

Patch choice from a distance and use of habitat information during foraging by the parasitoid *Ibalia leucospoides*

DEBORAH FISCHBEIN,^{1,2} JULIETA BETTINELLI,³ CARLOS BERNSTEIN² and JUAN C. CORLEY¹ ¹Grupo de Ecología de Insectos, Instituto Nacional de Tecnología Agropecuaria, Estación Experimental San Carlos de Bariloche, CC 277, Bariloche, Argentina, ²Laboratoire de Biométrie et Biologie Evolutive, UMR 5558, Université de Lyon, Villeurbanne, France and ³Department of Biology, University of New Mexico, Albuquerque, New Mexico, U.S.A.

Abstract. 1. In environments in which resources are distributed heterogeneously, patch choice and the length of time spent on a patch by foragers are subject to strong selective pressures. This is particularly true for parasitoids because their host foraging success translates directly into individual fitness.

2. The aim of this study was to test whether: (i) females of the parasitoid *Ibalia leucospoides* (Hymenoptera: Ibalidae) can discriminate among patches according to host numbers; (ii) the surrounding context affects the initial choice of patch, as well as time spent on patch; and (iii) the perceived quality of a given patch is affected by the quality of the surrounding patches.

3. Each female was randomly exposed to one of three different three-patch environments which differed in host number per patch, mean environment host number and host distribution among patches. For each treatment level, the first patch chosen and the time allocated to each patch visited by the female were recorded.

4. Females of *I. leucospoides* were able to discriminate different levels of host numbers among patches from a distance. The patch bearing the highest number of hosts was, predominantly, the first choice. Patch host number in association with mean habitat profitability influenced the length of time spent on the first patch visited. By contrast, variance in habitat profitability did not influence time allocation decisions. Contrary to the study prediction, there were no significant habitat-dependent time allocation differences among patches holding the same number of hosts.

5. The results indicate that, for *I. leucospoides*, patch exploitation decisions are partially influenced by information obtained from the habitat as a whole, a behaviour that may prove to indicate adaptive ability in highly patchy environments, as well as suggesting the presence of good cognitive abilities in this parasitoid species.

Key words. Foraging behaviour, marginal value theorem, parasitoid insects, patch decision rules.

Introduction

Animals usually live in patchy environments in which resources are heterogeneously distributed. In these conditions, mechanisms for resource patch choice and strategies for

determining the length of time spent on a patch are subject to strong selective pressures (Stephens & Krebs, 1986). This is particularly true for parasitoids, which are insects that lay their eggs in or on other arthropods, because in these animals host foraging success translates directly into offspring production and thus into individual fitness. This behavioural trait makes parasitoids ideal subjects in which to study foraging decisions. As a consequence, foraging strategies, such as host patch

Correspondence: Deborah Fischbein, Grupo de Ecología de Insectos, INTA EEA Bariloche, CC 277, San Carlos de Bariloche, 8400 Río Negro, Argentina. E-mail: dfischbein@bariloche.inta.gov.ar

choice and time spent on patch, and other factors influencing parasitoid foraging behaviour have been subject to significant research effort (see Wajnberg, 2006 for a review).

Parasitoid females frequently search for their hosts in highly variable environments. In such settings, adaptive foraging decisions depend on the accurate gathering and use of information. Accordingly, parasitoids may sample patches when searching in order to estimate the profitability of the current patch and of the surrounding habitat by continuously updating information. The use of information for patch exploitation has been studied vastly from both theoretical (McNamara & Houston, 1985; Bernstein *et al.*, 1988; Pierre *et al.*, 2003) and experimental (Hubbard & Cook, 1978; Waage, 1979; Hemerik *et al.*, 1993; Vos *et al.*, 1998; Thiel & Hoffmeister, 2006; Tentelier *et al.*, 2006; Tentelier & Fauvergue, 2007) viewpoints. Patch sampling, an information processing sequence, through which individuals compare *a priori* and *a posteriori* information, should help non-omniscient foragers to make better patch choices and usage decisions.

A great variety of environmental cues, such as chemical, visual and physical cues, are used by parasitoids as sources of information for both locating and assessing host patches (Vet & Dicke, 1992; Godfray, 1994). These cues of various natures can act as indicators of host presence, host species (Thiel & Hoffmeister, 2006) and host density (Waage, 1979; Li *et al.*, 1997; Shaltiel & Ayal, 1998; Wang & Keller, 2004; Tentelier *et al.*, 2005; Martínez *et al.*, 2006; Corley *et al.*, 2010), as well as of the presence of competitors in the current patch (Janssen *et al.*, 1995a,b; Bernstein & Driessen, 1996; Castelo *et al.*, 2003). The use of such information is expected to reduce uncertainty and therefore improve foraging success.

Making patch choice decisions on the basis of expected host availability (i.e. estimated through patch sampling or through stimuli discrimination from a distance) might ultimately lead to an adaptive exploitation of resources. However, the accuracy of such estimates depends on different factors, such as the number of patches already visited and the development of learning abilities. The inborn ability to estimate host availability can be highly inaccurate and lead to inefficient decisions at early stages in the learning process. Alternatively, the quality of the estimate can rely on the ability to respond to cues to host densities prior to patch exploitation (Geervliet *et al.*, 1998; Liu *et al.*, 2009). In many host–parasitoid systems, different cues, such as secondary chemical compounds released by plants, visual indications of plant consumption by herbivores and volatile kairomones released by hosts, can provide a rapid, albeit rough, estimate of host availability and represent the basis of an adaptive patch choice (Vet & Dicke, 1992; Turlings & Wäckers, 2004; Tentelier *et al.*, 2005; Tentelier & Fauvergue, 2007).

Once they are on a patch, parasitoids should be able to adjust the length of time they allocate to it in order to maximise their lifetime reproductive success. The marginal value theorem (MVT) (Charnov, 1976), the most influential rate maximisation model, predicts that an optimal forager should leave a resource patch when the instantaneous rate of fitness gain falls below the average rate of gain expected for the habitat. Therefore, optimal

residence time on a patch would increase with both increasing resource availability in the patch and decreasing availability in the habitat as a whole (i.e. habitat profitability). However, the MVT model does not suggest patch exploitation mechanisms that foragers should employ to achieve optimal residence time. Simple behavioural rules, such as the so-called rules of thumb (Iwasa *et al.*, 1981; McNair, 1982; Green, 1984; Stephens & Krebs, 1986), and the more complex and dynamic incremental and decremental patch-leaving rules have been proposed as such mechanisms (Waage, 1979; Driessen *et al.*, 1995; Wajnberg *et al.*, 2000; van Alphen *et al.*, 2003; Wajnberg, 2006).

The parasitoid *Ibalia leucospoides* Hochenwarth (Hymenoptera: Ibalidae) is a solitary, koinobiont and nearly proovigenic parasitoid (i.e. with an ovigeny index of 0.77; D. Fischbein, unpublished data, 2011) that attacks eggs and first-instar larvae of the woodwasp *Sirex noctilio* Boidin (Hymenoptera: Siricidae) (Chrystal, 1930; Madden, 1968; Spradbery, 1974). Woodwasps are primitive xylophagous insects that attack pine trees. *Sirex noctilio* is native to Mediterranean Europe, but over the last century has successfully invaded Australia, New Zealand, South Africa, South America and, more recently, North America (Hoebeke *et al.*, 2005). In most regions in which *S. noctilio* has established, it has rapidly become an important pest of pine tree forestations, mainly as a result of its outbreak population dynamics, during which tree mortality can be severe (Corley *et al.*, 2007). *Ibalia leucospoides* is one of several biocontrol agents adopted for the purposes of pest management of woodwasp populations (Hurley *et al.*, 2007; Corley & Bruzzone, 2009). The parasitoid, also native to Europe, was introduced into Australasia in the early 1960s, since when it has established throughout the invasion range of *S. noctilio*, mostly through accidental introductions together with its host (Madden, 1988). In field conditions, *I. leucospoides* may parasitise up to 40% of its hosts.

Because of its applied importance, there is a growing research effort on this parasitoid. Most studies have focused on its host location and patch use behaviour. Together with its eggs, the host wasp injects spore of its symbiotic fungus *Amylostereum areolatum* into pine trees. Then, woodwasp larvae develop and grow inside these trees by feeding on wood decomposed by the fungus (Madden, 1981). The chemical information derived from the host fungal symbiont is used by parasitoids during host searching and may provide information on host presence (Madden, 1968; Spradbery, 1974) and on the relative densities of hosts on patches (Martínez *et al.*, 2006). There is also evidence to suggest that *I. leucospoides* has a type III functional response to host density in pine logs (Fernández-Arhex & Corley, 2005) and that interference can occur when two females forage for a host in the same patch in simplified experimental conditions (Fernández-Arhex & Corley, 2010). To date, not many attempts have been made to evaluate host foraging behaviour by this parasitoid in a more natural, multiple patch environment (Corley *et al.*, 2010).

Whereas pine plantations are generally characterised by a regular spatial arrangement, trees attacked by *S. noctilio* are typically aggregated, especially during the long-lasting, endemic population phase (Corley *et al.*, 2007). The

distribution of attacks by *S. noctilio* within these clumps shows different degrees of heterogeneity, whereby clusters of attacked trees can show low or high degrees of variance in the number of hosts per tree, which can range from a few individuals to several hundred woodwasp larvae. During outbreak periods, overall infestation levels can be high, affecting most trees ($\geq 80\%$) and rendering spatial distribution less heterogeneous. Consequently, the abundance and spatial distribution of *S. noctilio* can vary not only among plantations, but within stands, and in the course of a single flight season as well as in subsequent generations, resulting in varying levels of heterogeneity. In this context, female *I. leucospoides* must deal with changes in both mean and variance habitat profitability.

This study tested the hypothesis that parasitoids choose host patches and adjust patch exploitation times according to different levels of host abundance and distribution among attacked trees. This hypothesis leads to various accompanying predictions. Firstly, female parasitoids are likely to assess patch profitability from a distance and, accordingly, to choose the best patch within a local environment, whatever the surrounding habitat characteristics may be. Secondly, a positive relationship between patch residence time and host numbers should emerge and the length of time allocated to patches will depend on the characteristics of the surrounding habitat. Therefore, parasitoids that experience local environments with different mean host numbers but similar host distribution among attacked trees (i.e. similar variance in host numbers per patch) will allocate more time to patches set in a poorer environment than to those in a richer one. In the same manner, parasitoids that experience local environments with the same mean host numbers but different host distribution among attacked trees will allocate their time among patches more equally in line with the decreasing heterogeneity of the environment (i.e. more similar host numbers per patch). Finally, a given patch with an absolute abundance of hosts will have higher relative profitability for the parasitoid when this patch is placed in poor habitats than in richer ones and, hence, will be exploited more intensively in the former context.

This study was focused on individual decision making by female parasitoids that had arrived at an aggregate of host-attacked trees. Accordingly, predictions were tested in three different three-patch environments characterised by different combinations of means and variances in habitat profitability. Host patches in the experimental set-up were recreated using pine tree logs infested in a controlled manner; the first patch contacted and the time allocated by parasitoids to each patch visited were analysed. Thus, the aim of this study was to test whether: (i) *I. leucospoides* females are able to perceive differences in patch host numbers from a distance as indicated by their selection of the best patch as their first choice; (ii) the surrounding context affects the choice of patch as well as the time spent on patch; and (iii) the perceived quality (quality rating) of a given patch is affected by the quality of the surrounding patches.

Materials and methods

Host and parasitoid wasps used in this study were obtained from pine (*Pinus contorta*) logs collected in the field, at several heavily attacked plantations located in northwest Patagonia, Argentina ($42^{\circ}02'S$, $71^{\circ}56'W$). Once felled, trees were cut into 1-m logs and kept individually in locker-type cages under indoor conditions until insect emergence. Each morning, newly emerged parasitoid females were collected from the cages and immediately placed in individual plastic vials (251 cm^3) for 7 days in a common chamber, free from host odours (temperature $23 \pm 1^{\circ}\text{C}$, RH 53%, LD 16:8 h). This time span was chosen to combine practical purposes (i.e. the matching of insects with the experimental set-up) with the use of middle-aged, more representative individuals. All wasps were virgins and were given unlimited access to a diluted honey solution (30% honey in distilled water) from emergence. On the day prior to the experiment, food was removed and replaced with distilled water only.

Experimental design

The aims of the experiment were to assess the ability of *I. leucospoides* females to detect the best patch of three offered from a distance and to establish whether patch residence time is proportional to host availability. The study also sought to establish whether mean host abundance in the local environment and host distribution among patches influence patch exploitation behaviour. For this purpose, female parasitoids were individually assigned at random to one of three different three-patch environments. The settings differed in host numbers at the individual log level (i.e. patch), in mean environment host numbers (the three logs), as well as in host distribution among patches (i.e. variance in host numbers per log). The settings are hereafter referred to as habitats LM-HV (low mean host numbers, high variance in host numbers), HM-LV (high mean host numbers, low variance in host numbers) and HM-HV (high mean host numbers, high variance in host numbers) (Table 1). The first host patch chosen (i.e. the first patch contacted by a parasitoid), subsequent patch visits and the time allocated to each patch visited were recorded as response variables. Therefore, if parasitoids are able to assess patch profitability without making direct contact with host patches, the patch with higher host numbers should be selected as their first choice, regardless of surrounding habitat characteristics. Additionally, if parasitoids are able to adapt their residence time in patches according to the surrounding patches, residence time should be longer in the poorer (LM-HV) than in the richer (HM-HV) habitat. In addition, if parasitoids can adjust their current patch time allocation to neighbouring patches, the time spent on patches should increase in similarity as the distribution of hosts among patches decreases in heterogeneity (e.g. HM-LV vs. HM-HV). Moreover, if parasitoids use the relative profitability of patches to adjust patch exploitation times, patches with similar absolute host numbers should be visited for less time when they are located in rich (HM-LV and HM-HV) than in poor (LM-HV) habitats.

Table 1. Females of the parasitoid *Ibalia leucospoides* were individually assigned to one of three different three-patch environments (habitats LM-HV, HM-LV and HM-HV).

| | <i>n</i> | Patch host numbers | | | Mean environment host number | Host distribution among patches (vc*) |
|---------------|----------|--------------------|--------|------|------------------------------|---------------------------------------|
| | | Low | Medium | High | | |
| Habitat LM-HV | 12 | 1 | 8 | 15 | 8 | 0.87 |
| Habitat HM-LV | 11 | 10 | 15 | 20 | 15 | 0.33 |
| Habitat HM-HV | 13 | 2 | 15 | 28 | 15 | 0.87 |

*vc, the variation coefficient, was used as a relative measure of variance in host distribution among patches (i.e. the ratio between the standard deviation of the mean environment host number and mean environment host number).

The environments differed in individual patch host numbers, mean environment host number and host distribution among patches (vc).

LM-HV, low mean host numbers, high variance in host numbers; HM-LV, high mean host numbers, low variance in host numbers; HM-HV, high mean host numbers, high variance in host numbers.

Because of the short duration of the insect emergence season (2 months approximately), and the time-consuming logistics associated with the experimental set-up (see below), completion of the research in a single season was unfeasible. The experiments were thus carried out in two different years, during daytime hours (11.00–20.00 hours) and at 23 ± 1 °C. During the first year, five, five and six replicates of the LM-HV, HM-LV and HM-HV habitat set-ups, respectively, were carried out. A further seven, six and seven replicates were added for each habitat scenario, respectively, during the second experimental year.

In order to create a symmetrical environment, three logs were placed in the corners of an imaginary isosceles triangle (30 cm on each side) inside a wire mesh cage (1 m³). To provide host patches, 'clean' (i.e. free from woodwasp attacks) pine logs, 0.8 m in length, were cut and allowed to dry at ambient temperatures for 10 days to ensure appropriate wood moisture conditions for woodwasp oviposition. Logs were then exposed to woodwasp females until the desired number of ovipositions had been achieved. Logs were then stored for another 10 days before the experiments to ensure that host development and fungal growth were suitable and attractive to *I. leucospoides* females. Data on the number of hosts per log (Table 1) were obtained by observing female woodwasps continuously and tallying each insertion of the ovipositor into the log. The number of host eggs laid was estimated according to Madden (1974). The position of a given log within the array was set at random.

A female wasp was introduced at the exact centre of the arrangement. After a 5-min adaptation period during which the wasp was kept inside a perforated plastic vial, the wasp was gently released and the trial initiated. In each replicate of the experiment, both the parasitoids and logs used were replaced. Wasps were observed continuously during an experiment. Patch residence times were recorded using a hand-held stopwatch. Although off-patch short excursions during host patch visits are not common in *I. leucospoides*, the end of a patch visit was arbitrarily defined as the point at which a wasp left the patch and remained off it for 20 min. The experiment was considered to have ended when, having left a patch and landed elsewhere, the wasp remained off any patch for ≥ 30 min.

Data analysis

A multinomial *logit* model was fitted to analyse the effects of the surrounding context on the first patch chosen. The initial model considered *patch chosen* (a qualitative three-level factor: high, medium, low) as the response variable, and *habitat* (a qualitative three-level factor: LM-HV, HM-LV, HM-HV) and *year* as explanatory variables. Starting with the most complex model, *patch chosen = habitat|year* (the latter term represents the sum of the effects of the two-way interaction and the two single variables), the non-significant factors and the interaction between factors were progressively removed until a minimal appropriate model was obtained. Model comparisons were computed using the standard likelihood method (Faraway, 2006). To test the hypothesis that the females chose logs at random, a G test for goodness of fit was carried out (Sokal & Rohlf, 1981).

The effects of host numbers in a patch and the habitat as a whole on time allocated to the patch visited were analysed using a generalised linear model assuming a gamma distribution of residuals and an inverse link function. The *patch host number* (a quantitative variable in this case, representing the number of hosts within the patch), the *habitats* (LM-HV, HM-LV and HM-HV) and *year* were introduced in the model as explanatory variables. A backward procedure was used to remove non-significant factors and interactions between factors in order to select the final model. Model comparisons were computed using the standard likelihood method. Residuals were examined to confirm that the final model accurately fitted the data. To test the effect of *habitats* on time assigned to a patch holding 15 hosts, when this patch was selected as a first choice, a generalised linear model based on an inverse link function and a gamma distribution was used. All data analyses were performed using the *R* statistical environment (R Development Core Team, 2011).

Results

Patch choice

The analysis of the first patch chosen out of the three offered showed no significant interaction between *habitat* and

year ($\chi^2 = 8.49$, d.f. = 4, $P = 0.07$). Additionally, and as predicted, the first patch chosen by *I. leucospoides* females was selected independently of *habitat* ($\chi^2 = 6.84$, d.f. = 4, $P = 0.14$) and *year* ($\chi^2 = 2.12$, d.f. = 2, $P = 0.34$). However, the results show that parasitoids were able to assess patch profitability without requiring direct contact with host patches by showing a propensity to alight on and exploit the patch bearing the highest number of hosts ($\chi^2 = 17.96$, d.f. = 2, $P < 0.001$) (Fig. 1).

The influence of patch host number and habitat on patch residence time

Only six of a total of 36 wasps visited more than one patch, irrespective of the local environment. Half of these wasps oriented directly to the best patch, exploited it and then moved to a subsequent patch. The time allocated to each patch visited tended to be positively related to host numbers on the patch. The remaining three wasps made a first, short visit to poorer patches and then moved to the patch with the highest number of hosts, in which they stayed and which they exploited. As only a limited number of wasps visited more than one patch, it was difficult to analyse data adequately in terms of patch residence time on all patches and therefore all statistical analysis was focused on patch residence time on the first host patch chosen.

Consistent with the study predictions, the time allocated to the exploitation of the first host patch visited increased with increasing patch host numbers ($\chi^2 = 12.61$, d.f. = 1, $P < 0.0001$). In addition, patch residence time was significantly affected by the interaction between *host number* in a patch and *habitat* (LM-HV, HM-HV, HM-LV; $\chi^2 = 7.79$, d.f. = 2, $P < 0.0001$). We attempted to understand this statistically significant interaction by comparing habitats according to their mean and variance in profitability (see below).

When habitat LM-HV was compared with habitat HM-HV, results suggested that parasitoids may use the relative profitability of patches to adjust their patch exploitation times.

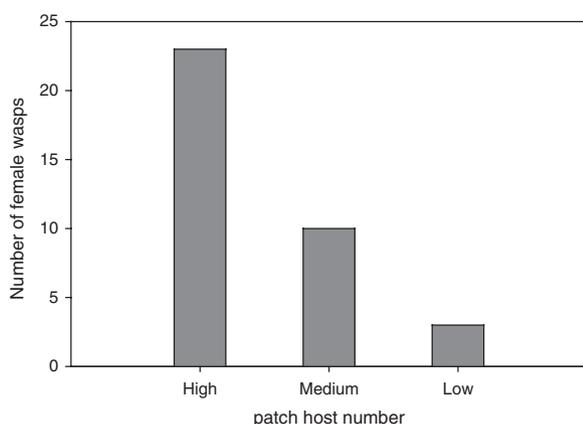


Fig. 1. Number of female wasps of *Ibalia leucospoides* that chose a given host patch for the first time, among the three patches simultaneously offered, as a function of patch host number (high, medium, low).

Patch residence time was significantly affected by the interaction between *host number* in a patch and *habitat* ($\chi^2 = 2.60$, d.f. = 1, $P = 0.01$). Therefore, female wasps were able to stay longer on patches (specifically, see patch containing 15 hosts; Fig. 2) in LM-HV conditions than in HM-HV conditions. Patches with different absolute numbers of hosts, but with the same relative profitability in habitat LM-HV and HM-HV, were assigned exploitation times according to their relative value (i.e. quality rating) (Fig. 2). However, patch residence time increased with the number of hosts on the patch ($\chi^2 = 13.06$, d.f. = 1, $P < 0.0001$).

When habitat HM-LV was compared with habitat HM-HV, the interaction between *host number* in a patch and *habitat* was significant ($\chi^2 = 3.80$, d.f. = 1, $P < 0.01$). However, this probably occurred as a consequence of the fact that only a single wasp (that in habitat HM-LV) visited the patch containing 10 hosts and allocated a disproportionate amount of time to it compared with the time allocated by the other wasps to patches of comparable richness. When the individual that had visited the patch bearing 10 hosts was removed from the analysis, the interaction between *host number* in the patch and *habitat* was no longer significant for habitats HM-LV and HM-HV ($\chi^2 = 0.39$, d.f. = 1, $P = 0.38$), and, contrary to the study prediction, *habitat* (i.e. variance in host numbers per patch) did not affect patch residence time ($\chi^2 = 0.29$, d.f. = 1, $P = 0.52$). Nonetheless, time spent on the first patch visited increased with host numbers in that patch ($\chi^2 = 11.98$, d.f. = 1, $P < 0.0001$).

To further study the use of patch relative profitability to adjust patch exploitation times, differences in the time assigned to patches holding 15 hosts when these patches were selected as first choice were analysed (these patches were included in the LM-HV, HM-LV and HM-HV habitats). In a manner that is partially consistent with the study prediction, females tended

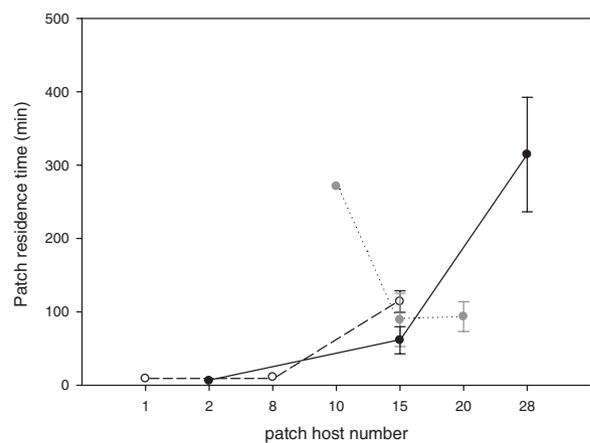


Fig. 2. Patch residence times (mean \pm standard error) on the first patch visited as a function of patch host number, for *Ibalia leucospoides* females exposed to different environmental conditions. ○, habitat LM-HV (low mean host numbers, high variance in host numbers); ◐, habitat HM-LV (high mean host numbers, low variance in host numbers); ●, habitat HM-HV (high mean host numbers, high variance in host numbers).

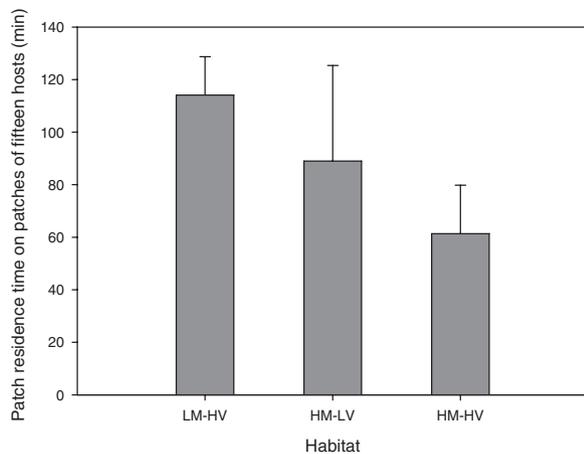


Fig. 3. Patch residence times (mean \pm standard error) on patches of 15 hosts chosen as first options in habitats LM-HV, HM-LV or HM-HV. LM-HV, low mean host numbers, high variance in host numbers; HM-LV, high mean host numbers, low variance in host numbers; HM-HV, high mean host numbers, high variance in host numbers.

to stay on the patch containing 15 hosts longer when this patch was located in the poorer habitat [mean \pm standard error (SE) in habitat LM-HV: 114.10 ± 14.63 min ($n = 10$)] than when it was placed in the richer habitat [mean \pm SE in habitat HM-LV: 89.00 ± 36.35 min ($n = 6$); mean \pm SE in habitat HM-HV: 61.33 ± 18.47 min ($n = 3$)] (Fig. 3). However, the differences among habitats were not significant ($\chi^2 = 0.86$, d.f. = 2, $P = 0.37$). The years in which the experiments were performed had no significant effect on any response variable analysed.

Discussion

Results show that *I. leucospoides* females may alight on and exploit, firstly, logs holding the highest number of hosts. This is particularly remarkable given that the first selection occurs from a distance. Once on the patch, the time allocated to the exploitation of the first host patch visited depended on host number in the patch in association with habitat profitability. This finding suggests that exploitation decisions may be influenced by information obtained from the surrounding patches.

Patch choice decisions

The most striking finding in this study is that *I. leucospoides* was capable of responding to differences in host patch quality without needing to make direct contact with logs in order to assess their profitability. *Ibalia leucospoides* seems to do this using chemical cues derived from the host fungal symbiont (Madden, 1968; Martínez *et al.*, 2006). As ovipositing woodwasps may disturb tree growth during their attacks, through a phytotoxic substance and fungus associated with oviposition, it is likely that tree location by foraging

parasitoids follows volatile cues emitted by stressed trees, such as monoterpenes (α - and β -pinene) (Madden, 1988). Odour cues derived mainly from the host symbiotic fungus probably help foraging wasps to optimise patch choice decisions even before they reach the patch (Martínez *et al.*, 2006; Corley *et al.*, 2010). However, we cannot discard the role played by volatiles derived from live but stressed trees in the field in parasitoid attraction and patch choice.

Choosing the best of three nearby patches suggests, from one perspective, proportionality between odour concentration and host number. Moreover, it requires at least a given ability to appraise several patches in the local environment and the capability to detect differences in volatile cues. It is generally assumed that parasitoids need to sample their environment first, mostly by making contact with host patches, in order to assess its profitability and make decisions (Hubbard & Cook, 1978; Waage, 1979; Driessen *et al.*, 1995). However, the present results suggest that *I. leucospoides* is able to make host-searching decisions by assessing initial host availability in patches, without the need for direct contact. In addition, assessment ability and patch choice in this parasitoid did not differ among habitats (i.e. independently of the characteristics of the habitat into which they were released, wasps tended to select the best log first), although at this stage we cannot rule out the possibility that this apparent lack of difference may be the consequence of a lack of power of our tests caused by small sample sizes.

In *I. leucospoides*, the strategy of choosing and staying longer in the best patch may result in a better outcome than a strategy of engaging in a process of sampling and continuous updating. A hypothetical explanation of the strategy of choosing a single patch must involve a highly variable environment. In pine plantations, *S. noctilio* densities and their spatial distribution among trees are known to vary, even during population outbreaks (Corley *et al.*, 2007). In these conditions, it is possible that a host-infested tree, within the aggregation of attacked trees, bears several to hundreds of host larvae, hence surpassing the parasitoid egg complement. Thus, for parasitoids, the ability to assess patch quality from a distance and respond accordingly by moving towards the best patch would be valuable: firstly, it may result in a time-saving strategy, and, secondly, making an appropriate choice gives the female parasitoid the chance to lay more eggs in a single tree with a high density of hosts. By making accurate choices and thoroughly exploiting a patch, *I. leucospoides* may protect itself against failure to find another good host patch, mortality during travel, and losses in terms of energy budget. It is also true that individual offspring production per patch can be independent of the number of hosts per patch (Tentelier *et al.*, 2008). In the wild, a low number of eggs laid by a female per patch in relation to the number of hosts available may occur as a result of either strong predation pressure or parasitoid redistribution among patches.

Patch residence time

Under the experimental conditions considered here, the first patch chosen by *I. leucospoides* was probably exploited

according to mean habitat profitability. Parasitoids may use the relative profitability of patches to adjust their patch exploitation times, but patch residence time also increases with the number of hosts in the patch. By contrast, variance in habitat profitability seems to have no influence on time allocation decisions. In accordance with the predictions of some theoretical studies (McNamara & Houston, 1985, 1987; Vos & Hemerik, 2003), the present results suggest that wasps may use the information available from nearby patches to make patch-leaving decisions. Additionally, the results qualitatively agreed with the general MVT predictions in that patch residence times by parasitoids increased with increasing host number. The increase in patch residence time may occur in consequence to a response of *I. leucospoides* to concentrations of host chemical cues.

Foraging theory predicts that the time allocated to a patch with a given host density depends upon the particular host environment. Thus, as habitat profitability increases, residence times on a patch of particular host availability should decrease (Charnov, 1976). Although we found that the number of hosts in the patch determined the time allocated to the first patch chosen in association with mean habitat profitability, we did not observe a statistically significant habitat-dependent time allocation difference with those patches bearing 15 hosts. This apparent mismatch is probably a consequence of the low power of the statistical test (low sample size) and not of parasitoid behaviour. Note that female wasps tended to spend more time on the patch with 15 hosts when this patch was within the poorer habitat (LM-HV) than when it was in the richest habitat (HM-HV).

In this study, the inclusion of an environment with low mean habitat profitability and low variance in host numbers per patch would have facilitated a factorial design. However, an environment that strictly follows these characteristics is difficult to design. Such an environment would have required a mean host number (for the environment) of eight with patches bearing different host numbers whilst conserving a variation coefficient of 0.33. An example of such a setting would include patches with six, eight and ten hosts. It is very unlikely that, in this or similar scenarios, these patches would be perceived as different by *I. leucospoides* females.

This study shows the relevance of quantitative differences in volatile-based cues and the roles they play in the process of patch selection. Once on a patch, animals may well use or overlook information about habitat characteristics. In this study, *I. leucospoides* showed a strong response to patch host abundance and the probable use of habitat information, but whether this leads to an increase in reproductive success requires further investigation. In any case, the ability to respond to differences in host numbers on patches is of great importance because it may indicate how well *I. leucospoides* individuals match their foraging effort to host availability.

Acknowledgements

We acknowledge financial support from the Agencia Nacional de Promoción Científica y Tecnológica (ANPCyT), Argentina

(PICT 0-1200/06 and PICT 2010-1775), Centre National de la Recherche Scientifique (CNRS), France (PICS 4144) and Instituto Nacional de Tecnología Agropecuaria, Argentina, and we thank two anonymous reviewers for their helpful comments on the manuscript.

References

- van Alphen, J.J.M., Bernstein, C. & Driessen, G. (2003) Information acquisition and time allocation in insect parasitoids. *Trends in Ecology & Evolution*, **18**, 81–87.
- Bernstein, C. & Driessen, G. (1996) Patch-marking and optimal search patterns in the parasitoid *Venturia canescens*. *Journal of Animal Ecology*, **65**, 211–219.
- Bernstein, C., Kacelnik, A. & Krebs, J.R. (1988) Individual decisions and the distribution of predators in a patchy environment. *Journal of Animal Ecology*, **57**, 1007–1026.
- Castelo, M.K., Corley, J.C. & Desouhant, E. (2003) Conspecific avoidance during foraging in *Venturia canescens* (Hymenoptera: Ichneumonidae): the roles of host presence and conspecific densities. *Journal of Insect Behavior*, **16**, 307–318.
- Charnov, E.L. (1976) Optimal foraging: the marginal value theorem. *Theoretical Population Biology*, **9**, 129–136.
- Chrystal, R.N. (1930) *Studies of the Sirex Parasites*, Oxford Forestry Memories No. 11. Oxford University Press, London, U.K.
- Corley, J.C. & Bruzzone, O.A. (2009) Delayed emergence and the success of parasitoids in biological control. *Biological Control*, **51**, 471–474.
- Corley, J.C., Villacide, J.M. & Bruzzone, O.A. (2007) Spatial dynamics of a *Sirex noctilio* woodwasp population within a pine plantation in Patagonia. *Entomología Experimentalis et Applicata*, **125**, 231–236.
- Corley, J.C., Villacide, J.M. & van Nouhuys, S. (2010) Patch time allocation by the parasitoid *Ibalia leucospoides* (Hymenoptera: Iballiidae): the influence of conspecifics, host abundance and distance to the patch. *Journal of Insect Behaviour*, **23**, 431–440.
- Driessen, G., Bernstein, C., van Alphen, J.J.M. & Kacelnik, A. (1995) A count-down mechanism for host search in the parasitoid *Venturia canescens*. *Journal of Animal Ecology*, **64**, 117–125.
- Faraway, J.J. (2006) *Extending the Linear Model with R*. Chapman & Hall, Boca Raton, Florida; London, U.K.
- Fernández-Arhex, V. & Corley, J.C. (2005) The functional response of *Ibalia leucospoides* (Hymenoptera: Iballiidae), a parasitoid of *Sirex noctilio* (Hymenoptera: Siricidae). *Biocontrol Science and Technology*, **15**, 207–212.
- Fernández-Arhex, V. & Corley, J.C. (2010) The effects of patch richness on con-specific interference in the parasitoid *Ibalia leucospoides* (Hymenoptera: Iballiidae). *Insect Science*, **17**, 379–385.
- Geervliet, J.B.F., Ariens, S., Dicke, M. & Vet, L.E.M. (1998) Long-distance assessment of patch profitability through volatile infochemicals by the parasitoids *Cotesia glomerata* and *C. rubecula* (Hymenoptera: Braconidae). *Biological Control*, **11**, 113–121.
- Godfray, H.C.J. (1994) *Parasitoids. Behaviour and Evolutionary Ecology*. Princeton University Press, Princeton, New Jersey.
- Green, R.F. (1984) Stopping rules for optimal foragers. *American Naturalist*, **123**, 30–40.
- 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*. *Journal of Animal Ecology*, **62**, 33–44.
- Hoebeker, E.R., Haugen, D.A. & Haack, R.A. (2005) *Sirex noctilio*: discovery of a Palearctic siricid woodwasp in New York. *Newsletter of the Michigan Entomological Society*, **50**, 24–25.

- Hubbard, S.F. & Cook, R.M. (1978) Optimal foraging by parasitoid wasps. *Journal of Animal Ecology*, **47**, 593–604.
- Hurley, B.P., Slippers, B. & Wingfield, M.J. (2007) A comparison of control results for the alien invasive woodwasp, *Sirex noctilio*, in the southern hemisphere. *Agricultural and Forest Entomology*, **9**, 159–171.
- Iwasa, Y., Higashi, M. & Yamamura, N. (1981) Prey distribution as a factor determining the choice of optimal foraging strategy. *American Naturalist*, **117**, 710–723.
- Janssen, A., Van Alphen, J.J.M., Sabelis, M.W. & Bakker, K. (1995a) Odour-mediated avoidance of competition in *Drosophila* parasitoids: the ghost of competition. *Oikos*, **73**, 356–366.
- Janssen, A., Van Alphen, J.J.M., Sabelis, M.W. & Bakker, K. (1995b) Specificity of odour-mediated avoidance of competition in *Drosophila* parasitoids. *Behavioral Ecology and Sociobiology*, **36**, 229–235.
- Li, C., Roitberg, B.D. & Mackauer, M. (1997) Effect of contact kairomone and experience on initial giving-up time. *Entomologia Experimentalis et Applicata*, **84**, 101–104.
- Liu, Q.Y., Thiel, A. & Hoffmeister, T.S. (2009) Odour-mediated patch choice in the parasitoid *Venturia canescens*: temporal decision dynamics. *Entomologia Experimentalis et Applicata*, **132**, 110–117.
- Madden, J.L. (1968) Behavioural responses of parasites to the symbiotic fungus associated with *Sirex noctilio* F. *Nature*, **218**, 189–190.
- Madden, J.L. (1974) Oviposition behaviour of the woodwasp *Sirex noctilio* F. *Australian Journal of Zoology*, **22**, 341–351.
- Madden, J.L. (1981) Egg and larval development in the woodwasp *Sirex noctilio*. *Australian Journal of Zoology*, **29**, 493–506.
- Madden, J.L. (1988) *Sirex* in Australasia. *Dynamics of Forest Insect Populations: Patterns, Causes and Implications* (ed. by A. A. Berryman), pp. 407–429. Plenum Press, New York, New York.
- Martínez, A., Fernández-Arhex, V. & Corley, J.C. (2006) Chemical information from the fungus *Amylostereum aerolatum* and host foraging behaviour in the parasitoid *Ibalia leucospoides*. *Physiological Entomology*, **31**, 336–340.
- McNair, J.M. (1982) Optimal giving-up time and the marginal value theorem. *American Naturalist*, **119**, 511–529.
- McNamara, J.M. & Houston, A.I. (1985) Optimal foraging and learning. *Journal of Theoretical Biology*, **117**, 231–249.
- McNamara, J.M. & Houston, A.I. (1987) Memory and the efficient use of information. *Journal of Theoretical Biology*, **125**, 385–395.
- Pierre, J.S., van Baaren, J. & Boivin, G. (2003) Patch leaving decision rules in parasitoids: do they use sequential decisional sampling? *Behavioral Ecology and Sociobiology*, **54**, 147–155.
- R Development Core Team (2011). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria [WWW document]. URL <http://www.R-project.org/> [accessed on 4 September 2011].
- Shaltiel, L. & Ayal, Y. (1998) The use of kairomones for foraging decisions by an aphid parasitoid in small host aggregations. *Ecological Entomology*, **23**, 319–329.
- Stephens, D.W. & Krebs, J.R. (1986) *Foraging Theory*. Princeton University Press, Princeton, New Jersey.
- Sokal, R.R. & Rohlf, F.J. (1981) *Biometry: The Principles and Practices of Statistics in Biological Research*. W.H. Freeman, New York, New York.
- Spradbery, J.P. (1974) The responses of *Ibalia* species (Hymenoptera: Ibalidae) to the fungal symbiontes of siricid woodwasp hosts. *Journal of Entomology*, **48**, 217–222.
- Tentelier, C. & Fauvergue, X. (2007) Herbivore-induced plant volatiles as cues for habitat assessment by a foraging parasitoid. *Journal of Animal Ecology*, **76**, 1–8.
- Tentelier, C., Wajnberg, E. & Fauvergue, X. (2005) Parasitoids use herbivore-induced information to adapt patch exploitation behaviour. *Ecological Entomology*, **30**, 739–744.
- Tentelier, C., Desouhant, E. & Fauvergue, X. (2006) Habitat assessment by parasitoids: mechanisms for patch use behaviour. *Behavioral Ecology*, **17**, 515–521.
- Tentelier, C., Guillemaud, T., Ferry, F. & Fauvergue, X. (2008) Microsatellite-based parentage analysis reveals non-ideal free distribution in a parasitoid population. *Molecular Ecology*, **17**, 2300–2309.
- Thiel, A. & Hoffmeister, T.S. (2006) Selective information use in parasitoid wasps. *Animal Biology*, **56**, 233–245.
- Turlings, T.C.J. & Wäckers, F.L. (2004) Recruitment of predators and parasitoids by herbivore-injured plants. *Advances in Insect Chemical Ecology* (ed. by R. T. Cardé and J. G. Millar), pp. 21–75. Cambridge University Press, Cambridge, U.K.
- Vet, L.E.M. & Dicke, M. (1992) Ecology of infochemical use by natural enemies in a tritrophic context. *Annual Review of Entomology*, **37**, 141–172.
- Vos, M. & Hemerik, L. (2003) Linking foraging behaviour to lifetime reproductive success for an insect parasitoid: adaptation to host distributions. *Behavioral Ecology*, **14**, 236–245.
- Vos, M., Hemerik, L. & Vet, L.E.M. (1998) Patch exploitation by the parasitoids *Cotesia rubecula* and *Cotesia glomerata* in multi-patch environments with different host distributions. *Journal of Animal Ecology*, **67**, 774–783.
- Waage, J.K. (1979) Foraging for patchily distributed hosts by the parasitoid, *Nemeritis canescens*. *Journal of Animal Ecology*, **48**, 353–371.
- Wajnberg, E. (2006) Time allocation strategies in insect parasitoids: from ultimate predictions to proximate behavioural mechanisms. *Behavioral Ecology and Sociobiology*, **60**, 589–611.
- Wajnberg, E., Fauvergue, X. & Pons, O. (2000) Patch leaving decision rules and the marginal value theorem: an experimental analysis and a simulation model. *Behavioral Ecology*, **6**, 577–586.
- Wang, X.G. & Keller, M.A. (2004) Patch-time allocation by the parasitoid *Diadegma semiclausum* (Hymenoptera: Ichneumonidae). III. Effects of kairomone sources and previous parasitism. *Journal of Insect Behavior*, **17**, 761–776.

Accepted 19 February 2012