Behav Ecol Sociobiol (2005) 58: 208–217
DOI 10.1007/s00265-004-0895-1

ORIGINAL ARTICLE

Yannick Outreman · Anne Le Ralec · Eric Wajnberg · Jean-Sébastien Pierre

Effects of within- and among-patch experiences on the patch-leaving decision rules in an insect parasitoid

Received: 2 August 2004 / Revised: 9 November 2004 / Accepted: 29 November 2004 / Published online: 26 February 2005

Abstract The present study aimed to address how an insect parasitoid makes patch-departure decisions from various types of host patches and how previous patch experiences in the environment modify this decision-making process. Experiments were done with the parasitic wasp *Aphidius rhopalosiphi* attacking the grain aphid *Sitobion avenae*. In the experiments, wasps were observed in a laboratory environment containing several patches of various host densities, and behavioural records were analysed using a Cox's proportional hazards model. Consideration of the effect of the within-patch experience gave a classic pattern of patch-leaving decision rules in parasitoids: *A. rhopalosiphi* used local information on host quality (i.e. numbers of ovipositions or rejections) and availability (i.e. patch density) to determine departure decision. However, consideration of previous patch experiences provided evidence that these departure rules are fundamentally dynamic, responding to the physiological state of the animal and the information it has about its environment. Results showed that *A. rhopalosiphi* decreased its tendency to leave the visited patch after an oviposition. However, when a female has already laid several other eggs in the environment, such an incremental mechanism gradually switched to a decremental one. Hence, *A. rhopalosiphi* responded to egg-load depletion by leaving the visited patches sooner and by depositing a smaller number of eggs in those patches, which probably led to a decreased level of superparasitism. Results also indicated that previous experiences enabled wasps to estimate spatial host distribution and then to adjust their behavioural decisions accordingly. Thus, *A. rhopalosiphi* was shown to adjust its patch residence time according to the quality and the number of the patches previously visited. These proximate mechanistic rules adopted by *A. rhopalosiphi* females are discussed in the context of general predictions from optimality models.

Keywords Multi-patch environment · Optimal foraging · Parasitoid · Patch-departure mechanism · Phenotypic plasticity

Introduction

Female parasitoids lay eggs on, in, or near host insects. Broadly speaking, lifetime reproductive success can therefore be limited by the number of eggs available for oviposition or by the time available for locating hosts (Heimpel and Rosenheim 1998). Hosts of many parasitoids are distributed non-randomly in the environment and often occur in discrete patches (Godfray 1994). Under such conditions, parasitic wasps must adjust their patch-residence time in order to maximise their progeny production. For this, parasitoids have to allocate accurately their foraging time among the different patches available in the habitat. This question has received considerable interest in the last few decades (Wajnberg et al. 1999; van Alphen et al. 2003). A number of theoretical models attempt to predict the patch time allocation that would ultimately maximise an individual's fitness. The most well-known model is based on the marginal value theorem developed by Charnov (1976). Ignoring possible complications due to egg-load limitation, this theorem suggests that the optimum time to leave a patch is when the instantaneous rate of fitness gain drops to the

Communicated by D. Gwynne

Y. Outreman (✉) · A. Le Ralec
Laboratoire Ecologie et Sciences Phytosanitaires, UMR
INRA-Agrocampus Rennes BiO3P,
65 rue de Saint-Brieuc CS 84215,
35042 Rennes Cedex, France
e-mail: yannick.outreman@rennes.inra.fr
Tel.: +33-2-23485568
Fax: +33-2-23485170

E. Wajnberg
Ecologie Comportementale des Parasitoïdes, INRA,
400 Route des Chappes,
BP 167 06903 Sophia Antipolis Cedex, France

J.-S. Pierre
UMR 6552, Université de Rennes I,
Campus Beaulieu,
35042 Rennes Cedex, France

maximum average rate that can be achieved in the environment. Whereas Charnov's model predicts general phenomena, it makes simplified assumptions about the constraints of foragers. For instance, animals are supposed to have a complete knowledge of the abundance and distribution of hosts in the habitat. Such an assumption is obviously unrealistic, especially in an unpredictable environment (Oaten 1977; Green 1980, 1984), and there is thus a need to link the functional, optimality predictions with the real proximate mechanisms involved (van Alphen and Vet 1986).

Several authors have long tried to understand the mechanistic rules, so-called rules of thumb, that animals might use to adjust their patch-residence time in an optimal way (Godfray and Shimada 1999). Waage (1979) proposed a mechanism determining departure from host patches for the moth parasitoid *Venturia canescens*. His model suggests that parasitic wasps enter a patch with an initial tendency to remain on it (i.e. responsiveness). This tendency is determined by the concentration of kairomones that is related to host density. When time elapses, the responsiveness decays at a constant rate down to a threshold at which the patch is abandoned. In this mechanistic model, each oviposition has an incremental influence on the current level of responsiveness and thereby increases patch-residence time. According to this model, the time spent on a patch should be influenced by host density. Such an incremental mechanism has been observed in several parasitoid species (see van Alphen et al. 2003 for a review). In some cases, however, an oviposition may have a decreasing effect on the tendency to remain on the patch. Such a decremental effect, a so-called "count-down mechanism" (Driessen et al. 1995), has been observed in a number of insect parasitoids (see van Alphen et al. 2003 for a review). This decremental patch-leaving mechanism is predicted to be adaptive when host patches are small (Strand and Vinson 1982) or when hosts are uniformly distributed (Iwasa et al. 1981; Driessen et al. 1995) or when the forager has reliable information about the quality of the visited patch (Driessen and Bernstein 1999). Finally, other authors have integrated the effect of encounters with already-parasitised hosts in these mechanistic models (for a review, see van Alphen et al. 2003). These models show that such encounters usually have a decremental effect on the responsiveness of the female to the patch (van Alphen and Vet 1986; van Alphen 1993).

Although prompted by experimental observations, Waage's model and variants are only a-priori hypotheses (Godfray 1994). Haccou et al. (1991) emphasised that such studies of empirical data based on a-priori models are problematic since only qualitative comparisons can be made between model predictions and observations. An alternative approach is to deduce the behavioural rule from the data with minimal prior assumptions. For this, several authors (Hemerik et al. 1993; van Roermund et al. 1994; van Steenis et al. 1996; Vos et al. 1998; Driessen and Bernstein 1999; Wajnberg et al. 1999) used Cox's (1972) proportional hazards model. From experimental data, the Cox's model quantitatively assesses the relative importance of different factors included in the process of patch-leaving decision. This approach can then accurately predict which patch-leaving rules are used in a specific situation. Most of the studies cited above concentrate on the effect of the experience acquired by the foraging parasitoids within a patch on their decision to leave it. Although these studies determine patch-departure mechanisms, they have limitations, such as ignoring the state of the animal and the information it has about the environment. Patch time-allocation strategy adopted by a parasitoid might indeed be affected by its previous foraging experiences in its habitat. Because parasitic wasps usually have a limited knowledge of the actual spatial host and patch distribution, previous foraging experiences could allow foragers to estimate spatial host distribution and to adjust their behavioural decisions accordingly (Oaten 1977). Information gathered on previously visited patches may provide a proximate mechanism to optimise patch-leaving decision rules (Vos et al. 1998). Previous foraging experiences in the prospected environment could also induce some variations in the physiological state of the wasp. Particularly, the number of eggs available in the female's ovaries decline during foraging and this may exert an important influence on the proximate mechanisms of patch-leaving decision.

Consequently, it is highly probable that patch-leaving decision rules in parasitoids are affected not only by within-patch experience but also by previous patch experiences in a habitat. This issue was addressed here by analysing how the parasitoid *Aphidius rhopalosiphi* De Stefani Perez (Hymenoptera: Braconidae), attacking the grain aphid *Sitobion avenae* Fabricius (Homoptera: Aphidinae), makes patch-departure decisions from various types of host patches, and how previous experiences in the environment modify its decision-making process. To achieve this, foraging parasitic wasps were observed in an environment containing several patches of various host densities, and behavioural records were analysed using a Cox's proportional hazards model.

Methods

Parasitoids and hosts

A. rhopalosiphi is a solitary parasitoid of the main aphid pests of cereal crops including the grain aphid, *S. avenae* (Krespi et al. 1994). *S. avenae* has a highly clumped distribution on cereal crops and, hence, *A. rhopalosiphi* faces discrete patches with a rather high variance in the number of individuals (Dedryver 1987). The potential fecundity of *A. rhopalosiphi* is about 140 ovocytes after the emergence (Shirota et al. 1983) and the average life span of adults is 11 days (Krespi 1990). *A. rhopalosiphi* used for these experiments originated from individuals captured in June 1996 in Rennes, France, which were reared in the laboratory on a mixed-age culture of *S. avenae*. The *S. avenae* strain, originating from one parthenogenetic female collected in 1990 in the same area, was reared on winter wheat, *Triticum aestivum*, cv. "Arminda". Colonies of both *A. rhopalosiphi* and *S. avenae* were maintained in climate rooms at 20°C, 70±10% RH, and 16L:8D photoperiod. Only second-instar *S. avenae* were used as hosts in experiments. To obtain females for experiments, mummies were collected from culture and placed individually in gelatine capsules. Newly emerged females were enclosed in plastic tubes (22×1 cm) containing moistened cotton, droplets of honey and one male for mating. Females were used only once. Just prior to each replicate, 1-day-old females were allowed to oviposit in three aphids placed on a wheat leaf. This allowed the wasp to gain experience in host handling and to reduce the possibility of any behavioural traits associated with first host encounters that might affect its search effort.

Experimental set-up

To investigate the effects of both previous experiences in the environment and within-patch experience on the patch-leaving decision rules, the foraging behaviour of individual *A. rhopalosiphi* females was observed in a glass cage (40×30×50 cm) containing several *S. avenae*-infested wheat plants. The set-up consisted of eight wheat plants, each containing only one leaf (about 15 cm height), placed in two parallel rows. Plants were 10 cm apart. Two plants were inoculated with 2, 2 with 6 and 2 with 12 unparasitised larvae of *S. avenae*; the 2 remaining plants were not infested. Such patch-density range is commonly encountered by *A. rhopalosiphi* females under natural conditions (Dedryver 1987). Plants were inoculated 3 h before the test. For each trial, the eight plants were randomly placed in the experimental set-up. Each of these eight plants was considered to be a patch.

The experimental procedure consisted of introducing one female in the centre of the laboratory cage. Observation began when the wasp entered and started to search on the first visited plant. The foraging behaviour of the individual females was observed and recorded continuously using the digital event-recorder "The Observer" (basic version 3.0 for Windows, Noldus Information Technology, Wageningen, The Netherlands). The beginning and the end of the following behaviours were recorded with an accuracy of 0.1 s: moving off or onto a patch, searching on a patch, standing still, preening, encountering and handling a host. In our experimental conditions, parasitoids were free to leave a patch by flying and no leaving by walking was observed. *A. rhopalosiphi* females adopted a particular behaviour before leaving a patch by flying. They stood still on the board of the leaf and took off a few seconds later. Such a particular behaviour was defined as the "patch-leaving event". However, females sometimes took off and subsequently relanded on that same plant (134 patch visits among the 774 studied). Females landed back on the same plant in two different situations. In most of the cases (123 out of the 134 immediate patch returns), a "patch-leaving event" was observed and the wasp simply re-landed on the same plant. This case was considered to be a new patch visit. Sometimes, however, hosts reacted to an attack, and this induced the wasps to fall down from the leaf before returning immediately to that plant by flying. In this case, these short excursions off the patch were not taken into account and their duration was included within the same patch visit. Patch-residence time was defined as the total time between entering and leaving the current patch by flying. In the present study, a host encounter was considered when a female stopped its searching activity after both location and contact with an aphid. During an encounter, the parasitoid displayed both antennal tapping and/or ovipositor stabbing behaviour. Piercing the skin of the encountered aphid with the ovipositor was interpreted and counted as an oviposition. Because *A. rhopalosiphi* is not able to recognise freshly parasitised hosts (Outreman et al. 2001a), females could accept for oviposition aphids that they have already parasitised. Conversely, any host encounter that did not lead to a stabbing behaviour was recorded as a host rejection. Attacked hosts were not replaced during the experiment (i.e. the patches suffered a continuous depletion). Finally, aphids could exude a small drop of waxy fluid from cornicles in response to the parasitoid attack. The sticky and hardening consistency of this secretion can glue the wasp's ovipositor or antenna during attack. This event, generally followed by the preening of the affected organ, was also recorded and termed "trapping".

When *A. rhopalosiphi* left a patch, it usually landed on the cage before resuming searching for a new patch. Thus, an observation consisted of a number of "on-patch" and "off-patch" bouts. The occurrence of these excursions outside the host patches presented the problem of how to define the end of an experiment. Usually, an arbitrary criterion is used in studies on patch-time allocation by parasitic wasps. Here, a replicate was terminated either after the parasitoid had visited all the eight patches or after 2 h of continuous observation, except when the female was still on a patch. In this last case, the replicate was terminated when she took off from that patch. Fifty-two females were tested in this experiment.

Cox's proportional hazards model

General model

A thorough description of the proportional hazards model (Cox 1972) can be found in Collett (1994). This model is formulated in terms of hazard rate. In the present context, this represented the probability per unit of time that a parasitic wasp leaves the visited patch, given that it is still on it (Haccou et al. 1991). The Cox's model assumes that the patch-leaving tendency is the product of a basic tendency to leave the patch (i.e. the baseline hazard) and a factor representing the joint effect of all the explanatory variables taken into account (i.e. the covariates). The model may be written as:

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

in which $h(t;z)$ is the hazard rate, $h_0(t)$ the baseline hazard, t the time elapsed since the female entered the current patch, and β_i the regression coefficients that give the relative contributions of the p covariates $z_i(t)$. A quantitative measure of the effect of any particular variable is given by the expression $\exp\{\Sigma\beta_i z_i\}$, the hazard ratio. If the hazard ratio is lower than 1, the female's patch-leaving tendency is reduced while a hazard ratio greater than 1 increased this tendency.

Covariates tested in our model

As pointed out by Haccou et al. (1991), it is unfeasible to consider all observable behavioural events that occur during the foraging behaviour in order to understand patch-leaving decision rules because this set would be obviously too large. Thus, the selection of covariates for the model was an important step in the analysis. These covariates were classified into two distinct groups. First, covariates related to the experience gained within the current patch were considered. Patch density, the number of ovipositions and host rejections, and their instantaneous rates are generally presumed to be important in patch-leaving models. Only the effects of oviposition and rejection rates up to three preceding ovipositions were tested in order to reduce the number of parameters to estimate. In addition, the number of "trappings" during the patch use was also included in the model. The patch density was added as fixed categorical covariate; the case corresponding to an empty patch was arbitrarily assumed to be the reference level corresponding to the baseline hazard with parameters set to zero. Second, a set of factors has been incorporated in the model to find how previous patch experiences affect the leaving tendency in parasitoids. Among these variables, the total number of ovipositions since the beginning of the experiment was considered in order to test the effect of physiological changes (i.e. egg-load depletion) on the patch-leaving decision in *A. rhopalosiphi*. Precise details about the explanatory variables initially included in the model are given in Table 1.

Statistical analysis

The purpose of the model was to estimate the influence of these covariates on the patch-leaving tendency in *A. rhopalosiphi* under all the conditions tested. For this, the effect of each variable and the overall significance of the fitting model were assessed using likelihood ratio tests (Collett 1994). Similar in Wajnberg et al. (1999), this test was used through an iterative procedure to identify the parameters having a significant influence on the females' patch-leaving tendency. In order to test possible interactions between factors, multiple pairs of covariates were included in the model. The adequacy of the final fitted model can be assessed by making residual plots. This showed that nothing was amiss. Thus, the final model was considered to properly describe the patch-leaving mechanisms used by *A. rhopalosiphi* females under the conditions tested. All computations were done with S-plus statistical software (MathSoft, Cambridge, Mass.).

Table 1 List of the covariates tested for their effect on the patch-leaving tendency of the parasitoid *Aphidius rhopalosiphi* foraging in a multi-patch environment containing several host patches of various densities of the grain aphid, *Sitobion avenae*[*T* time-dependent covariate (with values that can change between entering and leaving the current patch); *F* fixed covariate (with values that cannot change between entering and leaving the current patch)]. All these covariates were considered as quantitative except both the density of the current patch and the quality of the previously visited patches coded as factors

Covariates relevant to the within-patch experience
Density of the current patch (F)
Number of ovipositions on the current patch (T)
Number of host rejections on the current patch (T)
Number of "trappings" by cornicle secretion on the current patch (T)
Oviposition rate (−1): inverse of the time between the last and penultimate ovipositions (T)
Oviposition rate (−2): inverse of the time between the penultimate and antepenultimate ovipositions (T)
Oviposition rate (−3): inverse of the time between the antepenultimate and fourth preceding ovipositions (T)
Rejection rate (−1): total number of host rejections since the last oviposition divided by the time spent foraging since this oviposition (T)
Rejection rate (−2): total number of rejections since the penultimate oviposition divided by the time spent foraging since this oviposition (T)
Rejection rate (−3): total number of rejections since the antepenultimate oviposition divided by the time spent foraging since this oviposition (T)
Covariates relevant to the experience on the previously visited patches
Total number of previous patch visits (F)
Quality of the last visited patch (F), coded as follows:
0: if the last patch contained 0 or 2 hosts, or if it had already been visited or both
1: if the last patch contained 6 or 12 hosts and it had never been visited before
Quality of the penultimate visited patch (F) (coded as above)
Quality of the antepenultimate visited patch (F) (coded as above)
Number of previous visits to the current patch (F)
Number of ovipositions in the last visited patch (F)
Total number of ovipositions since the beginning of the experiment (T)

For graphical representation of the results, cumulative leaving-tendency functions were plotted for each level of the corresponding covariate (for details on estimation of cumulative leaving tendencies at different factor levels, see Kalbfleisch and Prentice 1980).

Results

Among the eight patches placed in the experimental arena, about 5.86±1.99 patches (mean±SD) were visited by the parasitic wasps. A total of 774 patch visits was observed. The fitting procedure led to a model including

Table 2 Estimated regression coefficients (β), standard errors (SE) and hazard ratios exp(β) for covariates that have a significant effect (P-value<0.05) on the patch-leaving tendency of *Aphidius rhopalosiphi* foraging in a multi-patch environment containing several host patches of various densities of the grain aphid, *Sitobion avenae*. χ^2 corresponds to the likelihood ratio tests. The overall significance of the fitting model: χ^2=686, *df*=14, P-value <0.001

	β	SE (β)	exp(β)	χ^2 (*df*)	P-value
Effect of the within-patch experience					
Density of the current patch					
Patch with no hosts	0.000	-	1.000	15.63 (3)	<0.005
Patch with 2 hosts	−0.224	0.1186	0.798		
Patch with 6 hosts	−0.355	0.1263	0.708		
Patch with 12 hosts	−0.518	0.1337	0.595		
Number of ovipositions on the current patch (1)	−0.271	0.0318	0.762	80.81 (1)	<0.001
Number of host rejections on the current patch (2)	0.075	0.0106	1.077	51.03 (1)	<0.001
Number of "trappings" by cornicle secretions on the current patch (3)	0.119	0.0364	1.127	10.69 (1)	<0.005
Oviposition rate one step backward	−3.559	0.9881	0.028	16.28 (1)	<0.001
Rejection rate one step backward	−2.510	0.9466	0.081	8.07 (1)	<0.005
Effect of the experiences on previously visited patches					
Total number of previous patch visits	0.016	0.0069	1.016	5.20 (1)	0.023
Quality of the last visited patch					
The last patch contained 0 or 2 hosts, or/and it had already been visited	0.000	–	1.000	16.52 (1)	<0.001
The last patch contained 6 or 12 hosts and it had never been visited before	−0.352	0.0972	0.703		
Number of visits to the current patch	0.236	0.0254	1.266	83.04 (1)	<0.001
Total number of ovipositions (4)	0.019	0.0033	1.020	34.12 (1)	<0.001
Pairwise interactions					
Interaction (1)∗(4)	0.002	0.0008	1.002	10.38 (1)	<0.005
Interaction (2)∗(3)	0.013	0.029	1.013	16.78 (1)	<0.001

12 parameters. Table 2 gives the estimated effect of all covariates having a significant influence on the patch-leaving tendency of *A. rhopalosiphi*.

Effects of within-patch experience

During the intra-patch foraging process, some factors had a strong influence on the decision of females to leave the current patch. Host density in the visited patch significantly affected patch residence time in *A. rhopalosiphi* (see Table 2). This effect is visualised on Fig. 1, representing the cumulative leaving tendencies on patches containing different numbers of hosts. *A. rhopalosiphi* had a higher leaving tendency on the low-density patches than on high-density ones.

During the experiment, an average of 93.49±40.51 host rejections and 36.27±13.46 ovipositions per wasp were observed. Thus, approximately 30% of the initial egg-load of the foragers was used during the experiment, suggesting significant egg-load depletion. According to results shown in Table 2, every oviposition in a given patch multiplied the chance per time unit that the wasp left that patch by a factor of 0.762. This indicates that *A. rhopalosiphi* females reduced their tendency to leave a patch after each oviposition. Conversely, the rejection of an aphid led to an increase in the patch-leaving tendency by a factor of 1.077. Observations showed that host rejections were induced by defensive behaviour of the hosts. Females rejected aphids that either exhibited mechanical defensive response during attack (i.e. quick motions of body and legs or escape reactions by walking) or had dried cornicle secretion on their body. Once emitted, this secretion rapidly solidified in the air, remaining on the tips of the cornicles, and hosts bearing dried secretion on their body repelled wasps. Finally, each time this secretion glued the wasp's ovipositor or antenna during an attack (wasps were trapped by cornicle secretions about 2.60±1.34 times during the test),

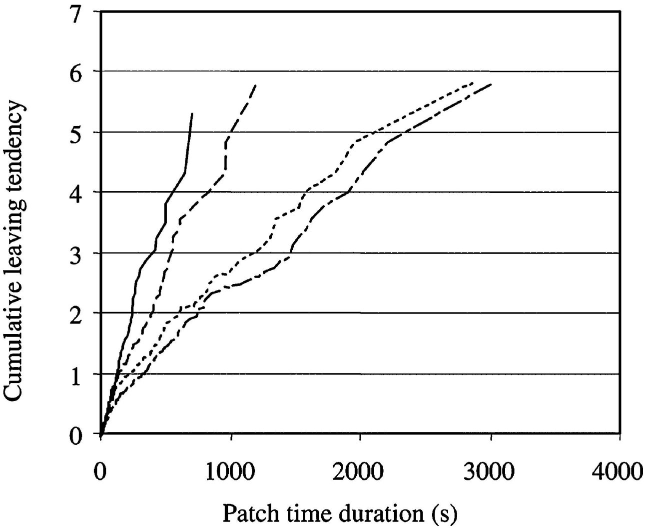

Fig. 1 Estimated cumulative patch-leaving tendency of the parasitoid *Aphidius rhopalosiphi* on wheat leaves containing 0 (——), 2 (— —), 6 (—-) or 12 (—-) larvae of the grain aphid *Sitobion avenae*, as hosts

its tendency to leave the patch significantly increased (see Table 2).

The most recent experienced oviposition and rejection rates also had a significant effect on the patch-leaving tendency. The higher the one step backwards oviposition rate, the lower the leaving tendency. Rejection rates up to the preceding oviposition also had a decreasing effect on the patch-leaving tendency. Thus, when there was a rapid succession of rejections since the previous oviposition, the effect of each host rejection on the leaving tendency was reduced or possibly reversed. Let N_r be the number of host rejections during the current visit, and R_1 the value of the rejection rates one step backwards in time at time t. According to eqn. 1, if after a host rejection the hazard ratio $\exp\{0.075\times N_r - 2.510\times R_1\}$ is less than 1, then this host rejection decreases the leaving tendency. From our data, only 495 out of 7,618 (i.e. 6.5%) rejection rates estimated reversed the negative host rejection effect on patch residence time. Therefore, the host rejection rate one step backwards in time essentially had a reducing, and rarely reversing, effect on the increase in leaving tendency induced by each host rejection.

Effect of experiences from previously visited patches

Results have shown that there was a significant variation in patch residence time according to the experience acquired on previously visited patches (see Table 2). The number of previous patch visits had an influence on the leaving tendency. Each new patch entry led to a weak increase in this tendency (here, by a factor of 1.016). The patch-residence time in *A. rhopalosiphi* was also significantly affected by the quality of the last-visited patch. As shown in Fig. 2, a female that had just left a high-quality patch spent more time in the next visited patch. If the encountered patch has already been visited (a patch was visited on average 2.54±1.93 times), the female left it more quickly. As can be seen in Fig. 3, the first visit to a patch lasted much longer than the subsequent ones. Lastly, the tendency of the females to leave was clearly related to the total number of eggs already laid since the beginning of the test; each egg laid since the beginning of the experiment led to an increase in patch-leaving tendency by a factor of 1.020. This result suggested that the decision of the wasp to leave the current patch was likely dependent upon its physiological state, i.e. its current egg-load.

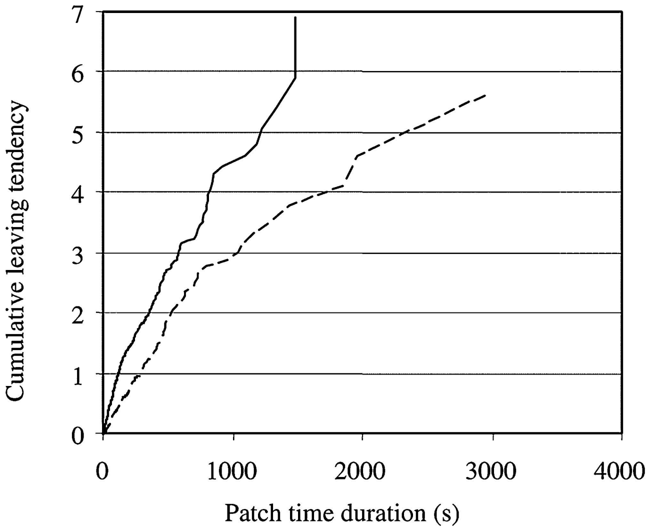

Fig. 2 Estimated cumulative patch-leaving tendency of the parasitoid *Aphidius rhopalosiphi* in an environment containing patches of various densities of the grain aphid *Sitobion avenae*, when the last visited patch was (–) high-quality or (—) low-quality

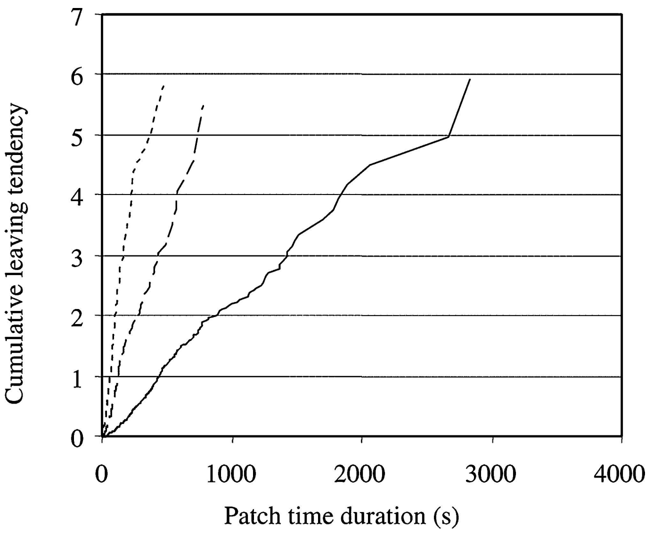

Fig. 3 Estimated cumulative leaving tendency in the parasitoid *Aphidius rhopalosiphi* on wheat leaves containing the grain aphid *Sitobion avenae,* as hosts (— first visit on the leaf; — second visit and —- subsequent visits to that leaf)

Pairwise interactions

A pairwise effect between the number of ovipositions during the current patch and the total number of ovipositions since the beginning of the experiment was found. This result suggests that the effect of an oviposition on the tendency to leave the current patch could be affected by the total number of eggs previously laid since the start of the test. These two covariates having opposite effects, the effect of an oviposition could be reduced and possibly reversed when the total number of eggs previously laid increases. Let N_o be the number of ovipositions in the current patch, N_t the total number of eggs laid since the beginning of the experiment and γ the estimated coefficient of the interaction term between these two effects. According to eqn. 1, the corresponding hazard ratio is $\exp\{0.019\times N_t - 0.271\times N_o + \gamma(N_o N_t)\}$ with $\gamma=0.002$ (see Table 2). A new oviposition, leading this hazard ratio to become greater than 1, will increase the leaving tendency. The conditions in which an oviposition led to an increase rather than a decrease in the leaving tendency are illustrated in Fig. 4. By raising N_t, ovipositions increased rather than decreased the patch-leaving tendency of *A. rhopalosiphi*.

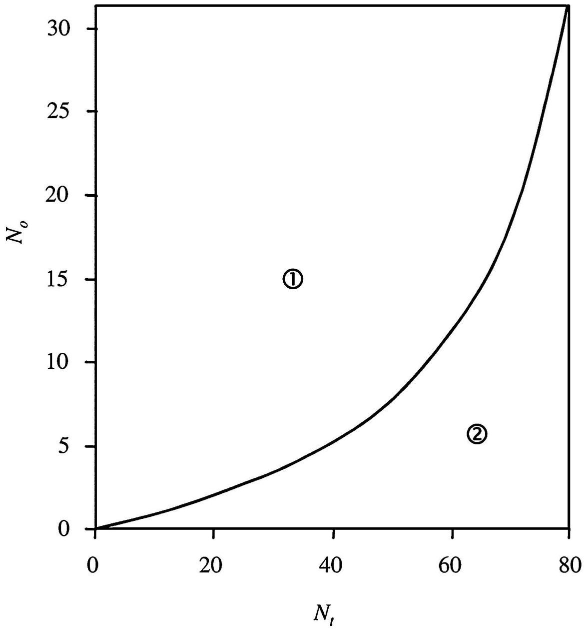

Fig. 4 Effect of an oviposition on the patch-leaving tendency of the parasitoid *Aphidius rhopalosiphi* in an environment containing patches of various densities of the grain aphid *Sitobion avenae* (N_t the total number of eggs already laid in the multi-patch environment; N_o the number of ovipositions in the current patch; ① region in which an oviposition decreases the tendency of the parasitoid to leave the current patch; ② region in which an oviposition increases the tendency of the parasitoid to leave the current patch; the *solid line* indicates the points at which the effect on an oviposition is reversed)

Finally, a pairwise effect between host rejection on the present patch and the number of "trappings" in that patch was found, suggesting that the increase in leaving tendency induced by a host rejection was higher after a female had been trapped in aphid cornicle secretions.

Discussion

Local information used for patch-leaving decision

The present study revealed that the experience acquired by *A. rhopalosiphi* females within patches of *S. avenae* had a significant influence on their decision to leave a patch. *A. rhopalosiphi* used local information on host quality (i.e. numbers of ovipositions or rejections) and availability (i.e. patch density) to determine the departure decision.

An increase in patch density had a decreasing effect on the tendency of females to leave a patch. Thus, the responsiveness of females to a patch was likely affected by their perception of the local host availability. For aphid parasitoids, patch assessment could be based on the amount of kairomone (Powell and Zhang 1983; Bouchard and Cloutier 1985), the degree of honeydew accumulation (Budenberg 1990), or the initial rate of encounter, as all these factors are positively related to aphid density (van Steenis et al. 1996). Accordingly, *A. rhopalosiphi* females tend to spend more time in the areas of high aphid density and this agrees with theoretical predictions of the marginal value theorem (Charnov 1976).

Among the behavioural events that occurred during patch depletion, the strongest effect was related to each oviposition, leading to a significant decrease in the leaving tendency. This is an incremental mechanism similar to the one described by Waage (1979) for the parasitoid *Venturia canescens*. Iwasa et al. (1981) suggested that the mechanism a forager used strongly depended on its information on patch quality. The incremental mechanism is generally thought to be associated with aggregated host distributions where the forager has little or no prior information on the host availability in a patch. In such a system, an oviposition may indicate that other hosts still remain to be discovered, and in response, parasitoids must increase their foraging time correspondingly. Under natural conditions, *A. rhopalosiphi* wasps faced discrete patches with a rather high variance in the number of individuals (Dedryver 1987). Thus, they are rarely well informed about the number of hosts available in the visited patch. Consequently, an incremental mechanism in *A. rhopalosiphi* seems to be adaptive as it enables the parasitoid to allocate its foraging time in high-density patches of its habitat. Besides this, wasps used the most recently experienced oviposition rate as a way of deciding when the patch should be left; the less time spent foraging between recent ovipositions, the lower the leaving tendency. This response seems to be adjusted to a clumped host distribution because attacking many hosts in a relatively short period is an indication that the patch is of high quality (Haccou et al. 1991). These two last patch-leaving mechanisms should allow *A. rhopalosiphi* to prolong the time spent in the high-density parts of its habitat.

A. rhopalosiphi contrasts with many other parasitoid species by its inability to recognise freshly parasitised hosts (Outreman et al. 2001a). When patch exploitation proceeded, there was then an increased risk of wasting eggs by attacking already parasitised hosts (i.e. superparasitism). Rosenheim and Mangel (1994) predicted that the risk of superparasitism is sufficient to promote early departure from partially exploited patches. This prediction implies that an oviposition should increase the patch-leaving tendency. Under experimental conditions presented to females, this tendency decreased with an increasing number of ovipositions in that patch. Hence, the risk of superparasitising freshly parasitised hosts did not seem to affect females' foraging strategy in the species studied.

Finally, disturbance induced by the foraging wasp within a host colony elicited agitation and aphid defence. Thus, females were faced with hosts that were difficult to handle and they often rejected some of them. Each host rejection induced a significant increase in the tendency of wasps to leave the patch. This decremental mechanism seems to be adaptive because encountering a defensive host could provide the female with some information regarding the decreasing value of the patch on which it is currently foraging. Moreover, results indicate that the intensity of the decremental effect associated with each rejection strongly depended on the state of the animal. The reduction in patch time induced by each rejection was indeed higher when wasps had been trapped in aphid cornicle secretion, indicating that they became more susceptible to host defensive behaviours. These last results show to what extent host behaviour can influence both patch-leaving decision-making and reproductive success of parasitoids. The host colonial response led to a lower parasitisation rate by inducing earlier departures of wasps from partially exploited patches containing hosts difficult to handle (Outreman et al. 2001b).

Past experiences in the host system and patch-leaving decision

Using the effect of information available within a single patch only ignores the fact that the patch-departure decision of a forager might also depend on its past experiences in its habitat. Under field conditions, aphid density on patches varies considerably and time-allocation decisions became important for successful foraging. However, wasps have only a limited knowledge of the host system properties. Recent foraging experiences could then allow parasitic wasps to estimate both the availability and spatial distribution of hosts in the local environment and to adjust their foraging decisions accordingly (Oaten 1977; McNamara and Houston 1985; Stephens and Krebs 1986; Bernstein et al. 1988; Mangel and Clark 1988; Bernstein et al. 1991; Fauchald 1999).

Present results show that patch-time allocation by *A. rhopalosiphi* was strongly affected by previous patch experiences. The strongest effect was related to the quality of the last visited patch. The patch-leaving tendency was lower when parasitoids had previously visited high-quality patches, indicating the high expectation of parasitoids on the profitability of the subsequent patch after a rewarding experience. Winder et al. (1999) suggested that the spatial distribution of the grain aphid *S. avenae* in winter wheat presents high-density patches on a small scale nested within low-density patches on a larger scale. In this case, a parasitoid wasp that finds a plant with many hosts is likely to find the next nearby plant visited to be also heavily infested. The foraging female should thus increase its foraging time in the subsequently visited plant. However, if success has recently been low, the parasitoid is probably situated within a low-density patch area, and the female should decrease her foraging time in the future patch. The forager's recent experience could then result in higher time allocation toward an area of higher profitability. However, the hosts' searching pattern of *A. rhopalosiphi* females has never been accurately studied under natural conditions. After leaving a given patch, do they tend to land on the nearby plants or do they fly further away? Given the *S. avenae* spatial distribution, foragers should search for small-scale patches by increasing their turning rate and reducing distances travelled. Careful analyses of searching behaviour of *A. rhopalosiphi* would be useful in order to validate our suggestions. Finally, it is worth noting that only the quality of the last visited patch was taken into account by *A. rhopalosiphi*. Considering only the most recent experience should allow a quick reaction to current patch quality (Haccou et al. 1991).

The total number of previous patches visited significantly increased the leaving tendency on the patch currently exploited. This result is consistent with the marginal value theorem developed by Charnov (1976). When patches are visited after relatively short travel times, the tendency of the parasitoids to leave a patch should increase. However, variation in patch-time allocation with an increasing number of visits could also be determined by some other factors such as reduced motivation to search because of egg depletion, habituation to kairomone concentration or tiredness (van Alphen and Galis 1983).

Finally, patches of the habitat are likely to undergo depletion. The probability for a wasp to encounter an already depleted patch might increase with time. Results have shown that a return visit to a patch was always much shorter than the first visit. A similar result was found for several other parasitoid species (Waage 1979; Galis and van Alphen 1981; Haccou et al. 1991; Hemerik et al. 1993; Bernstein and Driessen 1996; Wajnberg et al. 1999). A parasitoid might recognise locations it has visited before on the basis of visual cues or it may respond to chemical cues that have been deposited by itself. Such chemicals serve as a patch marker and the ability to respond to them has been reported in various parasitoid species (see Bernstein and Driessen 1996 for a review). No patch-marking behaviour was observed in *A. rhopalosiphi*. However, host stimuli could lead to recognition of already depleted patches. As shown above, aphids could present dried cornicle secretion on their body and, thus, the perception of such aphids can indicate to the females that the patch has been previously depleted. Females that recognise already depleted patches should spent less time foraging on them.

Past experiences and oviposition effect: a switching rule

Mechanisms determining departure from host patches have been studied in a number of insect parasitoids. Thus far, in each study either an incremental or a decremental effect of oviposition on leaving tendency has been identified. In the present study, however, both mechanisms were found. Results obtained in the present study indicate that an increasing ovipositional experience in the habitat gradually switched the incremental mechanism to a decremental one. Accordingly, when an *A. rhopalosiphi* wasp has already laid many eggs in its environment, an oviposition in the visited patch leads to a decrement rather than an increment of patch residence time.

Some optimisation models maximising lifetime reproductive success predict foraging strategies by parasitoids to be fundamentally dynamic (Iwasa et al. 1984; Mangel 1987; Houston et al. 1988; Mangel 1989a, 1989b; Sirot and Bernstein 1997). According to these models, the motivation to oviposit is determined by the interplay of physiological state variables and ecological state variables. Mangel's model (1989a) predicts that, when egg load is high, the parasitoid should attack a large number of hosts because the expected number of future encounters is not sufficient to ensure that all eggs would be laid. This suggests that parasitoids should have a high "site fidelity" and be willing to superparasitise when the egg complement is large. Thus, the parasitoid should become reluctant to superparasitise when it runs short of eggs and when the global host availability is particularly high (Mangel 1987). These predictions can be understood in terms of a trade-off between present and future reproductive success. Animals should be more selective (i.e. should lay only in few hosts to avoid superparasitism) if there is a high probability of laying all its eggs before death (Mangel 1989a).

The present results are consistent with these predictions. When the egg complement was high, an oviposition in a patch decreased the tendency of *A. rhopalosiphi* to leave the patch. In spite of the risk of superparasitism, females had a high site fidelity. Previous experiences in the environment induced changes in patch-leaving rules. Parasitoids gradually switched to a decremental mechanism with an increasing ovipositional experience. Thus, *A. rhopalosiphi* responded to egg-load depletion by leaving the visited patches sooner and by depositing a smaller number of eggs in those patches. This switching rule associated with the physiological status likely leads to a decreasing level of superparasitism induced by the lack of host discrimination.

Conclusions

Our goal here was to understand patch-departure decision-making in an aphid parasitoid from both the mechanistic and functional point of view. Effects of both within-patch experience and previous experiences on other patches were tested to generate hypotheses on the kind of patch-leaving rules animals use. Consideration of the effect of the within-patch experience gave a classical pattern of patch-leaving decision rules whilst consideration of previous experiences provided evidence that these rules are fundamentally dynamic, responding to the physiological state of the animal and the information it has about its environment. As a result, the state of the wasps changed dynamically as a consequence of their decisions, and this in turn influenced the decisions in a feedback loop. Moreover, the resulting leaving strategy can be expected to work well in an environment with a strongly variable number of hosts per patch, indicating that there was a strong selection to react accurately to host distribution. However, conditions offered to the parasitoids in the experiment differed in some respects from the natural situation. One aspect is the fact that during a season with high parasitoid density, several *A. rhopalosiphi* females could search simultaneously on the same wheat plant. This situation suggests some interference between females and this probably induces variations in the patch-departure decision rules (Wajnberg et al. 2004). This subject is open to further behavioural research.

Acknowledgements We are grateful to C. Bernstein and three anonymous referees for their useful comments and suggestions on an earlier draft of the manuscript. J. van Alphen, C.A. Dedryver, M. Hochberg and M. Plantegenest are acknowledged for stimulating discussions about this work. We thank also F. Lefèvre and B. Chaubet for their technical assistance. This study was supported by grants from the Ministère de l'Agriculture and from the Ministère de l'Education, de la Recherche et de la Technologie, France. All the experimental procedures conformed to French law.

References

Alphen JJM van (1993) Patch residence time and encounters with parasitized hosts: a reaction. Neth J Zool 43:340–349

Alphen JJM van, Galis F (1983) Patch time allocation and parasitization efficiency of *Asobara tabida*, a larval parasitoid of *Drosophila*. J Anim Ecol 52:937–952

Alphen JJM van, Vet LEM (1986) An evolutionary approach to host finding and selection. In: Waage JK, Greathead D (eds) Insect parasitoids. Academic, London, pp 23–61

Alphen JJM van, Bernstein C, Driessen G (2003) Information acquisition and time allocation in insect parasitoids. Trends Ecol Evol 18:81–87

Bernstein C, Driessen G (1996) Patch-marking and optimal search patterns in the parasitoid *Venturia canescens*. J Anim Ecol 65:211–219

Bernstein C, Kacelnik A, Krebs JR (1988) Individual decisions and the distribution of predators in a patchy environment. J Anim Ecol 57:1007–1026

Bernstein C, Kacelnik A, Krebs JR (1991) Individual decisions and the distribution of predators in a patchy environment. II. The influence of travel costs and structure of the environment. J Anim Ecol 57:1007–1026

Bouchard Y, Cloutier C (1985) Role of olfaction in host finding by aphid parasitoid, *Aphidius nigripes* (Hymenoptera: Aphidiidae). J Chem Ecol 11:801–808

Budenberg WJ (1990) Honeydew as a contact kairomone for aphid parasitoids. Entomol Exp Appl 55:139–147

Charnov EL (1976) Optimal foraging: the marginal value theorem. Theor Popul Biol 9:129–136

Collett D (1994) Modelling survival data in medical research. Chapman and Hall, London

Cox DR (1972) Regression models and life tables. Biometrics 38:67–77

Dedryver C (1987) Biologie, écologie et dynamique de population des pucerons des céréales en climat océanique. PhD thesis, University of Paris XI

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, Alphen JJM van, Kacelnik A (1995) A count-down mechanism for host search in the parasitoid *Venturia canescens*. J Anim Ecol 64:117–125

Fauchald P (1999) Foraging in a hierarchical patch system. Am Nat 153:603–613

Galis F, Alphen JJM van (1981) Patch time allocation and search intensity of *Asobara tabida* Nees (Braconidae), a larval parasitoid of *Drosophila*. Neth J Zool 31:596–611

Godfray HCJ (1994) Parasitoids. Behavioral and evolutionary ecology. Princeton University Press, Princeton

Godfray HCJ, Shimada M (1999) Parasitoids: a model system to answer questions in behavioral, evolutionary and population biology. Res Popul Ecol 41:3–10

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

Haccou P, De Vlas SJ, Alphen JJM van, Visser ME (1991) Information processing by foragers: effects of intra-patch experience on the leaving tendency of *Leptopilina heterotoma*. J Anim Ecol 60:93–106

Heimpel GE, Rosenheim JA (1998) Biol Control 11:160–168

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

Houston A, Clark C, McNamara J, Mangel M (1988) Dynamic models in behavioral and evolutionary ecology. Nature 332:29–34

Iwasa Y, Higashi M, Yamamura N (1981) Prey distribution as a factor determining the choice of optimal foraging strategy. Am Nat 117:710–723

Iwasa Y, SuzukiY, Matsuda H (1984) The oviposition strategy of parasitoids. I. Effects of mortality and limited egg number. Theor Popul Biol 25:205–227

Kalbfleisch JD, Prentice RL (1980) The statistical analysis of failure time data. Wiley, New York

Krespi L (1990) Etude de la biocénose parasitaire des pucerons des céréales dans le bassin de Rennes: cas particulier d'*Aphidius uzbekistanicus* Luz. PhD thesis, University of Rennes I

Krespi L, Dedryver CA, Rabasse JM, Nénon JP (1994) A morphometric comparison of aphid mummies containing diapausing vs. non-diapausing larvae of *Aphidius rhopalosiphi* (Hymenoptera: Braconidae, Aphidiinae). Bull Entomol Res 84:45–50

Mangel M (1987) Oviposition site selection and clutch size in insects. J Math Biol 25:1–22

Mangel M (1989a) An evolutionary interpretation of the "motivation to oviposit". J Evol Biol 2:157–172

Mangel M (1989b) Evolution of host selection in parasitoids: does the state of the parasitoid matter? Am Nat 133:688–705

Mangel M, Clark CW (1988) Dynamic modelling in behavioral ecology. Princeton University Press, Princeton

McNamara J, Houston A (1985) A simple model of information use in the exploitation of patchily distributed food. Anim Behav 33:553–560

Oaten A (1977) Optimal foraging in patches: a case for stochasticity. Theor Popul Biol 12:263–285

Outreman Y, Le Ralec A, Plantegenest M, Pierre JS (2001a) Superparasitism limitation in an aphid parasitoid: cornicle secretions avoidance and host discrimination. J Insect Physiol 47:339–348

Outreman Y, Le Ralec A, Wajnberg E, Pierre JS (2001b) Can imperfect host discrimination explain partial patch exploitation in parasitoids? Ecol Entomol 26:271–280

Powell W, Zhang ZL (1983) The reactions of two cereal aphids parasitoids, *Aphidius uzbekistanicus* and *A. ervi* to host aphids and their food-plants. Physiol Entomol 8:439–443

Roermund HJW van, Hemerik L, Lenteren JC van (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

Rosenheim JA, Mangel M (1994) Patch-leaving rules for parasitoids with imperfect host discrimination. Ecol Entomol 19:374–380

Shirota Y, Carter N, Rabbinge R, Ankersmit GW (1983) Biology of *Aphidius rhopalosiphi*, a parasitoid of cereal aphids. Entomol Exp Appl 34:27–34

Sirot E, Bernstein C (1997) Food searching and superparasitism in solitary parasitoids. Acta Oecol 18:63–72

Steenis MJ van, El-Khawass KAMH, Hemerik L, Lenteren JC van (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

Stephens DW, Krebs JR (1986) Foraging theory. Princeton University Press, Princeton

Strand MR, Vinson SB (1982) Behavioral response of the parasitoid *Cardiochiles nigriceps* to a kairomone. Entomol Exp Appl 31:308–315

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 (1979) Foraging for patchily-distributed hosts by the parasitoid, *Nemertis canescens*. J Anim Ecol 48:353–371

Wajnberg E, Rosi MC, Colazza S (1999) Genetic variation in patch time allocation in a parasitic wasp. J Anim Ecol 68:121–133

Wajnberg E, Curty C, Colazza S (2004) Genetic variation in the mechanisms of direct mutual interference in a parasitic wasp: consequences in terms of patch-time allocation. J Anim Ecol 73:1179–1189

Winder L, Pery JN, Holland JM (1999) The spatial and temporal distribution of the grain aphid *Sitobion avenae* in winter wheat. Entomol Exp Appl 93:277–290