae* females are known to mark their hosts after each oviposition (Salt, 1937). Therefore, the females of this species can discriminate between healthy and already attacked hosts (Klomp et al., 1980). To this end, olfactory cues are sometimes involved during host antennal inspection (Bruins et al., 1994); but, in most cases, sensory receptors are used during probing of the host with the ovipositor (Le Ralec and Wajnberg, 1990).

The strain used in the experiment originates from a population that was collected several years ago from parasitized European corn borer (i.e., *Ostrinia nubilalis* Hübner; Lep. Pyralidae) eggs in Alsace, France. From the time of capture onwards, the strain was maintained under laboratory conditions on *E. kuehniella* eggs at 25 °C, LD 12:12.

For this study, less than 24 h old *T. brassicae* females were each offered a single patch of nine UV-killed *E. kuehniella* eggs. These were arranged on a 3 × 3 regular square grid pattern, with a distance of one mm between the hosts aligned in rows and columns. The host patches, built just before the experiment, consisted of different proportions of non-attacked hosts and hosts that were already attacked by a conspecific female 24 h before the experiment. After being attacked, and before being used to build the patches, the hosts were stored at 25°C. The healthy hosts were also stored under the same conditions. Four treatments were compared (number of replicates in parentheses): patches with only healthy hosts (31), patches with six healthy hosts and three attacked hosts (30), patches with three healthy hosts and six attacked hosts (31), and patches with only already attacked hosts (29). For the two intermediate cases, the two types of hosts were placed along the diagonal of the square pattern. This set-up was used in order to modify the quality of the patch without changing its surface. This appeared to be important since it has been shown that the time allocated by some parasitoids could vary according to the patch area, without a change in host density or quality (van Lenteren and Bakker, 1978). Females were all virgin, honey-fed, and naive (i.e., without previous experience with hosts) and were isolated at random, before adult emergence, from the mass-reared population. This protocol was chosen in order to run the experiment under conditions that were as standardized as possible. All experiments were carried out during daytime at 25±1°C and 60±5% RH. Females were used only once and were free to leave the patch whenever they wanted. Hosts were not replaced during the observation, so patches may have suffered a continuous depletion.

The behavior of each female was observed continuously from the moment the parasitoid entered the patch for the first time up to the moment it left the patch for more than 60 s. On some occasions, the females left the patch and walked a few millimeters away before returning to the hosts. Like in Driessen and Bernstein (1999), these short excursions were included in the computation of the patch residence time.

Using an event recorder, the beginning and the end of the following behaviors were recorded during the whole observation with an accuracy of 0.1 s: (1) entering or (2) leaving the patch, (3) antennal drumming on a host, (4) drilling a host with the ovipositor, (5) ovipositing in a host, and (6) walking between hosts. The location of the host on which behaviors 3 to 5 were observed was also recorded. A drilling behavior followed by an oviposition behavior was considered as a successful host attack behavior. When there was no oviposition after a drilling behavior, the host was considered to be rejected.

These data were used to test whether the females' patch exploitation strategy was in accordance with the predictions of the MVT. The total patch residence time was thus computed, and also the level of the patch profitability before leaving. This last parameter should ideally correspond to the rate of reproductive success just before leaving the patch, and is usually estimated by the rate of encounters with hosts during the last min before the patch is abandoned (e.g., Cook and Hubbard, 1977; Hubbard and Cook, 1978; Waage, 1979). However, in the present study, both healthy and already attacked hosts were present on the patch, therefore attacking a host does

not necessarily produce the same level of reproductive success to the forager. We thus preferred to estimate patch profitability by the actual rate of progeny production during the last min before the patch is left. For this, a complementary experiment was performed with two *T. brassicae* lines originating from the same population, but differing by a single neutral random amplified polymorphic DNA marker (i.e., marker N4, located on linkage group number III, Laurent et al., 1998). Using these two lines, we estimated that the attack of a healthy host or of a host already parasitized 24 h before by an other female leads to an adult progeny with a probability of 0.8634 ($n = 205$) and 0.0519 ($n = 77$), respectively. When a healthy host is attacked twice during the same patch visit (i.e., self-superparasitism), the total progeny production reaches an average of 1.2952 ($n = 105$). These three parameters were used to estimate accurately the reproductive success of all females before the patch is left.

The proportional hazards model

The patch leaving mechanisms used by the females were analyzed by means of a Cox proportional hazards model (also called a Cox regression model). A thorough description of this model can be found in the literature dealing with survival analysis (e.g., Collett, 1994; Kalbfleisch and Prentice, 1980). Briefly, in our case this model expresses the data in terms of leaving tendency (the so-called hazard rate), which is the probability per unit of time that a female leaves the patch, given that she is still on it. This leaving tendency can be modified by some pre-defined explanatory factors (i.e., covariates) according to the following equation:

$$h(t) = h_0(t) \exp \left\{ \sum_{i=1}^p \beta_i z_i \right\} \quad (1)$$

in which $h(t)$ is the hazard rate, $h_0(t)$ is the innate patch leaving tendency (so-called baseline hazard), t the time passed since the female entered the patch, and β_i the regression coefficients that give the relative contributions of p covariates z_i . These coefficients, and thus the influence of the covariates to be tested, can be interpreted through the exponential term, the so-called hazard ratio. A hazard ratio greater than one will indicate an increasing effect on the females' patch leaving tendency, while a hazard ratio lower than one will be interpreted in the opposite way. Covariates can be time-dependent or fixed. The baseline hazard is the patch leaving tendency when all the covariates are equal to zero.

Usually, the number of hosts successfully attacked and the number of hosts rejected during the patch visit are the main covariates whose influence on the females' leaving tendency are tested with such a model. This enables the quantifying of the associated incremental or decremental effect on patch residence time (e.g., Haccou et al., 1991; Hemerik et al., 1993; van Roermund et al., 1994; Wajnberg et al., 1999). However, in the present study, the quality of each host on the patch was known throughout the experiment, so that more accurate covariates could be defined. Six time-dependent covariates were used: the number of successful attacks or rejections of: (1) a healthy host, (2) a host previously attacked by the same female (self-superparasitism), or (3) a host already attacked by another female 24 h before the experiment (conspecific-superparasitism). The initial quality of the patch was added as a fixed categorical covariate, the case corresponding to nine healthy hosts being arbitrarily assumed to be the reference level corresponding to the baseline hazard with a parameter set to zero. Thus, only three parameters need to be estimated for this factor (see Collett, 1994; Wajnberg et al., 1999, for a detailed explanation). Finally, in order to check whether there

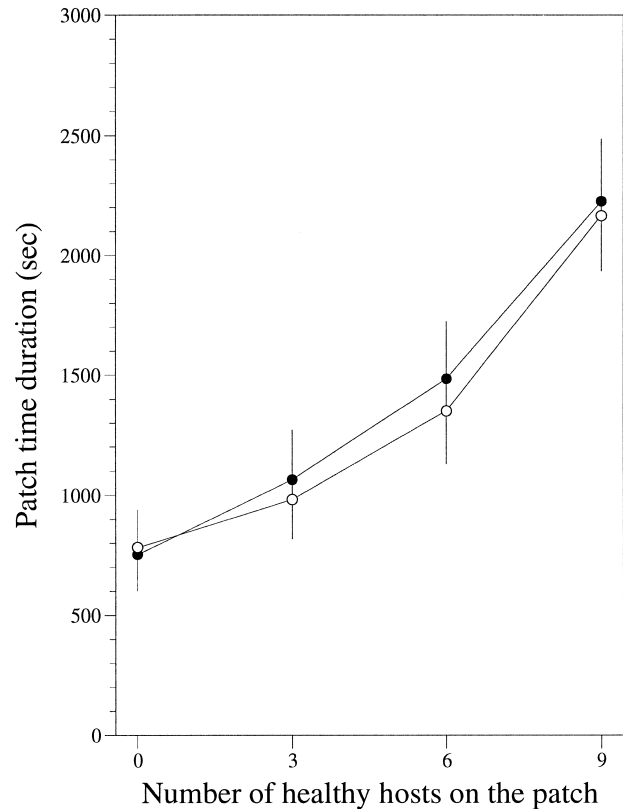


Figure 1

Average (\pm SE) observed (black circles) and simulated (white circles) patch residence times on patches of nine hosts containing different initial numbers of healthy hosts. Both averages and standard errors are computed from the Kaplan-Meier estimator of the corresponding survivor functions. The number of replicates from the simulated data are the same as for the observed ones.

was a change in the patch leaving mechanisms with the quality of the patch, the interactions between all the time-dependent covariates and the fixed covariate were also added to the model. Thus, the full model included 27 parameters. They were estimated from the data by partial likelihood maximization (Cox, 1975).

The significant effects of the covariates were tested using a standard likelihood ratio test. Like in Wajnberg et al. (1999), this test was used through an iterative procedure to identify the parameters having a significant influence of the females' patch leaving tendency. The adequacy of the final fitted model can be assessed by making residual plots (see Wajnberg et al., 1999, for an example of such a plot). This showed that nothing was amiss. Thus, the final model was considered to properly describe the patch leaving mechanisms used by *T. brassicae* females under all the conditions tested. All computations were done in S-Plus (Venables and Ripley, 1994).

RESULTS

As can be seen in Figure 1, *T. brassicae* females spent more time on patches containing a higher initial proportion of healthy hosts (Log-rank test: chi square = 22.92, $df = 3$, $p < .001$). Moreover, Figure 2 shows the number of progeny produced per time unit, and Figure 3 the distribution of the rates of reproductive success just before the patch is left. These final rates of reproductive success appeared to be statistically similar, whatever the initial quality of the patch the females were foraging on (Kruskal-Wallis test: chi square = 5.45, $df =$

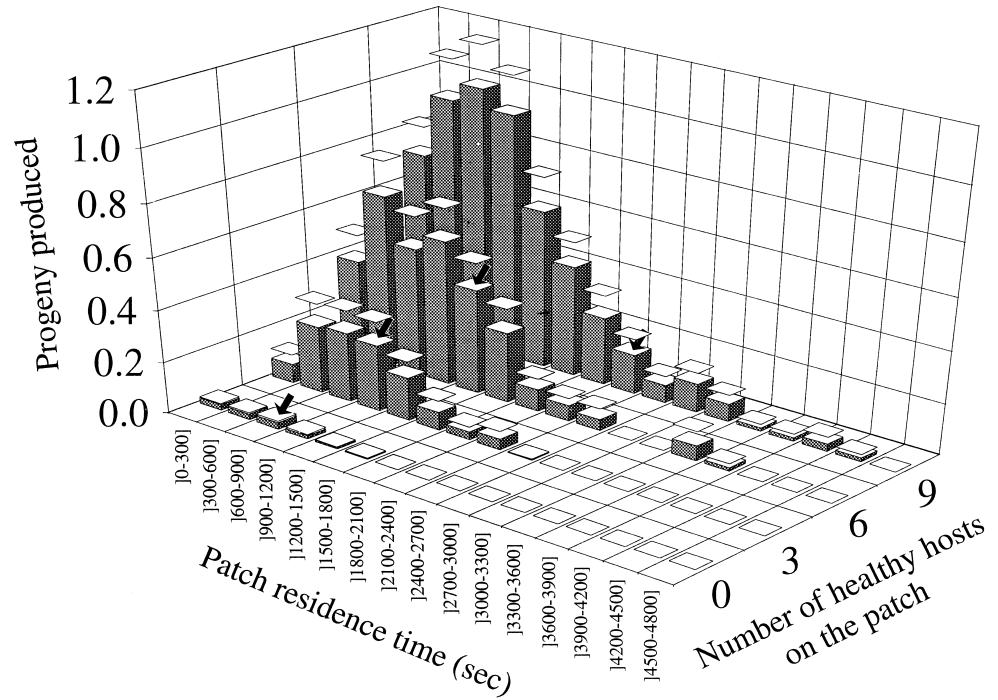


Figure 2
Average progeny produced at each 5-min interval during the total residence time on patches of nine hosts containing different initial numbers of healthy hosts. Additional upper limits correspond to standard errors. Arrows indicate values corresponding to the average patch time duration of the measured *T. brassicae* females (see Figure 1).

3, NS; see Figure 3). An important proportion of the data plotted in Figure 3 are null values. This seems to suggest that the strategy adopted by the females consists of depleting completely the patch before leaving it. However, as can be seen on Figure 2, that shows average values, some progeny can still

be produced after the patch is left. Moreover, an average of 3.74, 2.73 and 1.36 healthy hosts remained unattacked when the females left patches containing nine, six and three initially unparasitized hosts, respectively. Therefore, the patch exploitation strategy adopted by *T. brassicae* females appears to be more complex than a simple complete exploitation before leaving. The rates of reproductive success that are plotted in Figure 3 were computed over the last 5-min period spent on the patch. The Kruskal-Wallis test used to compare the final rates of reproductive success in the four situations remains non-significant if the estimate was done over an interval of time ranging from 1 to 10 min before the patch is left. Therefore, females spent statistically more time on patches of higher quality and seem to reduce them to the same level of profitability before leaving. Thus, their patch exploitation strategy appeared to be in accordance to some of the predictions of the MVT.

A Cox regression model was fitted to the behavioral data in order to identify the patch leaving mechanisms used by the females under the different conditions compared. Table 1 gives the estimated effect of all the covariates having a significant influence on the patch leaving tendency of the wasp females.

The tendency of the females to leave was clearly related to the initial quality of the patch they were foraging on. The leaving tendency on a patch containing only hosts already attacked by a previous female was 2.85 higher than on a patch containing only healthy hosts. Furthermore, each successful oviposition on a healthy host decreased the patch leaving tendency by a factor of 0.78. This indicates that *T. brassicae* females are using an incremental mechanism to control their patch residence time. On the other hand, when a female rejected a healthy host or a host that it previously attacked, its leaving tendency significantly increased by a factor of 1.22 and 1.07, respectively. These two types of host rejection have thus a decremental effect on patch residence time. In contrast, ovipositing a second time (or more) in a healthy host (i.e., self-superparasitism), and attacking or rejecting a host that was previously attacked by another female did not show any

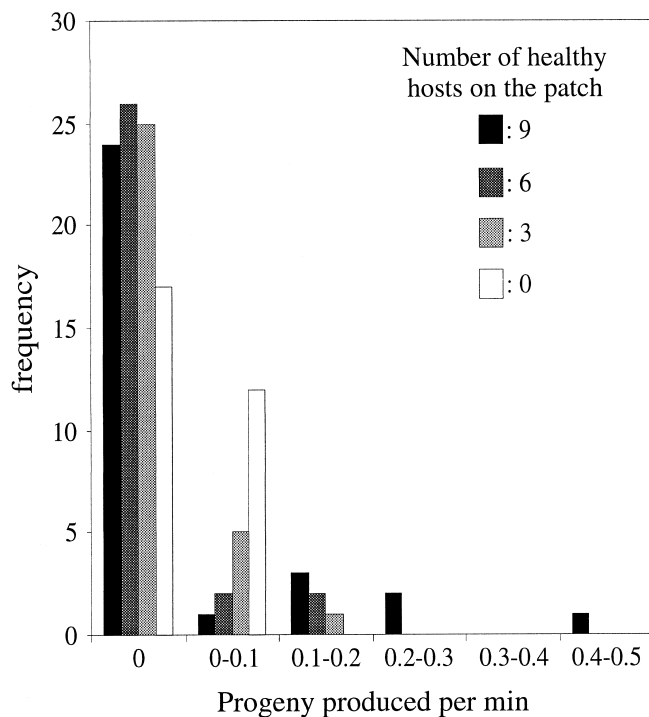


Figure 3
Frequency distribution of the number of progeny produced per time unit during the terminal 5-min period on patches of nine hosts containing different initial numbers of healthy hosts. Average values are not statistically different (Kruskal-Wallis test: chi square = 5.45, df = 3, NS).

Table 1

Estimated regression coefficients (β), standard errors (se) and hazard ratio ($\exp(\beta)$) for only those covariates that had a significant effect ($p < .05$) on the patch leaving tendency of *T. brassicae* females

	β	se	$\exp(\beta)$	χ^2 (df)	p value
Patches with 9 healthy hosts	0.00	—	1.00	8.20 (3)	0.042
Patches with 6 healthy hosts	0.72	0.32	2.06		
Patches with 3 healthy hosts	0.74	0.36	2.10		
Patches with 0 healthy hosts	1.05	0.40	2.85		
Oviposition in a healthy host	-0.25	0.09	0.78	7.92 (1)	0.005
Rejection of a healthy host	0.20	0.06	1.22	9.71 (1)	0.002
Rejection of a host already attacked by the same female	0.07	0.03	1.07	5.56 (1)	0.018

χ^2 correspond to the likelihood ratio tests. All of them were computed with all the other significant terms present in the model. Patches with nine healthy hosts were assumed to be the reference level (i.e., baseline hazard with a coefficient set to zero).

influence on the patch leaving tendency (all chi square at $p > .05$). Finally, no significant interactions were observed between the effect of the patch quality and the effect of each oviposition in a healthy host, rejection of a healthy host or a host that was previously attacked by the same female (all chi square at $p > .05$). Therefore, the patch leaving mechanisms discussed so far did not change according to the quality of the patch exploited by the females.

A simulation model

Are the different leaving rules discussed so far a sufficient set of mechanisms leading the females to adopt a patch exploitation strategy that is in accordance to the theoretical predictions of the MVT? If this is true, what is the importance of each of these rules in fitting to such optimal predictions? In order to answer these two questions, a Monte Carlo procedure, based on the results of the Cox regression model, was developed in order to simulate the patch exploitation behavior of *T. brassicae* females on patches of different quality. The idea of using a Cox regression model as a basis for building a simulation model of patch exploitation in parasitic wasps has been already suggested by several authors (Driessen and Bernstein, 1999; van Roermund et al., 1994; van Roermund et al., 1997; Vos et al., 1998). Some of them actually proposed detailed procedures simulating specific situations (Driessen and Bernstein, 1999; van Roermund et al., 1997). The model developed in the present study is built on a more general procedure that can be easily adapted to any kind of situation.

The Monte Carlo model was developed according to two successive steps. The first one was based on a six-states Markov chain, and used to generate the different behavioral events occurring during the patch exploitation. These events were then used as inputs for a second step that was built around the results of the Cox regression model. The six behavioral states used in the Markov chain were a successful attack or a rejection of a healthy host, a host previously attacked either by the same female or by a conspecific. The patch was assumed to be exploited randomly by the females, so the probability of starting the behavioral sequence in each of these states was set according to both the initial quality of the patch and the rejection rates of the three types of host, as estimated from the experimental data. Then, the inter-state transition probabilities were modified according to the type of host successfully attacked. Therefore, this procedure takes patch depletion into account through a monotonous decrease in the probability of encountering a healthy host each time such a host is successfully attacked. Based on the experimental data, the times between the moment the patch is entered and each

of the behavioral states, and the inter-state transition times were drawn from two-parameter exponential distributions (i.e., exponential distributions with a minimal time-lag), whose features were estimated from the experimental data (see Haccou and Meelis, 1992, for a detailed description of such statistical distributions). The behavioral sequence was generated up to the maximal observed patch residence time (i.e., 5835.9 s). For a given simulation, and from the moment the female entered the patch, the behavioral sequence was used at each time step to compute both the waiting time t_1 before the next coming event, and the waiting time t_2 before the patch is left. This second waiting time was drawn randomly using the results of the Cox regression model. The detailed procedure is described in the Appendix. If t_1 was smaller than t_2 , the female was supposed to keep on foraging on the patch, experiencing the next coming event, and the procedure was resumed at this next event. In the other case, the patch was supposed to be left, and both the patch time duration and the rate of reproductive success during the last 5-min period were outputted.

The simulation model was first used with the regression parameters estimated from the experimental data (see Table 1). This was done only for verification, and, despite the fact this was not a real validation done on independent behavioral data, it would reveal whether some important factors were omitted. As can be seen in Figure 1, which gives an example of the simulated patch time durations obtained on the four types of patches, the model generated patch residence times that were in close agreement with the experimental observations. In order to study the effect of different patch exploitation strategies on the ability of the females to fit the predictions of the MVT, the simulation model was then used with different combinations of the regression parameters. Five different sets of patch leaving rules were compared: (1) the real patch leaving mechanisms, with parameter values estimated from the experimental data (i.e., with an incremental effect associated to each successful oviposition, and decremental effects associated to the rejection of a healthy host or a host already attacked by the same female, see Table 1); (2) the same set of mechanisms but with the incremental effect of each successful oviposition set to its opposite value, leading to a decremental mechanism; (3) and (4) the observed set of patch leaving mechanisms (see Table 1) but with the decremental effects of the two types of host rejection set to their opposite values, respectively; (5) all the three patch leaving mechanisms observed set simultaneously to their opposite values. In all the cases, parameters related to the quality of the patch remained unchanged. In each case, 200 simulations were done, each of them simulating the same number of rep-

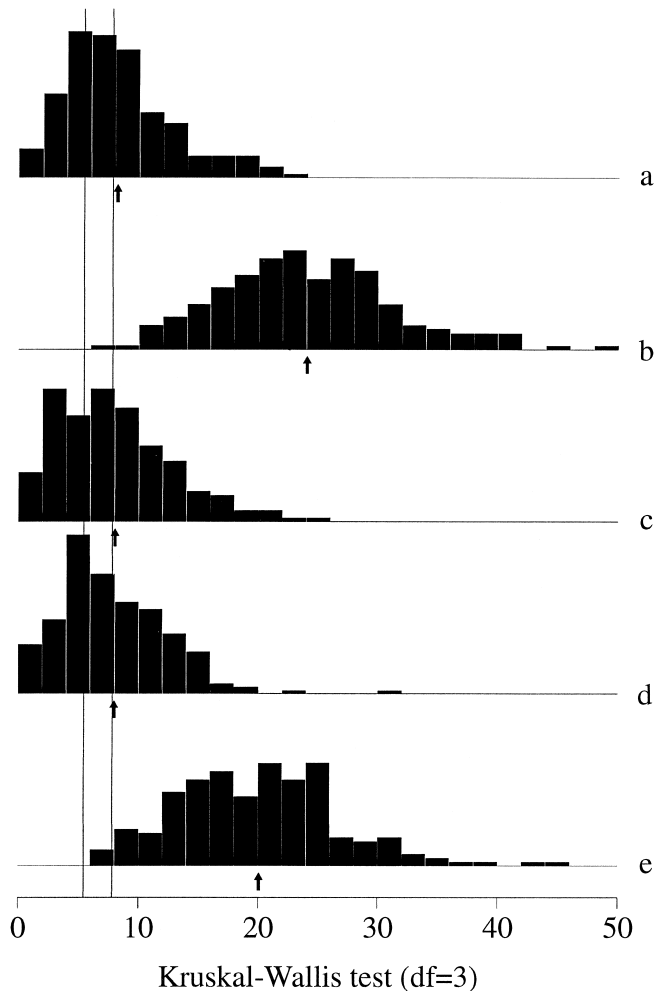


Figure 4
Frequency distributions of Kruskal-Wallis tests (i.e., chi square) done to compare the rates of progeny production during the terminal 5-min period on the patch with the following five different simulated sets of patch leaving rules: (a) the set of patch leaving mechanisms observed on *T. brassicae* females (see Table 1); (b) the same mechanisms but with the incremental effect of each oviposition in a healthy host set to its opposite value; (c) and (d): like in (a) but with the decremental effect of the two types of host rejections set to their opposite values, respectively; and (e) like in (a) but with the three patch leaving mechanisms set simultaneously to their opposite values. Each histogram represents the distribution of 200 tests. Arrows show their average values. The two vertical lines represent: (1) the chi square observed on the experimental data (i.e., 5.45, see Figure 3) and (2) the 5%-risk critical threshold value for a chi square with $df = 3$ (i.e., 7.81), respectively.

licates on the different patch qualities than the number of females observed experimentally. Finally, as in Figure 3, the ability of these different patch leaving strategies to produce results that are in accordance to the predictions of the MVT was assessed. For each simulation, the final rates of reproductive success on the different patch qualities were compared by means of a Kruskal-Wallis test. In each case, the frequency distribution of the 200 tests will thus indicate whether the females behave in an optimal way or not. Figure 4 gives the frequency distributions of these tests for the five patch exploitation strategies compared.

More than 54% (i.e., 109 out of 200) of the simulations done with the regression parameters estimated from the experimental data led to Kruskal-Wallis tests below the 5%-risk

threshold value of 7.81 (Figure 4a). However, if each successful oviposition had a decremental effect on the patch residence time instead of the incremental effect observed (see Table 1), only one Kruskal-Wallis test out of 200 remained non-significant (Figure 4b). Thus, the observed incremental effect of each oviposition in a healthy host seems to be an important mechanism ensuring the ability of the females to reach theoretical predictions of the MVT. On the other hand, Kruskal-Wallis tests were not affected by substituting the decremental mechanisms associated to the rejection of a healthy host or a host already attacked by the same female by opposite incremental effects. In both cases, more than 54% of the chi square tests were non-significant (Figure 4c,d). Therefore, these two patch leaving decision rules do not seem to have an important influence on the ability of the females to behave according to the MVT predictions. Finally, when all these three patch leaving rules were changed simultaneously into their opposite effects, only 4 out of 200 chi square tests remained non-significant (Figure 4e). According to the previous results, this is likely due to only the effect of each oviposition in a healthy host.

These results indicate that, within the set of the patch leaving mechanisms studied, the incremental effect of each successful oviposition in a healthy host appeared to play the most important role for the females to behave according to the MVT predictions. In order to understand this result more accurately, another set of simulations was carried out in order to perform a sensitivity analysis on the only parameter showing a significant influence. The same procedure was used, but only with different values (i.e., from -1.50 to 0.25) of the regression parameter describing the effect of each successful oviposition. All the other parameters remained unchanged. The results are presented in Figure 5.

As long as a regression parameter lower or equal to the real observed value of -0.25 is used, more than 50% of the simulations led to Kruskal-Wallis tests below the 5%-risk threshold value. This indicates that, as long as each successful oviposition had an incremental effect, and whatever its intensity, the patch exploitation strategy adopted by the foraging females remains in accordance to the theoretical predictions of the MVT. On the other hand, if higher values of the regression parameter are used, and especially when positive value are considered (i.e., when each oviposition led to a decremental mechanism), more and more Kruskal-Wallis tests became significant, indicating that females behave in a less and less optimal way.

DISCUSSION

T. brassicae females stayed statistically longer on patches containing a higher initial proportion of healthy hosts. On the other hand, the rates of progeny produced just before the patch is left remained statistically the same. This suggests that patches were all reduced to the same level of profitability before being left. Thus, the patch exploitation strategy adopted by the foraging females appears to be in accordance with some of the predictions of the MVT. This theorem implicitly assumes that foragers have a thorough knowledge of the quality and distribution of all the patches in the habitat. For this, they are assumed to sample a large number of patches in order to rapidly assess their profitability (Cook and Hubbard, 1977; Galis and van Alphen, 1981; Godfray, 1994). However, the results presented in this study were obtained on naive females, and only their first patch visit was considered. This suggests that, as soon as they emerge, females should have some innate, not necessarily accurate patch leaving rules leading them to adopt a patch exploitation strategy that is on average in accordance with the quality of the patches they will

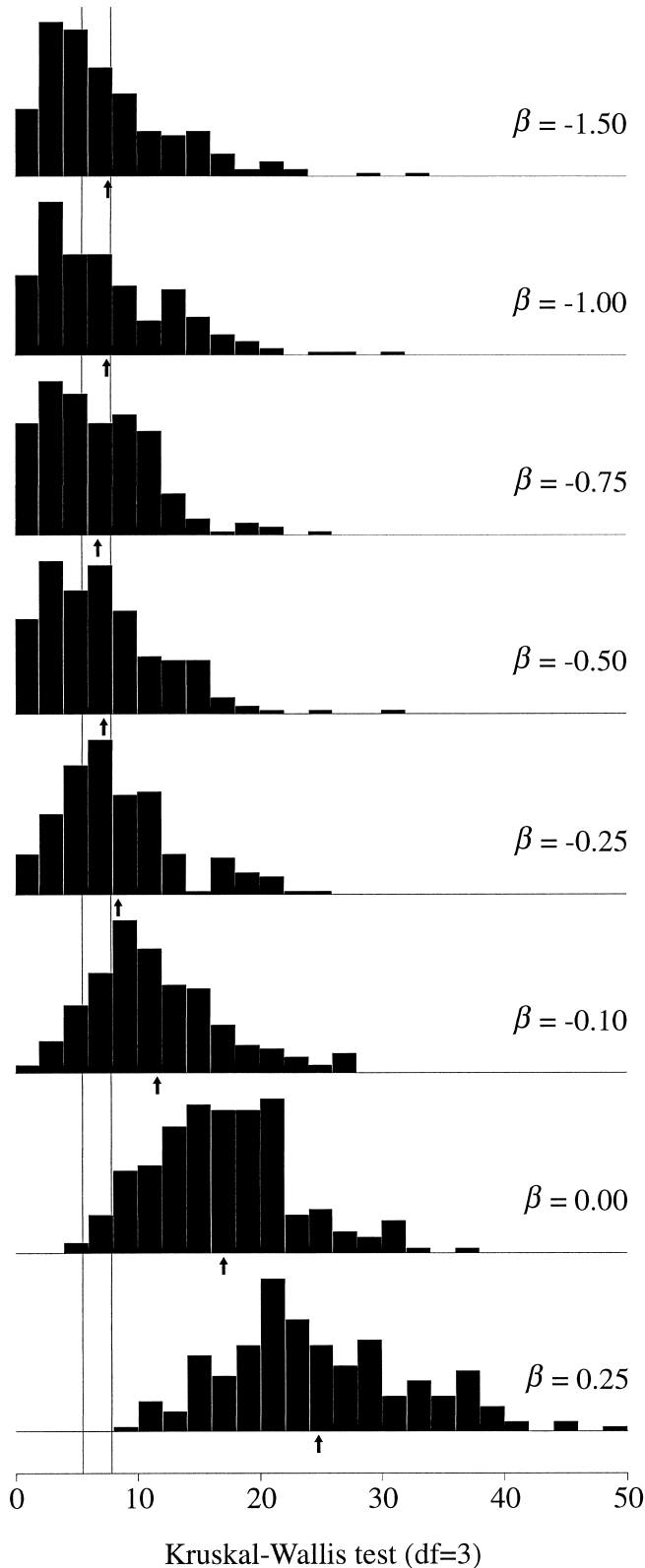


Figure 5
 Frequency distributions of Kruskal-Wallis tests (i.e., chi square) done to compare the rates of progeny production during the terminal 5-min period on the patch when different values of the regression parameter (β) associated to the effect of each oviposition in a healthy host, are used. Negative values of this parameter correspond to an incremental effect. Positive values simulate a decremental mechanism. The regression parameter estimated on

encounter. As soon as the first patch is discovered, their foraging strategy would thus be already in accordance with the predictions of the MVT, without prior knowledge of the quality of all the available patches in the habitat. This ability could then be improved during the following patch visits (Vos et al., 1998).

The proximate mechanisms involved deserve to be analyzed and several hypotheses can be proposed. According to Waage's (1979) model, the patch residence time is supposed to depend on the initial degree of responsiveness to the patch that is related to the number of hosts available. However, in the present study, patches offered to the females were all constituted of nine hosts, and the amount of kairomone provided by a healthy host or a host previously attacked by another female should be the same. Thus, in the present case, the change observed in the patch residence time with the quality of the patch should not be related to a change in the initial responsiveness of the females. Sometimes, it has also been demonstrated that females could spend less time on patches that were previously marked by a conspecific foraging female (Bernstein and Driessen, 1996; Galis and van Alphen, 1981; van Lenteren and Bakker, 1978; Waage, 1979). However, in the present study, patches were built just before the experiment, and the previous conspecific females used to produce the hosts already attacked did not have any chance to mark the patch itself. Other mechanisms should thus be proposed to explain the reduction in the time spent on patches containing a higher initial proportion of already attacked hosts. A third hypothesis has been suggested by Rosenheim and Mangel (1994). An imperfect ability to discriminate between healthy and already attacked hosts within the same patch should lead the females to experience a higher risk of superparasitism, with a corresponding reduction in reproductive success. Under such a hypothesis, the presence of already attacked hosts within the patch may lead the females to leave earlier. In the present case, this hypothesis is unlikely because *Trichogramma* females are known to be able to accurately discriminate between healthy hosts and hosts that are already parasitized (Salt, 1937). Therefore, more complex patch leaving rules are likely to be involved, and we decided to analyze these by means of a Cox regression model.

Using such a regression model, we first found that each successful oviposition in a healthy host significantly reduced the patch leaving tendency of the females. This indicates that *T. brassicae* females were using an incremental mechanism similar to the one described by Waage (1979). This incremental effect is likely to be related to the fact that, following oviposition, *Trichogramma* females are known to increase their turning tendency together with a reduction in their walking speed. Such an arrestment response leads to an increasing tendency to remain on the patch after each oviposition (Gardner and van Lenteren, 1986; Yano, 1978). This incremental mechanism is supposed to be adaptive when the hosts exhibit a clumped distribution (i.e., with a large variance in patch density), or if foraging females are unable to assess accurately the number of hosts that are expected in the patch under exploitation (Iwasa et al., 1981).

Ovipositing a second time (or more) in a healthy host or in a host that was previously attacked by another female did not have any influence on the patch leaving tendency of the

←

real data was -0.25 (see Table 1). Each histogram represents the distribution of 200 tests. Arrows show their average values. The two vertical lines represent (1) the chi square observed on the experimental data (i.e., 5.45, see Figure 3) and (2) the 5%-risk critical threshold value for a chi square with $df = 3$ (i.e., 7.81), respectively.

females. Thus, neither self- nor conspecific superparasitism seem to provide the forager information regarding the future value of the patch and thus does not seem to modify its readiness to leave. On the other hand, rejecting a healthy host or a host previously attacked by the same female led to a significant increase in the tendency to leave the patch. As a general rule, the rejection of a host has repeatedly been considered to provide the female with some information regarding the decreasing value of the patch. Thus, the resulting increasing tendency to leave is usually considered to be adaptive (van Alphen, 1993; van Alphen and Vet, 1986; van Lenteren, 1991; Wajnberg et al., 1999). However, no significant effect was observed when the host rejected was one that was previously attacked by a conspecific female. This surprising result seems to indicate that indirect interference (Visser and Driessen, 1991) would not have any influence on the tendency of the females to leave the patch, and this is in contradiction with what is usually expected (van Alphen and Vet, 1986). In the case of *Trichogramma*, only direct mutual interference would have a significant influence (Kfir, 1983).

Finally, the patch leaving rules that have been discussed so far (i.e., incremental effect of each oviposition in a healthy host and decremental effects of each rejection of a healthy host or a host previously attacked by the same female) do not seem to change significantly according to the quality of the patch exploited by the females. The only significant effect was that the patch leaving tendency was higher on patches containing a higher proportion of already attacked hosts. In turn, this led to an increase in giving-up times (i.e., the time period from the last successful oviposition until the patch is abandoned) with an increase in the quality of the patch (Log-rank test: chi square = 10.50, df = 3, $p < .02$). Such a result has been already observed on other parasitoid species (e.g., Nelson and Roitberg, 1995) and is in accordance with the optimal predictions of the model developed by McNair (1982). The variation in the patch leaving tendency with the quality of the patch can thus be considered to be adaptive.

As pointed out by Godfray (1994), there is currently a lack of studies relating the type of proximate patch leaving rules that are revealed by means of the statistical approach used here with the ultimate predictions of the MVT. Indeed, studies showing the ability of the foragers to follow the predictions of the MVT are usually not focusing on the mechanistic rules involved (e.g., Bonser et al., 1998). Reciprocally, the analyses of the patch leaving rules adopted by the females are not necessarily done within the framework of the optimal predictions of the MVT (e.g., Driessen and Bernstein, 1999; Waage, 1979). In the present study, we thus tried to relate these two complementary approaches. By using the results of the Cox regression model discussed above, we developed a Monte Carlo procedure simulating the patch exploitation strategy of a wasp female on patches of different profitability. Several other methods were already proposed by some authors in order to simulate patch exploitation strategy in parasitic wasps (Driessen and Bernstein, 1999; Roitberg and Prokopy, 1984; van Roermund et al., 1997; Waage, 1979). The model presented here is the only not fully parametric one allowing to take into account accurately and simultaneously: (1) the effects of numbers and timings of the different events appearing on the patch (e.g., host attacks or rejections), (2) the stochastic nature of these events, (3) the effect of time-dependent mechanisms, and (4) the fact that the leaving tendency of the females can be a function of time (i.e., with patch residence times not necessarily distributed exponentially). Using this simulation model, we demonstrated that the patch leaving rules adopted by the females seem to provide them with an efficient and rather simple way to fit to the optimal predictions of the MVT. Within the set of the leaving mechanisms

that are used, the incremental effect of each successful oviposition in a healthy host appeared to be, at least qualitatively (see Figure 5), the most important one to achieve this optimal goal. On the other hand, the two other mechanisms (i.e., decremental effects of rejecting a healthy host or a host previously attacked by the same female) did not appear to play an important part (see Figure 4). Using another type of simulation procedure, Driessen and Bernstein (1999) developed a model of patch departure parameterized for *Venturia canescens* (Gravenhorst) females foraging in a habitat containing an important amount of patches of hosts. The inter-patch travel time was set to zero so that females could visit all the available patches within a single foraging bout. Under such simulated conditions, these authors showed that a decremental effect of each oviposition would lead to a higher rate of progeny production because such a mechanism would lead the female to visit a higher number of patches per time unit. On the other hand, when travel time between patches is infinite, so that only one patch is visited, an incremental mechanism was shown to produce the highest rate of progeny production. In the present study, only one patch visit is also considered, and we found an incremental mechanism to perform better according to an other criterion, the terminal rate of reproductive success before leaving the patch. Our results are thus in agreement with those found by Driessen and Bernstein (1999) and provide a more general framework suggesting that, when only one patch is visited, an incremental effect of each successful oviposition would lead the females to behave in a more optimal way.

The patch exploitation strategy of *T. brassicae* females is likely to change during successive visits to patches of host of different profitability. Thus, experiments are now being performed in order to identify any kind of change in the patch leaving rules adopted by the females that are offered in succession patches of different quality. Any modification observed will then be included in the simulation model developed in the present study in order to see whether the foraging females are also sampling their environment in order to get closer to the optimal predictions of the optimal foraging models.

APPENDIX

According to the Cox regression model, the hazard function for the i 'th female is:

$$h_i(t) = h_0(t) \exp\{\beta^T Z_i(t)\} \quad (\text{A1})$$

where β is the vector of the regression parameters and $Z_i(t)$ the vector of the fixed and time-dependent covariates. Integrating both sides of this expression leads to the cumulative hazard function, conditional on the covariates $Z_i(t)$:

$$H_i(t) = \int_0^t h_i(u) du = \int_0^t h_0(u) \exp\{\beta^T Z_i(u)\} du. \quad (\text{A2})$$

In order to estimate this function, we first need to estimate the cumulative baseline hazard function:

$$H_0(t) = \int_0^t h_0(u) du. \quad (\text{A3})$$

For this, the so-called Breslow's (1974) estimator is usually used. It leads to a step function whose jumps are, if $t_{(j)}$ is the j 'th patch time duration among all the observed patch residence times, arranged in increasing rank order:

$$\hat{\Delta}_0(t_{(j)}) = \hat{H}_0(t_{(j)}) - \hat{H}_0(t_{(j-1)}). \quad (\text{A4})$$

Let $\hat{\beta}$ be the estimated vector of the regression parameters.

Thus, the cumulative hazard function for the i 'th female, conditional on the covariates $Z_i(t)$, can be estimated by:

$$\hat{H}_i(t) = \sum_{t(j)=t} \hat{\Delta}_0(t_{(j)}) \exp\{\hat{\beta}^T Z_i(t_{(j-1)})\} \quad (\text{A5})$$

which is also a step function whose jumps are:

$$\hat{\Delta}_i(t_{(j)}) = \hat{H}_i(t_{(j)}) - \hat{H}_i(t_{(j-1)}). \quad (\text{A6})$$

Using the product integral proposed by Gill and Johansen (1990), these values can be used to estimate the corresponding distribution function:

$$\hat{F}_i(t) = 1 - \prod_{t(j)=t} [1 - \hat{\Delta}_i(t_{(j)})]. \quad (\text{A7})$$

This function provides the cumulative distribution of the patch times for the j 'th female, conditional on the covariates $Z_i(t)$, these patch times being measured from the moment the female enters the patch. However, what we need instead are the distributions of the patch residence times measured from the last behavioral event that appeared on the patch. Such distributions should be estimated after each new coming behavioral event.

Let us suppose that the last behavioral event occurred at time X , and let $Y = T - X$ the time elapsed between X and the patch time duration T . Then, using the change of variable $t = s + X$, the Cox regression model presented in (Equation A1) for T is equivalent to the following one for Y :

$$h_i(s + X) = h_0(s + X) \exp\{\beta^T Z_i(s + X)\} \quad (\text{A8})$$

The corresponding estimated distribution function of Y , $\hat{F}_{i,Y}$ is thus the same as the one described in (Equation A7), except that only the jumps of the cumulative hazard function that appeared after the time of the last event are taken into account. For each female, and after each event appearing on the patch, this distribution function was estimated using the behavioral sequence generated with the Markov chain described in the text.

Finally, a value u is drawn randomly from a Uniform distribution over the interval $[0, 1]$. The simulated patch residence time x , measured from the last behavioral event that appeared on the patch at X , is then $\hat{F}_{i,Y}^{-1}(u)$ which is the smallest value satisfying $\hat{F}_{i,Y}(x) \geq u$ (Rubinstein, 1981):

$$\hat{F}_{i,Y}^{-1}(u) = \inf\{x: \hat{F}_{i,Y}(x) \geq u\}. \quad (\text{A9})$$

We thank C. Bernstein and G. Driessen for their continuous encouragement and criticism. For their critical reading of the manuscript, we thank C. Bernstein, G. Driessen, L. Lapchin and J.S. Pierre. We thank N. Ledger for reading the English version of the manuscript, C. Curty and J. Pizzol for their valuable help in experimental work, and P. Chavigny for performing the analysis with the molecular markers.

REFERENCES

- Bell WJ, 1991. Searching behaviour. The behavioural ecology of finding resources. London: Chapman and Hall.
- Bernstein C, Driessen G, 1996. Patch-marking and optimal search patterns in the parasitoid *Venturia canescens*. *J Anim Ecol* 65:211–219.
- Bonser B, Wright PJ, Bament S, Chukwu UO, 1998. Optimal patch use by foraging workers of *Lasius fuliginosus*, *L. niger* and *Myrmica ruginodis*. *Ecol Entomol* 23:15–21.
- Breslow NE, 1974. Covariance analysis of censored survival data. *Biometrics* 30: 89–99.
- Bruins EBAW, Wajnberg E, Pak GA, 1994. Genetic variability in the reactive distance in *Trichogramma brassicae* after automatic tracking of the walking path. *Entomol Exp App* 72:297–303.
- Charnov EL, 1976. Optimal foraging: the marginal value theorem. *Theor Popul Biol* 9:129–136.
- Collett D, 1994. Modelling survival data in medical research. London: Chapman and Hall.
- Cook RM, Hubbard SF, 1977. Adaptive searching strategies in insect parasites. *J Anim Ecol* 46:115–125.
- Cox DR, 1972. Regression models and life tables. *Biometrics* 38:67–77.
- Cox DR, 1975. Partial likelihood. *Biometrika* 62:269–276.
- Driessen G, Bernstein C, 1999. Patch departure mechanisms and optimal host exploitation in an insect parasitoid. *J Anim Ecol* 68:445–459.
- Driessen G, Bernstein C, van Alphen JJM, Kacelnik A, 1995. A count-down mechanism for host search in the parasitoid *Venturia canescens*. *J Anim Ecol* 64:117–125.
- Galis F, van Alphen JJM, 1981. Patch time allocation and search intensity of *Asobara tabida* Nees (Braconidae), a larval parasitoid of *Drosophila*. *Neth J Zool* 31:596–611.
- Gardner SM, van Lenteren JC, 1986. Characterisation of the arrestment responses of *Trichogramma evanescens*. *Oecologia* 68:265–270.
- Gill RD, Johansen S, 1990. A survey of product-integration with a view towards application in survival analysis. *Ann Statist* 18:1501–1555.
- Green RF, 1980. Bayesian birds: A simple example of Oaten's stochastic model of optimal foraging. *Theor Popul Biol* 18:244–256.
- Green RF, 1984. Stopping rules for optimal foragers. *Am Nat* 123:30–40.
- Godfray HCJ, 1994. Parasitoids. Behavioral and evolutionary ecology. Princeton, New Jersey: Princeton University Press.
- Haccou P, Meelis E, 1992. Statistical analysis of behavioural data. An approach based on time-structured model. Oxford: Oxford University Press.
- Haccou P, de Vlas SJ, van Alphen JJM, Visser ME, 1991. Information processing by foragers: effects on intra-patch experience on the leaving tendency of *Leptopilina heterotoma*. *J Anim Ecol* 60:93–106.
- Hassell MP, 1978. The dynamics of arthropod predator-prey systems. Princeton, New Jersey: Princeton University Press.
- Hemerik L, Driessen G, Haccou P, 1993. Effects of intra-patch experiences on patch time, search time and searching efficiency of the parasitoid *Leptopilina clavipes*. *J Anim Ecol* 62:33–44.
- Hubbard SF, Cook RM, 1978. Optimal foraging by parasitoid wasps. *J Anim Ecol* 47:593–604.
- Iwasa Y, Higashi M, Yamamura N, 1981. Prey distribution as a factor determining the choice of optimal foraging strategy. *Am Nat* 117: 710–723.
- Kalbfleisch JD, Prentice RL, 1980. The statistical analysis of failure time data. New York: Wiley.
- Kfir R, 1983. Functional response to host density by the egg parasite *Trichogramma pretiosum*. *Entomophaga* 28:345–353.
- Klomp H, Teerink BJ, Ma WC, 1980. Discrimination between parasitised and unparasitised hosts in the egg parasite *Trichogramma embryophagum* (Hym.: Trichogrammatidae): A matter of learning and forgetting. *Neth J Zool* 30:254–277.
- Krebs JR, Ryan JC, Charnov EL, 1974. Hunting by expectation or optimal foraging? A study of patch use by Chickadees. *Anim Behav* 22:953–964.
- Laurent V, Wajnberg E, Mangin B, Schiex T, Gaspin C, Vanlerberghe-Masutti F, 1998. A composite genetic map of the parasitoid wasp *Trichogramma brassicae* based on RAPD markers. *Genetics* 150:275–282.
- Le Ralec A, Wajnberg E, 1990. Sensory receptors of the ovipositor of *Trichogramma maidis* Pintureau & Voegelé (Hym.: Trichogrammatidae). *Entomophaga* 35:293–299.
- Li C, Roitberg BD, Mackauer M, 1993. Patch residence time and parasitism of *Aphelinus asychis*: a simulation model. *Ecol Model* 69: 227–241.
- McNair JM, 1982. Optimal giving-up time and the marginal value theorem. *Am Nat* 119:511–529.
- McNamara JM, 1982. Optimal patch use in a stochastic environment. *Theor Popul Biol* 21:269–288.
- Nelson JM, Roitberg BD, 1995. Flexible patch time allocation by the leafminer parasitoid, *Opius dimidiatus*. *Ecol Entomol* 20:245–252.
- Roitberg BD, Prokopy RJ, 1984. Host visitation sequence as a determinant of search persistence in fruit parasitic tephritid flies. *Oecologia* 62:7–12.
- Rosenheim JA, Mangel M, 1994. Patch-leaving rules for parasitoids with imperfect host discrimination. *Ecol Entomol* 19:374–380.
- Rubinstein RY, 1981. Simulation and the Monte Carlo method. New York: John Wiley & Sons.

- Salt G, 1937. The sense used by *Trichogramma* to distinguish between parasitised and unparasitised hosts. *Proc R Soc Lond B* 122:57–75.
- Shaltiel L, Ayal Y, 1998. The use of kairomones for foraging decisions by an aphid parasitoid in small host aggregations. *Ecol Entomol* 23: 319–329.
- Stephens DW, Krebs JR, 1986. *Foraging theory*. Princeton, New Jersey: Princeton University Press.
- van Alphen JJM, 1993. Patch residence time and encounters with parasitised hosts: A reaction. *Neth J Zool* 43:340–349.
- van Alphen JJM, Vet LEM, 1986. An evolutionary approach to host finding and selection. In: *Insect parasitoids* (Waage J, Greathead D, eds). London: Academic Press; 23–61.
- van Lenteren JC, 1991. Encounters with parasitized hosts: To leave or not to leave a patch. *Neth J Zool* 41:144–157.
- van Lenteren JC, Bakker K, 1978. Behavioural aspects of the functional response of a parasite (*Pseudeucoila bochei* Weld) to its host (*Drosophila melanogaster*). *Neth J Zool* 28:213–233.
- van Roermund HJW, Hemerik L, van Lenteren JC, 1994. Influence of intrapatch experiences and temperature on the time allocation of the whitefly parasitoid *Encarsia formosa* (Hymenoptera: Aphelinidae). *J Insect Behav* 7:483–501.
- van Roermund HJW, van Lenteren JC, Rabbinge R, 1997. Analysis of foraging behavior of the whitefly parasitoid *Encarsia formosa* on a leaf: A simulation model. *Biol Control* 8:22–36.
- van Steenis MJ, El-Khawass KAMH, Hemerik L, van Lenteren JC, 1996. Time allocation of the parasitoid *Aphidius colemani* (Hymenoptera: Aphidiidae) foraging for *Aphis gossypii* (Homoptera: Aphidae) on cucumber leaves. *J Insect Behav* 9:283–295.
- Venables WN, Ripley BD, 1994. *Modern applied statistics with S-Plus*. New York: Springer-Verlag.
- Visser ME, Driessen G, 1991. Indirect mutual interference in parasitoids. *Neth J Zool* 41:214–227.
- Vos M, Hemerik L, Vet LEM, 1998. Patch exploitation by the parasitoids *Cotesia rubecula* and *Cotesia glomerata* in multi-patch environments with different host distributions. *J Anim Ecol* 67:774–783.
- Waage JK, 1978. Arrestment responses of the parasitoid, *Nemeritis canescens*, to a contact chemical produced by its host, *Plodia interpunctella*. *Physiol Entomol* 3:135–146.
- Waage JK, 1979. Foraging for patchily-distributed hosts by the parasitoid, *Nemeritis canescens*. *J Anim Ecol* 48:353–371.
- Wajnberg E, Hassan SA, 1994. *Biological control with egg parasitoids*. Wallingford, England: CAB International.
- Wajnberg E, Rosi MC, Colazza S, 1999. Genetic variation in patch time allocation in a parasitic wasp. *J Anim Ecol* 68:121–133.
- Yamada Y, 1988. Optimal use of patches by parasitoids with a limited fecundity. *Res on Popul Ecol* 30:235–249.
- Yano E, 1978. A simulation model of searching behaviour of a parasite. *Res Popul Ecol* 20:105–122.