

Influence of environmental conditions on patch exploitation strategies of parasitoids

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In patchy environments, patch-leaving decision rules are a key component of the foraging behavior of parasitoids that have to share their searching time between the different host patches to optimize the number of ovipositions. It has been experimentally shown that one of the proximate cues involved in patch-leaving decision is the number of ovipositions performed by the parasitoid while in the patch. Ovipositions can have either a decremental or an incremental effect on the patch residence time depending on parasitoid species. Previous theoretical studies have suggested that environmental conditions and the ability of parasitoids to reliably estimate the number of available hosts on a patch when entering it should influence how patch departure depends on ovipositions. We developed an individual-based model to test a large variety of patch-leaving decision rules in different environmental conditions. This model includes a more realistic representation of individual acquisition of information than previous theoretical work. In accordance with previous results, we show that the best use of information depends on environmental conditions. Moreover, we identify the environmental factors that have a decisive influence on the most appropriate type of rule (incremental or decremental). Decremental mechanisms are most efficient only in restricted conditions characterized by a large number of patches and few parasitoids. The sensitivity of decision rules to frequency-dependent processes was tested by numerical invasibility experiments. Rare mutants using any alternative rule never outperform populations using a high-performance rule. Incremental rules seem to be more sensitive than decremental ones to frequency-dependent processes. *Key words:* individual-based model, kairomone, optimal foraging, ovipositions, patch-leaving decisions, patchy environment. [*Behav Ecol* 18:742–749 (2007)]

In the wild, most animals forage for patchily distributed resources. In these conditions, efficient foraging requires the acquisition of relevant information from the environment and implies making seemingly complex decisions. These decisions may be based on answers to the following questions: Where to forage? How long to forage for? Should the forager join other animals exploiting an area rich in food resources? These individual-level decisions affect both the distribution of the forager population and the depletion of the resource. As a consequence, these decisions will strongly influence population-level processes (Houston and McNamara 1997; Basset et al. 2002). This is especially true for parasitoids searching for hosts because of the close link that exists between the number of hosts attacked by a parasitoid and its fitness. Therefore, patch exploitation strategies used by these animals should be under strong selective pressure. Determining which strategies are used by the animals and by what mechanisms these animals may arrive at these strategies is an important area of research in behavioral ecology.

Several theoretical models predicting the optimal time for which a forager should exploit each visited patch have been proposed. The 2 most widely cited models are the marginal value theorem (MVT, Charnov 1976) and the ideal free distribution (IFD, Brown 1969; Orians 1969; Fretwell and Lucas 1970; Parker 1970; Royama 1970). These 2 models refer to different organization levels. The MVT considers the individual, whereas the IFD considers the population. They also tackle different problems: when the forager should leave

a patch, for the MVT, and how a population of foragers should distribute among patches, for the IFD model. But, these 2 concepts are not unrelated. Bernstein et al. (1988, 1991) showed that using MVT-like decision making leads foragers to a spatial distribution close to the IFD. These early models were strictly functional (i.e., the predictions only consider the fitness consequences for the forager) and assumed that the forager had full knowledge of the relevant information.

Despite modifications of the assumptions of the initial models to add more realism (Oaten 1977; Stephens and Charnov 1982; Sutherland and Parker 1985; Parker and Sutherland 1986; Tregenza 1995), the MVT and the IFD often fail to match experimental results (for reviews concerning the MVT, see Pyke 1984; Nonacs 2001 and for a review concerning the IFD, see Tregenza et al. 1996). This may be so because the models assume omniscient animals, whereas real foragers rely on different mechanisms and limited information. In order to take these features into account, another approach assuming that animals rely on minimal information and on simple rules of thumb to make patch-leaving decisions has therefore been developed. Three kinds of rules are usually proposed as leading potentially to optimal patch residence times: 1) fixed-number rules (Gibb 1962), in which the animal leaves the patch as soon as it consumes a fixed number of prey; 2) fixed-time rules (Krebs 1973), in which the animal stays in the patch for a fixed period of time; and 3) fixed-GUT rules (Krebs et al. 1974), in which the animal leaves the patch after a given period of time without finding prey (the giving-up time—GUT). More complex rules, based on these simple ones, have also been proposed (Green 1980, 1984; McNair 1982).

Experiments mostly conducted with parasitoids have shown that real foragers can integrate different information and use rather complex rules to make patch-leaving decisions (see Driessen et al. 1995; Van Alphen et al. 2003 for reviews; see also Wajnberg et al. 2003; Wang and Keller 2003; Boivin et al. 2004; Lucchetta et al., forthcoming). To describe the foraging

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behavior of the parasitoid *Venturia canescens*, Waage (1979) proposed a model suggesting how animals may combine 3 different sources of information: 1) the concentration of chemicals deposited by the hosts (kairomones), 2) the time already spent on the patch, and 3) ovipositions. Although this model seems to satisfactorily describe Waage's experimental observations, its efficiency has yet to be examined in relatively complex environments. As in the fixed-GUT rules, in this model (Waage 1979) each oviposition increases the tendency to stay on the patch. These models are said to use an incremental mechanism. By contrast, the fixed-time and fixed-number rules use a neutral and a decremental mechanism, respectively.

Although many parasitoids are known to use incremental mechanisms, many others use decremental mechanisms (Driessen and Bernstein 1999; Van Alphen et al. 2003; Wajnberg et al. 2003; Wajnberg 2006). That ovipositions have incremental effects in some species and decremental effects in others is an interesting problem. In a seminal article, Iwasa et al. (1981) suggested that the distribution of hosts determined which rules would lead to an optimal strategy. Parasitoids foraging for uniformly distributed hosts are expected to use a fixed-number rule because the current availability of prey depends only on the initial, fixed, number of hosts, and the number of hosts already attacked. If hosts are randomly (Poisson) distributed, current host availability is a function of the time already spent foraging, and ovipositions are optimized by using a fixed-time rule. For parasitoids foraging for hosts with aggregated distribution (i.e., a high variability in the number of hosts per patch), current host availability depends on both the time spent foraging and the number of hosts already attacked, and the best rule is of the fixed-GUT kind. Green (1980, 1984) and McNair (1982) compared, for different spatial resource distributions, the efficiency of patch-leaving decision rules based on realistic proximal cues used by foragers (in particular parasitoids). They suggested that the structure of the environment determines the most adapted rule.

However, in these theoretical studies, realism is sacrificed to achieve mathematical tractability. The rules considered are much simpler than those used by real parasitoids, and the results are only obtained under restricted conditions. Moreover, these studies focused on the individual-level and neglected frequency-dependent processes.

More empirical studies suggested that there may exist a link between the reliability of the information parasitoids have on the initial quality of a patch and the use of information from ovipositions in patch-leaving decisions. Decremental (or "countdown") rules could be more appropriate when the initial information is reliable (Shaltiel and Ayal 1998; Driessen and Bernstein 1999), while incremental rules would be appropriate wherever initial information is unreliable (Van Alphen et al. 2003). This assertion has been confirmed by simulation of a single parasitoid foraging in a patch not yet depleted by previous visits (Driessen and Bernstein 1999); however, this was never studied for more general circumstances.

We aimed to examine the relationship between the reliability of the information parasitoids can obtain and the patch-leaving rules they should use. We are particularly interested in investigating whether differences in environmental conditions could explain the prevalence of incremental or decremental mechanisms. To avoid the constraints of a classical mathematical approach (in particular the assumption of the infinite size of the environment and the oversimplified representation of individual information acquisition and decision making), we used an individual-based model. First, we investigated the robustness of the previous theoretical results by testing the 3 kinds of rules considered by Iwasa et al. (1981) in an environment constituted by a finite number of patches and in a pop-

ulation, as opposed to individuals, context. Second, we considered more complex rules. In particular, we added a potential ability for parasitoids to estimate the initial quality of the patch in which they are foraging. Third, we studied the invasibility of the different rules by numerical experiments.

THE MODEL

Parasitoids in a heterogeneous environment

Our model simulates the searching behavior of a number of parasitoids, within a single generation, foraging for hosts in a patchy environment. As observed in many parasitoid species (Van Lenteren 1981), we assume that parasitoids are able to avoid superparasitism so that hosts become unavailable for parasitism as soon as attacked. The number of available hosts and parasitoids searching (searchers) in each patch changes as hosts are captured and parasitoids enter and leave the patch.

The initial parasitoid distribution is set at random. At each time step, the total number of attacks by the parasitoids in each patch is calculated as a function of the number of available hosts and searchers by assuming a linear functional response with mutual interference. Based on Hassell and Varley (1969), the total number of attacks generated in a given patch N_{att} is

$$N_{att} = QP_s^{1-m}H, \quad (1)$$

where Q is the quest constant (i.e., the searching efficiency of parasitoid foraging on its own), m is the mutual interference coefficient, H is the number of susceptible hosts, and P_s is the number of searchers, in the patch.

Equation 1 gives a real number. As attacks are discrete (integer) events, we transform this real number into an integer (N_{eff}) using the following rule:

$$\begin{cases} N_{eff} = \text{integer part of } N_{att} & \text{if } h > \text{fractional part of } N_{att}, \\ N_{eff} = (\text{integer part of } N_{att}) + 1 & \text{otherwise} \end{cases} \quad (2)$$

where h is randomly drawn for each time step and patch from a [0,1] uniform distribution.

We assume that each parasitoid is able to make, at most, one attack per time step. As a consequence, the maximum possible number of attacks per time step is given by the number of searchers in the patch. As we assume that parasitoids always avoid superparasitism, the number of attacks is also limited by the number of available hosts on the patch.

At the end of each time step, the number of hosts attacked is subtracted from the number of susceptible hosts. In each patch, the N_{eff} attacks are assigned to an equal number of randomly chosen parasitoids among searchers in the patch. After that, migrants are identified according to the patch-leaving decision rule considered (see below). As a first approximation, we assume that differences between interpatch distances have a negligible effect on the traveling time. This is an acceptable assumption if we consider a small-scale environment when compared with the dispersal ability of the animals (Bernstein et al. 1988). Other more realistic scenarios can be envisaged, but we considered this beyond the scope of this first work. Traveling time is fixed at 2 time steps. During this time, migrants are absent from any patch and do not interfere with searching parasitoids. We also assume that parasitoids are unable to assess the quality of a patch before reaching it, and consequently, they are randomly distributed among patches. At the end of the migration period, migrant parasitoids become again searchers.

Patch-leaving decision rules

We consider, in the first part of our work, that animals use one of the following simple rules of thumb: fixed-number rules, fixed-time rules, or fixed-GUT rules. The parameter values used in the simulations of these simple rules are given in Table 1.

In the second part of our work, we consider more complex and realistic mechanisms. We define, based on Waage (1979), responsiveness as the tendency to stay in a patch. We assume that a parasitoid leaves its current patch when its responsiveness drops below zero. Parasitoids may use 3 sources of information concurrently (instead of a single one as in simple rules of thumb) to decide whether to leave a patch. The sources of information are the initial number of hosts on the patch (parasitoids determine this by detecting kairomone concentration, Shaltiel and Ayal 1998), the time they already spent on the patch, and the number of own ovipositions. Consequently, decision rules are characterized by 4 parameters affecting responsiveness. The initial responsiveness R_0 is set, when a parasitoid first arrives to patch, by ω and κ as a linear function of the host density, H , in the patch:

$$R_0 = \omega + \kappa H. \quad (3)$$

The host-density-independent component of the initial responsiveness is given by ω and sets the patch departure time for parasitoids entering an empty patch. The ratio of ω and κ is a measure of the influence of the initial host density on the tendency to stay on a patch: the higher the κ/ω ratio, the more the initial host density influences the patch-leaving decision. At each time step, the responsiveness of each parasitoid is updated, according to the rule being considered and the parasitoid's individual experience during this period. At the i th time step, the responsiveness of a given parasitoid, R_i , is calculated as:

$$R_i = R_{i-1} - \tau + I, \quad (4)$$

where τ is a parameter controlling the influence of the time spent in a patch. If the particular rule assumes the time spent in the patch has no influence, τ equals zero, else τ equals one. We consider that τ can take only these 2 values to limit the redundancy between rules. If all the other parameters describing the rule are decreased in absolute value, the influence of the time spent in the patch is increased. The parameter I controls the influence on responsiveness of each attack and is defined as following:

$$\begin{cases} I = \alpha \text{ if the parasitoid makes an attack during} \\ \quad \text{the current time step} \\ I = 0 \text{ otherwise} \end{cases}. \quad (5)$$

For incremental rules, α is positive. Therefore, each oviposition increases responsiveness and, thus, the patch residence time. For decremental rules, α is negative, and each attack decreases responsiveness and, thus, the patch residence time. Neutral rules are those in which attacks do not influence the patch residence time ($\alpha = 0$).

The different values used for parameters α , ω , τ , and κ are given in Table 2. Note that rules in which α and κ are equal to 0 correspond to fixed-time rules, and rules in which $\kappa = \tau = 0$ and $\alpha < 0$ correspond to fixed-number rules. To ensure that the rules are comparable across different environmental conditions, κ is scaled by the mean number of hosts per patch. The total number of parameter value combinations is 2178. However, some of these combinations lead to the same rule. For example, when the time spent in the patch has no influence ($\tau = 0$), the rule is the same for all values of $\alpha > 0$:

Table 1

Values of key parameters used for simple rules

	Single parasitoid	Parasitoid population of 50 individuals
Fixed number (number of attacks)	1–4 ^a 1–10 ^b	{2, 4, 6, ..., 198, 200}
Fixed time (time in a patch)	1–30	{5, 10, 15, ..., 95, 100}
Fixed GUT (time without finding a host)	1–13	{3, 6, 9, ..., 57, 60}

^a Uniform and random environments.

^b Aggregated environment.

parasitoids will never change patches and stay indefinitely in the first patch they enter. Therefore, we have removed some redundant combinations and retained 1585 combinations corresponding to 495 incremental rules, 100 neutral rules, and 990 decremental rules. Despite this selection, different combinations can lead to similar rules for some of the environmental conditions we have considered.

Environmental conditions

Environmental conditions in our model are characterized by the initial host distribution, the number of patches, and the number of parasitoids.

We consider uniform, random, and aggregated initial host distributions. In uniform environments, simulations start with all patches containing the same number of hosts. In random environments, the initial number of hosts in each patch is given by a Poisson distribution. In aggregated environments, the initial number of hosts in each patch is given by a negative binomial distribution with an aggregation parameter, k , equal to unity.

For simple rules, 3 conditions differing in the numbers of patches and of parasitoids are tested. These are a single parasitoid in an environment composed of an infinite number of patches (this is simulated by assuming a single patch whose number of hosts is reset each time the parasitoid "moves" to another patch), a single parasitoid in an environment comprising 20 patches, and a parasitoid population (50 individuals) in an environment comprising 20 patches. The parameter values defining the simulation conditions (summarized in Table 3) coincide with those considered by Iwasa et al. (1981).

For complex rules, a larger range of environmental conditions is tested. Four values for the number of patches (10, 20,

Table 2

Values of parameters used for the description of complex rules

Host-density independent component of the initial responsiveness (ω)	0, 5, 10, 15, 20, 30, 40, 60, 100
Host-density-dependent component of the initial responsiveness (κ)	(0, 1, 2, 4, 6, 8, 10, 15, 20, 30, 40)/ \bar{H} ^a
Influence of the time in the patch on the responsiveness (τ)	0, 1
Influence of attacks on the responsiveness (α)	–25, –20, –15, –10, –5, 0, 5, 10, 15, 20, 25

^a \bar{H} is the mean initial number of hosts per patch.

Table 3
Values of environmental parameters used for simulations with simple rules

	Infinite environment	Finite environment
Number of patches, Z	∞	20
Number of parasitoids, P	1	1 and 50
Initial mean number of hosts per patch, \bar{H}	$5 \times P$	$5 \times P$
Searching efficiency, Q	$0.25/\bar{H}$	$0.25/\bar{H}$
Traveling time (in time steps)	2	2
Mutual interference coefficient, m	—	0.3 (for $P = 50$)
Maximal length of the simulations (in time steps)	400	1000

50, and 100) and 6 values for the total number of parasitoids (1, 5, 10, 20, 50, and 100) are combined. In these simulations, the initial mean number of hosts per parasitoid is kept constant to allow comparison of results. Searching efficiency is standardized, so that for a single parasitoid in a patch containing the mean initial number of hosts, the probability of finding a host, in a single time step, is 0.2. Parameter values are summarized in Table 4. Environmental conditions for which the initial mean number of parasitoids per patch would be lower than 1 are not considered.

Representation of results

Simulations for every combination of rules and environmental conditions were repeated 100 times. In each simulation, we assume that all parasitoids use the same patch-leaving decision rule.

We compare the efficiency of the different rules of thumb measured as the total number of attacks performed by the parasitoids during a given length of time. For that, we first identify the most efficient rule for each kind (fixed number, fixed time, fixed GUT) and then compare across these 3 rules. Tukey–Kramer honestly significant difference tests are used for multiple mean comparisons.

The aim of this work is not to precisely determine which rule is optimal in a given environment but to investigate whether the difference of the influence of a given stimulus (oviposition on a host) could be explained by differences in environmental conditions. This is why we concentrate on the type of the most efficient rules, without looking into the precise parameter values used to set the rules. We explore the behavior of the more complex rules by first identifying the “good rules.” These are defined for a given time horizon and for given environmental conditions by using a criterion that allows to discriminate between rules but that takes into account the variance in rule efficiency due to the stochastic

Table 4
Values of environmental parameters used in simulations with complex rules

Number of parasitoids, P	1, 5, 10, 20, 50, 100
Number of patches, Z	10, 20, 50, 100
Initial mean number of hosts per patch, \bar{H}	$40 \times (P/Z)$
Searching efficiency, Q	$0.2/\bar{H}$
Traveling time (in time steps)	2
Mutual interference coefficient, m	0.3
Maximal length of the simulations (in time steps)	400

processes incorporated to the model. The rules are sorted according to the average (over 100 replicates) of the total number of attacks they lead to. Good rules is the set of consecutive rules, whose 90% confidence limits overlap that of the best rule. The best rule is the rule that, for the considered time horizon and environmental conditions, leads to the highest total number of attacks.

Invasibility analysis

The efficiency of the different rules is assessed by comparing simulations in which it was assumed that all individuals of the parasitoid population use the same patch-leaving decision rule. This ignores frequency-dependent processes. For example, mutual interference between parasitoids and modification of the healthy host distribution due to patch exploitation may affect the performance of the rules. Therefore, we carried out a series of numerical experiments to test whether frequency-dependent processes would alter the previously obtained results.

For these experiments, 51 environmental conditions (combination of a number of patches, a number of parasitoids, a host distribution and a time horizon) have been randomly chosen among the 128 used for testing complex rules in which the number of parasitoids is greater than 1 and good rules do not include the 3 types of rules (decremental, neutral, incremental) simultaneously. For each of these environmental conditions, we identify the most efficient rule of each type represented in the good rules and test it in an invasibility experiment. The 75 experiments consist of introducing into a population of residents using one of the previously identified “good rule” a single, mutant individual using each of the 1585 rules successively. We then compare the performance of the mutant to the performance of nonmutant individuals. This is done by calculating the mean difference (over 100 replicates) between the total number of attacks made by the mutant and the mean number of attacks made by nonmutants and comparing it to 0 (t -test, $\alpha = 0.05$). These confrontation experiments simulate the parasitoids’ behavior only during a single generation. However, we can consider that the results reveal the ability of the residents to withstand invasion by a mutant by assuming that parasitoids of the resident strategy form a stable system with their hosts.

RESULTS

Simple rules

A single parasitoid in an infinite environment

We first simulated a single parasitoid in an environment containing an infinite number of patches. We tested many fixed-number, fixed-GUT, and fixed-time rules in a uniform, a random, and an aggregated environment. As a consequence of the infinite number of patches, the overall value of the environment remains constant through time as does the long-term rate of attacks. The total number of attacks at a time horizon long enough as to ensure independence of the initial conditions is then a reliable estimate of rules efficiency.

The results were qualitatively in agreement with the analytical results obtained by Iwasa et al. (1981) under similar conditions. According to the environment, the most efficient rules belong to the following types: fixed number in a uniform environment, fixed time in a random environment, and fixed GUT in an aggregated environment (Figure 1). Our results also gave the relative performances of the different rules in a given environment. In the uniform environment, fixed-number rules performed only marginally better than fixed-time and fixed-GUT rules, whereas in random or aggregated environments

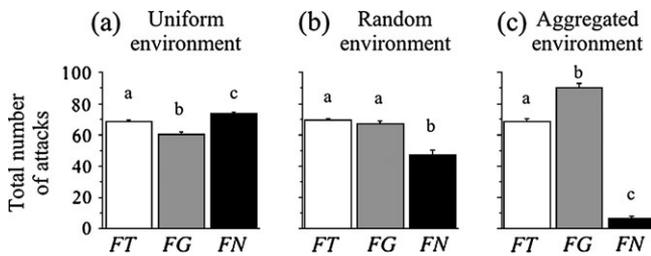


Figure 1

Relative efficiency of the different types of rule of thumb in the different environments for a single parasitoid foraging in an infinite number of patches. Diagrams show the number of attacks (over 100 repeats) performed by a parasitoid using the best rule of each type during 400 time steps (mean and 95% confidence interval). White bars are for fixed-time rules (FT), gray bars are for fixed-GUT rules (FG), and black bars are for fixed-number rules (FN). The same letter indicates that the total numbers of attacks are not significantly different ($\alpha = 0.05$). Parameter values used for these simulations are summarized in Tables 1 and 3.

fixed-number rule performed poorly in comparison. Fixed-time rules appeared to be intermediate, never clearly overperforming or underperforming compared with the other rules. Finally, fixed-GUT rules, although best adapted to aggregated environments, are also suited to other conditions.

A single parasitoid in a finite environment

We considered a single parasitoid foraging in a limited environment of 20 patches to test the influence of environment size.

With the number of patches now being finite, the overall value of the environment decreases with time as the patches are exploited by the parasitoid. Therefore, the efficiency of the different rules change with time. The performance of the best rule of each type (measured by the total number of attacks) for the different environments is shown in Figure 2. As expected, for a small number of time steps ($T = 100$), the results were similar to those obtained in infinite environments (compare Figures 1 and 2). For larger numbers of time steps, fixed-number rules became progressively less efficient, independent of the environment considered. In the aggregated environment, the superiority of fixed-gut rules over fixed-time rules decreases as simulation time progresses.

A parasitoid population in a finite environment

We simulated a parasitoid population of 50 individuals, all using the same patch-leaving decision rule. The environment consisted of 20 patches.

For random and uniform environments, the most efficient rule for each of the 3 types led to a similar number of attacks, independent of the number of time steps (Figure 3a,b). However, for intermediate and long simulations, fixed-number rules are in all cases significantly less efficient than the best rule, which is systematically a fixed-GUT rule. For the aggregated environment, fixed-GUT rules were somewhat more efficient than fixed-time and fixed-number rules for short ($T = 100$) and intermediate ($T = 600$) simulations (Figure 3c). However, for long simulations ($T = 1000$), the difference between fixed-time and fixed-GUT rules decreased. Relatively to the other types of rules, fixed-number rules became progressively less efficient with simulation time.

The rules so far tested have been simplistic, in the sense that they rely on a single source of information. This is not consistent with experimental results (see Van Alphen et al. 2003 for a review) showing that parasitoids are able to use more complex rules that combine several sources of information.

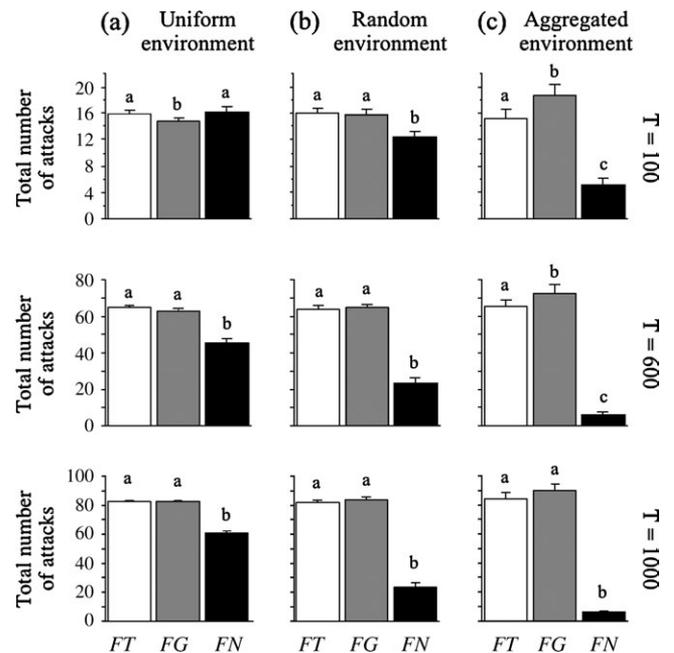


Figure 2

Relative efficiency of the different types of rule of thumb in the different environments for a single parasitoid foraging in an environment comprising 20 patches. Diagrams show the number of attacks (over 100 repeats) performed by a parasitoid using the best rule of each type over different times (mean and 95% confidence interval). White bars are for fixed-time rules (FT), gray bars are for fixed-GUT rules (FG), and black bars are for fixed-number rules (FN). The same letter indicates that the total numbers of attacks are not significantly different ($\alpha = 0.05$). Parameter values used for these simulations are summarized in Tables 1 and 3.

Complex rules

For short simulations in uniform environments (Figure 4), where a limited number of parasitoids search in a large number of patches, the best rules involve a decremental mechanism. The probability of a parasitoid entering an already visited patch is very low. These conditions are similar to those considered by Iwasa et al. (1981). In conditions with contrasting environments, such as many parasitoids searching in few patches, the best rules were incremental. Incremental rules became progressively more efficient, compared with the other rules, at longer simulation times (Figure 4a).

The results obtained for random environments (Figure 4b) were similar to those observed in uniform environments, particularly concerning incremental rules. However, in environments with a restricted number of parasitoids and a large number of patches, the advantage of decremental rules was much less evident than for uniform environments.

For aggregated environments (Figure 4c), conditions in which decremental rules are more efficient than incremental ones were even more restrictive than for random environments. Independent of simulation time, incremental rules performed at least as well as other types of rules for most environmental conditions. For long simulation times, the best rule for each type resulted in equivalent performances.

Invasibility analysis

Among the 75 experiments, the nonmutant rule is incremental in 35 cases, neutral in 25 cases, and decremental in 15 cases. This distribution matches the proportion of cases in which each type of rule is represented in good rules ($\chi^2 = 0.146$,

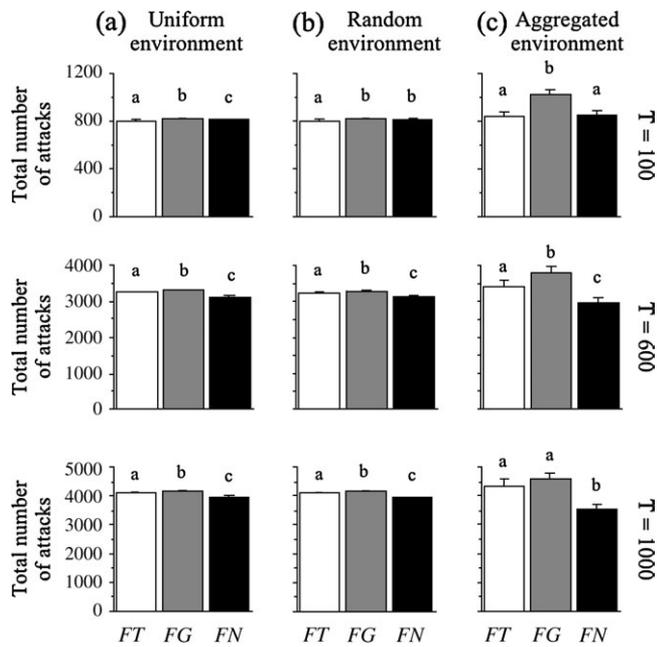


Figure 3
Relative efficiency of the different types of rule of thumb in the different environments for a parasitoid population foraging in an environment comprising 20 patches. Diagrams show the number of attacks (over 100 repeats) performed by the parasitoid population using the best rule of each type over different times (mean and 95% confidence interval). White bars are for fixed-time rules (FT), gray bars are for fixed-GUT rules (FG), and black bars are for fixed-number rules (FN). The same letter indicates that the total numbers of attacks are not significantly different ($\alpha = 0.05$). Parameter values used for these simulations are summarized in Tables 1 and 3.

$P = 0.930$). The results show that in no case a mutant using a type of rule that is not included in the good rules could significantly outperform a resident good rule. Conversely, in many cases, the resident could not outperform the challenger and both resident and mutant coexisted at least for very low densities of the mutant. When the resident strategy was incremental, a decremental mutant could persist in 29 invasibility experiments over 35. When the resident strategy was decremental, an incremental mutant could persist in only 7 invasibility experiments over 15. The difference of susceptibility to an invasion leading to coexistence between types of rules is highly significant (Fisher's exact test, $P = 0.016$).

DISCUSSION

In this study, we compare the performance of different kinds of patch-leaving decision rules parasitoids might use when foraging for hosts in a patchy environment. For this, we use an individual-based model in which we consider different environmental conditions and a large number of possible rules. These rules rely on proximal cues that provide parasitoids with information on which they base their decision. We show that environmental conditions change the way parasitoids should use the information, particularly information provided by ovipositions. When the parasitism rate is low (i.e., if the number of patches is large and the number of parasitoids low), independent of the initial host distribution, a parasitoid relying on other sources of information in addition to ovipositions, such as chemical or visual cues of host density, would maximize its searching success by using a decremental leaving rule. Otherwise, each oviposition should increase the ten-

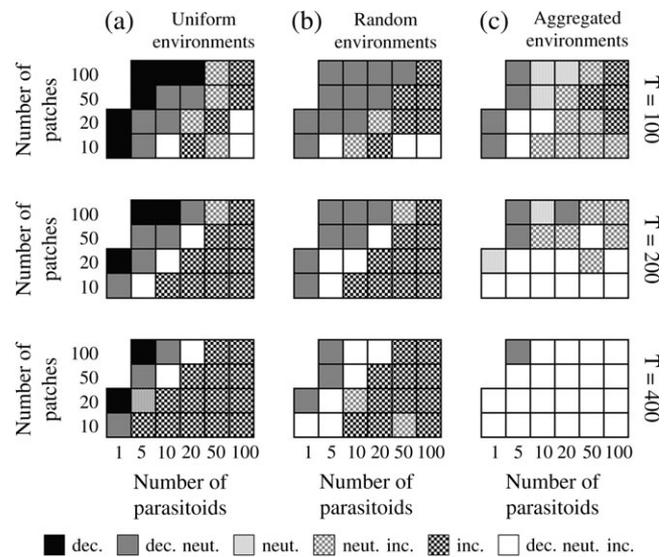


Figure 4
Types of mechanism (incremental, neutral, and decremental) represented in the good rules (see main text) for the different environmental conditions. Parameter values used for these simulations are summarized in Tables 2 and 4.

dency for the animal to stay in the patch (i.e., it should use an incremental rule).

Analytical work by Iwasa et al. (1981) identified the simple rules of thumb that perform best depending on host distribution. Our simulations, carried out in similar conditions, qualitatively confirm their conclusions and show that quantitative differences in performance depend strongly on host distribution. For example, fixed-GUT rules (which rely on an incremental mechanism) give a clear advantage for an aggregated distribution of resources. In underdispersed environments, fixed-time rules perform only marginally better, with the different rules leading to equivalent results. Generally, fixed-time and fixed-GUT rules perform adequately in a variety of circumstances. This suggests that parasitoids foraging in changing environments and unable to modify their rule of thumb should adopt either a fixed-time or fixed-GUT leaving rule.

In their model, Iwasa et al. (1981) make 2 key assumptions. First, they assume that a single forager exploits the environment and that changes in host availability are restricted to those that are the consequence of the foraging activity of the parasitoid. Second, they assume that the number of patches is so large that the probability of re-entering an already visited patch is negligible. This guarantees that a forager entering a patch will find it in a prime state. In these conditions, and if the environment is uniform (i.e., all patches have the same initial value), the forager knows exactly, at any time, the quantity of resources remaining in its current patch and the quantity it will find if it moves to another patch. Consequently, it can optimize its gains by using a decision rule based only on the number of attacks already performed in the patch. However, if one of these 2 assumptions is relaxed, it can be expected that fixed-number rules become progressively less suitable. We have confirmed this by showing how the relative efficiency of fixed-number rules rapidly decreases if the size of the environment is limited or the number of foragers is large.

Driessen et al. (1995) and Driessen and Bernstein (1999) suggested that, independent of the host distribution, decremental rules are well adapted provided that parasitoids take kairomone concentration into account in their patch-leaving decisions. Our results are somewhat in contradiction with this

hypothesis by revealing cases in which decremental rules are outperformed by other rules, even if the former include kairomone concentration in the decision mechanism. As Iwasa et al. (1981), Driessen et al. (1995) considered a parasitoid foraging on its own and ignored the effect of other parasitoids on patch depletion. They also assumed that local kairomone concentration is a reliable indicator of the patch value when the parasitoid arrives at the patch. However, Shaltiel and Ayal (1998) and Vos et al. (1998) showed that this is not always the case. Host availability or kairomone concentration can change independently due to high migration or predation rates or climatic factors, such as precipitation. Although none of these factors is included in our simulations, we can conjecture that kairomone concentration is not always a good indicator of the actual number of hosts available to the parasitoid. This is so because when a parasitoid enters a patch, the number of available hosts may differ from the initial number due to previous visits by itself or by conspecifics. The probability of a parasitoid entering an already visited patch increases as the total number of patches decreases, the number of parasitoids increases, or the period of parasitoid activity lengthens.

Our results suggest that the conditions in which decremental rules are well adapted are restricted. However, experimental work has shown that the number of parasitoid species using decremental mechanisms is not negligible (Driessen and Bernstein 1999; Van Alphen et al. 2003; Wajnberg et al. 2003; Wang and Keller 2003; Boivin et al. 2004; Wajnberg 2006). Several factors may explain this apparent contradiction. First, the conditions we have identified as favorable to decremental mechanisms, that is, environments with a large number of host patches and a low parasitoid density, are probably not rare in natural conditions. For example, the low rate of parasitism of about 3% observed in *Ectomyelois ceratoniae* in natural conditions (Schneider 2003) suggests a low density of its parasitoid, *V. canescens*, compared with the number of available hosts. Driessen et al. (1995) showed that *V. canescens* adopts a decremental rule.

Second, the reliability in assessing the initial patch value is a key factor for parasitoids using a countdown mechanism. We assume that the initial tendency to stay in a patch is determined by the kairomone concentration that is proportional to the initial density of hosts. As already pointed out, the reliability of the information given by kairomone concentration could be uncertain. Previous experimental work (Shaltiel and Ayal 1998; Tentelier et al. 2005) suggested that some parasitoids are probably able to evaluate more precisely the patch value when entering the patch than our virtual parasitoids.

Third, the patch-leaving decision rules assumed in our model involve 3 sources of information. This results in rules that are more realistic than those previously considered in theoretical studies.

However, experimental work has shown that parasitoids can use more complex patch-leaving decision rules, combining a larger range of proximal cues. Encounters with parasitized hosts have been identified as increasing the tendency to leave a patch (Sugimoto et al. 1987; Hemerik et al. 1993; Wajnberg et al. 1999, 2000, 2003). Some parasitoids are also able to avoid visiting patches that have been already exploited (by themselves or conspecifics) by detecting chemical marks (see Bernstein and Driessen 1996 for a review) or host products, such as faeces, silken threads, or exuviae (Ohara et al. 2003) deposited during previous visits. The number of patches already visited has also been identified as a factor increasing the tendency of many parasitoid species to leave a patch (Vos et al. 1998; Wajnberg et al. 1999; Tenhumberg, Keller, Possingham, and Tyre 2001; Tenhumberg, Keller, and Possingham 2001). Encounters with conspecifics, which is only indirectly included in our model through mutual interference, can have a direct effect

on the tendency to leave a patch, independent of the effect of parasitoid density on the probability of attack (Visser et al. 1992; Wajnberg et al. 2004). All these factors allow parasitoids to gain more reliable information on the actual number of hosts available on a given patch and should widen the environmental conditions for which decremental mechanisms are preferable.

Fourth, we assumed in our model that hosts are excluded from the pool of available hosts as soon as they have been parasitized. Therefore, we assumed that the parasitoids could discriminate between parasitized and healthy hosts and, thus, never superparasitize. This is observed in certain parasitoid species but not in others (Van Lenteren 1981). Rosenheim and Mangel (1994) demonstrated theoretically that parasitoids that cannot discriminate perfectly between healthy and parasitized hosts should leave the patch earlier to reduce the risk of superparasitism. Tenhumberg, Keller, Possingham, and Tyre (2001) showed that a decremental mechanism could be a behavioral response for these species.

Finally, the results of our numerical invasion experiments raise 2 important points. First, our findings on the relationship between the environmental conditions and the best way to use information provided by ovipositions are robust in face of frequency-dependent processes in the sense that mutants using a type of rules not included in the good rules never outperform a resident good rule. Second, many conditions were found in which a good rule could be invaded by an alternative rule but without the former being replaced by the latter, (i.e., leading to the coexistence of more than one type of rules). These results suggest that in many conditions, mixed patch-leaving strategies might be evolutionary stable. This topic deserves full exploration, but this is beyond the aims of the present work. Furthermore incremental rules seem to be less resistant to an invasion leading to the coexistence of different types of rules than decremental ones. This suggests that often in situations in which incremental rules are more efficient than decremental ones, individuals using a decremental rule could persist in a mixed population, at least at low numbers. Beauchamp (2000) also concluded to the persistence of different patch-leaving decision rules in the same population of foragers, but a direct comparison with our results is difficult as the rules considered by this author rely on learning process and do not take proximal cues into account.

Patch-leaving decisions are a key component of parasitoid behavior, which links individual processes to population-level phenomena. Two main approaches have, until now, been used to analyze the diversity of patch-leaving rules used by parasitoids. Adaptive studies have explored the rules animals are expected to use depending on environmental conditions. This approach has privileged mathematical tractability and sacrificed biological realism. The models assume simpler rules than those used by parasitoids and simpler environmental conditions than found in the wild. Conversely, studies aiming to determine the proximate cues and patch-leaving mechanisms used by parasitoids rely on statistical approaches. This results in realistic descriptions of animal behavior but generally ignores evolutionary processes. Our study has used individual-based simulations to try to incorporate both approaches. This work points out at the pitfalls of sacrificing biological realism for the sake of mathematical tractability and provides a simple explanation of the diversity of patch-leaving decisions used by foragers to exploit patchily distributed resources. These decisions are based on the reliability of information provided by different cues.

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