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SHORT COMMUNICATION

Parasitoids use herbivore-induced information to adapt patch exploitation behaviour

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Abstract. 1. Optimal foraging models ultimately predict that female parasitoids should exploit rich host patches for longer than poorer ones. At the proximate level, mechanistic models and experimental studies show that parasitoids use both chemicals produced by their hosts and direct encounters with their hosts to estimate patch quality. Although it has been extensively studied in the context of host location, the use of herbivore-induced plant response by insect parasitoids has never been considered in the context of patch time allocation.

2. In this study, the respective roles of herbivore-induced plant response and direct contact with hosts on the foraging behaviour of *Lysiphlebus testaceipes* females on an aphid patch were quantified. For this, the level of herbivore-induced plant response and the number of aphids on the leaf bearing the patch were manipulated independently. Different levels of plant response were obtained by varying the duration of infestation on another leaf.

3. Parasitoid residence time and number of attacks increased with both the level of plant response and the number of aphids.

4. These results suggest that *L. testaceipes* females use the combination of herbivore-induced response of plants and direct encounters with hosts to assess patch quality and adjust their patch use behaviour.

Key words. *Aphis gossypii*, incremental effect, *Lysiphlebus testaceipes*, patch time allocation, proportional hazards model, reliability, synomones, tritrophic interactions.

Introduction

Parasitoid wasps often lay their eggs in or on hosts that are patchily distributed in the environment (Godfray, 1994). Under such conditions, one way they can maximise their lifetime reproductive success is to optimise the time they spend on patches (Stephens & Krebs, 1986). The marginal value theorem (Charnov, 1976) states that when a resource depletes with patch exploitation, foragers should leave the patch they are on when their instantaneous rate of gain drops to the maximal average of gain in the habitat. In other words, foragers should leave a patch when, on average, they can gain more elsewhere. A subsequent prediction is that when there are different patch qualities in the environment, foragers should stay longer on rich patches than on poor ones. If foragers leave every patch at the optimal time, they maximise their long-term rate of fitness gain, i.e. the total gain of fitness over their lifespan.

One notoriously unrealistic assumption of the marginal value theorem is that foragers have a perfect knowledge of the quality of every patch available in the environment. Because real animals cannot be omniscient, mechanistic models have been developed to identify what proximate information parasitoids use to assess patch quality and meet optimality criteria (review in van Alphen *et al.*, 2003). The seminal model developed by Waage (1979) suggests that the quantity of kairomones produced by hosts can give parasitoids an initial estimate of patch quality, and should thus set their initial motivation to stay on the patch. Examples of kairomones identified in this context are honeydew (Shaltiel & Ayal, 1998) and host mandibular

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gland secretion (Waage, 1978). The initial motivation can then be updated during patch exploitation by events providing additional information on patch quality. Such events can be encounters with parasitised and unparasitised hosts, or with competitors (van Alphen *et al.*, 2003; Wajnberg *et al.*, 2004). Up to now, all intra-patch sources of information known to be used by parasitoids to adapt their patch residence time come only from either hosts or competitors.

Herbivore-induced responses of plants could also serve parasitoids of phytophagous insects to make a reliable estimate of the number of hosts present in a patch. The rationale of such a hypothesis is that plants infested with phytophagous insects sometimes emit a blend of volatile compounds which can in turn attract entomophagous insects (Turlings & Wäckers, 2004). Moreover, the quantity of some compounds present in the blend increases with the number of herbivores feeding on them (Schmelz *et al.*, 2003). For example, in the case of infestation with aphids, the level of emission of volatiles by plants is related to the duration of infestation (Du *et al.*, 1998). Because the number of aphids also increases with the duration of infestation, the amount of volatiles emitted by infested plants could be a reliable indicator of aphid density on the plants. Indeed, parasitoids that perceive the quantitative variations in volatile emissions can use them as potential cues to fly to the most infested plants (Geervliet *et al.*, 1998; Guerrieri *et al.*, 1999). Even when a plant bears more than one patch, parasitoids could use local emission of volatiles to adjust their residence time in each patch. Although infested plants can emit volatiles systemically, the blend emitted by infested parts differs quantitatively and qualitatively from the systemic response (Röse *et al.*, 1996; Rodriguez-Saona *et al.*, 2002; Scutareanu *et al.*, 2003; Arimura *et al.*, 2004).

The present study aims to identify the role of information given by hosts and by host-induced response of plants in patch use behaviour by insect parasitoids. To do this, parasitoids are tested on patches for which the level of herbivore-induced plant response and the number of aphids are manipulated independently. Assuming that the response of plants is correlated to the duration of infestation and that parasitoids use it as information on patch quality, it is predicted that the residence time and number of attacks of parasitoids on host patches should increase with the duration of the plants' infestation. As shown for other species (van Alphen *et al.*, 2003), it is also expected that the number of hosts in the patch will affect patch use behaviour through direct interactions between parasitoids and hosts.

Materials and methods

Study system

The tritrophic system used in this study involves cucumber plant *Cucumis sativa* L. (Cucurbitales: Cucurbitacae), the cotton aphid *Aphis gossypii* Glover (Homoptera: Aphididae) and the parasitoid *Lysiphlebus testaceipes* Cresson (Hymenoptera: Braconidae). *Lysiphlebus testaceipes* can develop on more than 100 aphid species on a wide variety of plants, including *A. gossypii* on cucumber (Pike *et al.*, 2000). Cucumber plants do emit herbivore-induced volatiles. When infested with *A. gossypii*, the emission of several chemical compounds increases in both infested and uninfested leaves (C. Tentelier, T. C. J. Turlings, and X. Fauvergue, unpublished data). Among the compounds systemically emitted is 6-methyl-5-hepten-2-one, the emission of which is also elicited in wheat seedlings infested with bird cherry-oat aphid (Quiroz *et al.*, 1997) and broad bean infested with pea aphid (Du *et al.*, 1998).

Parasitoids used in this study were young (< 10 h) mated *L. testaceipes* females. They came from a strain reared for more than 200 generations under laboratory conditions on *A. gossypii* as a host insect and cucumber (*C. sativa* var. 'Carmen') as a host plant. Mummified aphids were collected from the rearing and kept individually in small glass vials until emergence of adult parasitoids. Emerging parasitoids were sexed and paired for 1 h. Females were then held in glass vials containing a droplet of honey for a duration of 5 min to 8 h, until they entered the test patch.

Experimental set-up

In order to test if parasitoids use information from both the plant and the aphids to adjust their patch residence time, a 4×3 factorial experiment was carried out where the duration of infestation of the plant by aphids and the number of aphids in the patch were manipulated independently. For this, small cucumber plants (*C. sativa* var. 'serit') with two leaves were used. On one leaf, an aphid colony was reared in order to elicit a response from the plant. The colony was founded by putting a single adult *A. gossypii* female on the leaf and letting it feed and reproduce for 1 , 3, or 7 days. This resulted in colonies of respectively, 11 (10–12), 23 (22–25), and 70 (65–76) aphids (average and 95% confidence interval). A control was added, where no aphid was put on the leaf. Such an increase in durations of infestation is assumed to lead to a corresponding increase in the production of herbivore-induced volatiles by the plant (Du *et al.*, 1998). Glue was placed around the petiole of the infested leaf to prevent the dispersal of aphids to other parts of the plant. Before the behavioural test, all these aphids were gently removed from the leaf with a paintbrush. On the other leaf, an experimental patch was created by placing aphids on the leaf with a paintbrush 5 min before the test. The number of aphids on the patch reflected colonies of 1, 3, and 7 days. Aphids were aggregated in such a way that the area of the colony remained constant ($\approx 3\ \text{cm}^2$) whatever the number of aphids, so that it was the density of aphids in the patches that was manipulated. A test began when a female parasitoid released on the patch performed the first host attack and lasted until she moved further than 1 cm from the nearest aphid for more than 60 s. While the parasitoid was foraging on the patch, the temporal coordinate of each attack was recorded with 0.1 s accuracy on a computer running an event-recorder software. An attack was recorded when the female bent her abdomen between her legs and inserted her ovipositor for more than 1 s into the aphid (Völkl & Mackauer, 2000). Seventeen replicates were done for each of the 12 levels of treatment.

Statistical analysis

To quantify the effects of hosts and host-induced plant response on patch time allocation by *L. testaceipes* females, the data were analysed with a Cox proportional hazards model. Since the seminal work of Haccou *et al.* (1991), this kind of statistical model has been widely used in behavioural studies, particularly to describe mechanisms underlying patch-leaving decisions of parasitoids (van Alphen *et al.*, 2003). This approach allows one to quantify how events occurring during patch exploitation, like ovipositions, affect patch residence time. The model describes the influence of covariates on the leaving tendency of a parasitoid (i.e. the probability per unit of time that the wasp leaves the patch, given that it is still on it) according to the equation:

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

where $h(t)$ is the patch-leaving tendency after a time t spent on the patch, $h_0(t)$ is the baseline-leaving tendency, p is the number of covariates and β_i is the regression coefficient of the covariate z_i. If a coefficient β_i is such that the exponential term (the hazard ratio) is greater than one, then the corresponding covariate z_i has an increasing effect on the parasitoids' leaving tendency, and therefore, a decremental effect on the parasitoids' motivation to stay on the patch. A β_i value leading to a hazard ratio smaller than one will be interpreted in the opposite way. Covariates incorporated in the model were the duration of plant infestation and the density of aphids on the patch, which are both fixed covariates, and the number of host attacks, which is a time-dependent covariate. To test the effect of infestation duration, the baseline hazard was set to the control (i.e. 0 day infestation). For the number of aphids on the patch, it was set to the lowest density. All possible two-by-two interactions between these three covariates were also included in the full model. The coefficients β_i were estimated from the data by means of partial likelihood maximisation (Collett, 1994). Reduction to the most parsimonious model was made using a series of standard likelihood ratio tests (Wajnberg *et al.*, 1999), and adequacy of the final model was assessed by plotting deviance residuals against rank of patch time duration. Computations were carried out in S-Plus (Venables & Ripley, 1994).

To test the effect of plant response and aphid density on the total number of attacks performed by parasitoids on host patches, a generalised linear model based on a log link function and a Poisson distribution was used. Analyses based on likelihood ratio statistics and Pearson's χ^2 tests were used to test main effects and interaction. Validity of the model was assessed by checking plots of residuals against predicted values. Analyses were carried out using the Genmod procedure in the SAS statistical package, version 8.0 (SAS Institute Inc., 1999).

Results and discussion

Patch residence time and total number of attacks by *L. testaceipes* females were highest when infestation duration and aphid density indicated highest patch quality. The proximate cues affecting patch residence time were the herbivore-induced plant response, the density of aphids on patches, and attacks on aphids (Table 1). These results indicate that parasitoids use information from both plants and hosts to adapt their patch use behaviour. The remainder of this paper discusses how *L. testaceipes* females can increase their knowledge of patch quality by combining cues coming from different trophic levels.

As predicted, parasitoids' residence time and number of attacks on host patches increased with the duration of infestation of cucumber plants by *A. gossypii* (for residence time, see Table 1 and Fig. 1; for number of attacks, $n = 203$, $\chi^2 = 42.19$, $P < 0.0001$). This shows that female *L. testaceipes* use herbivore-induced plant response as a cue for patch exploitation. The overall positive effect was

Table 1. Estimated coefficients (β), standard errors (SE), and hazard ratios [exp(β)] for the covariates that remained in the most parsimonious model, i.e. those having a significant effect ($P < 0.05$) on the patch-leaving tendency of *Lysiphlebus testaceipes* females.

Covariates	β	SE	exp(β)	χ^2 (d.f)	*P*-value
Attacks	−0.282	0.0483	0.754	37.03 (1)	<0.0001
0 day infestation	0.000	–	1.000	8.49 (3)	0.037
1 day infestation	−0.514	0.3481	0.598		
3 day infestation	−0.140	0.3459	0.869		
7 day infestation	−0.915	0.3479	0.401		
Low aphid density	0.000	–	1.000	18.41 (2)	0.0001
Medium aphid density	−1.616	0.4498	0.199		
High aphid density	−1.882	0.4478	0.152		
Interaction: Duration of Infestation × Aphid Density	–	–	–	15.83 (7)	0.027
Interaction: Attacks × Aphid Density	–	–	–	12.60 (2)	0.002

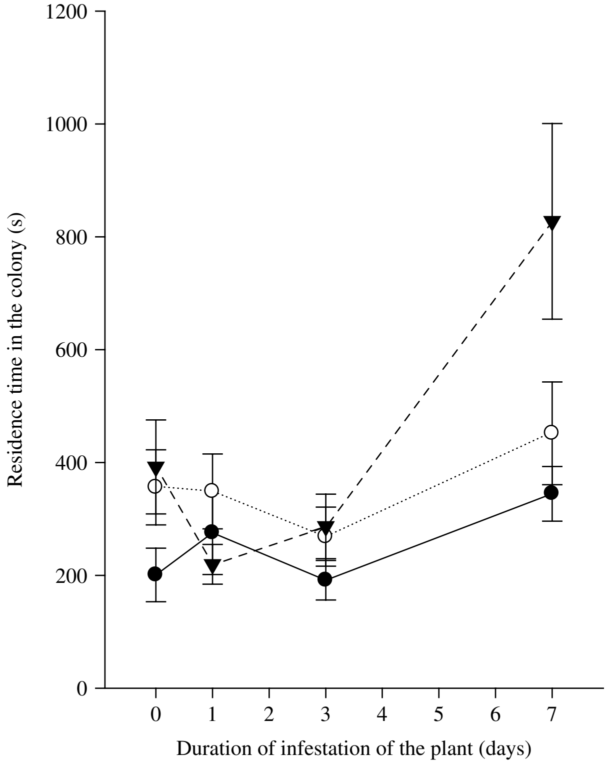

Fig. 1. Average (± SE) residence time of *Lysiphlebus testaceipes* females on patches in which both aphid density and the level of aphid-induced plant response were manipulated. Parasitoids' residence time was observed on patches with low (—●—), medium (···○···), and high (– – ▼ – –) densities of *Aphis gossypii*, supported by cucumber plants infested for 0, 1, 3, or 7 days.

mainly due to the 7 days of infestation, for which patch residence time and number of attacks were longer than for other levels of infestation. This qualitative difference between recent (0 , 1, and 3 days) and older infestation (7 days) might reflect some threshold level, either in the emission of a response by the plant or in the parasitoid's capacity to detect it. Although it has been extensively studied in the context of host location (Vet *et al.*, 2002; and references therein), the use by parasitoids of herbivore-induced plant response has never been considered in the context of patch time allocation. Rather, studies of patch time allocation have focused on the use of kairomones (chemical compounds produced by the hosts) by parasitoids to form their initial estimate of the number of hosts on a patch (review in van Alphen *et al.*, 2003). For the particular case of aphid parasitoids, the initial estimate of patch quality increases with the amount of honeydew produced by aphid nymphs, when the parasitoids have direct contact with honeydew (Budenberg, 1990; Cloutier & Bauduin, 1990; Grasswitz & Paine, 1993; Shaltiel & Ayal, 1998). In the present experiment, however, the effect of infestation duration cannot be due to honeydew because parasitoids were not released on the leaf where the aphid colony had developed. Thus, the effect of infestation duration on the patch residence time of *L. testaceipes* females is clearly due to the response of the plant to aphid infestation.

Information that parasitoids gain from herbivore-induced plant response is complemented by direct encounters with hosts. Increasing aphid density led to an increase in patch residence time and in total number of attacks ($n = 203$, $\chi^2 = 75.28$, $P < 0.0001$). Although this positive effect could be due to visual cues (Battaglia *et al.*, 2000; Völkl, 2000) or aphid cornicle secretions (Grasswitz & Paine, 1992), it was most probably a consequence of the incremental effect of attacks on females' motivation to stay on the patch (Table 1). Such an incremental effect of attacks characterise patch use in several other parasitoid species (review in van Alphen *et al.*, 2003). It was first described on *Venturia canescens* by Waage (1979) who proposed a mechanistic model where a parasitoid's initial motivation to stay is related to the amount of kairomone emitted by the hosts and declines with the time spent on the patch, until a threshold value upon which the parasitoid leaves the patch. Each time a host is attacked, the motivation to stay is incremented by a given value. Such a mechanism has been shown to be adaptive when initial information on patch quality is unreliable (Iwasa *et al.*, 1981; Driessen & Bernstein, 1999). In this case, there are at least two reasons why information provided by plants on patch quality may actually be unreliable. The first is that the response of plants may not increase linearly with the number of hosts, as suggested above. The second is that the herbivore-induced response of plants that is perceived by parasitoids is probably systemic (Paré & Tumlinson, 1999) and therefore provides information on the overall abundance of aphids on the whole plant rather than on the quality of the particular patch visited by the parasitoid. For cases where all hosts are aggregated on one single patch, information from the plant would be reliable, but for plants bearing more than one patch, as it is generally the case with aphids, a direct cue from hosts would be necessary to refine the estimate of patch quality. In the system used in this study, aphid infestation actually elicits a systemic response of cucumber plants (C. Tentelier, T. C. J. Turlings and X. Fauvergue, unpublished data). Hence, the parasitoids might need to complement the information given by plants with direct information from hosts.

Statistically significant interactions between aphid density and other covariates document the way parasitoids integrate information from plants and from their hosts. First of all, the interaction between aphid density and the level of plant response affected patch residence time (Table 1). The effect of aphid density on patch residence time was clear only on plants infested for 7 days (Fig. 1). This suggests that the parasitoids' sensitivity to aphid density could depend on the response of the plant through a potentiation mechanism (Shettleworth, 1998). Parasitoids would be sensitive to direct cues from their hosts only if they had perceived cues from the plant. Secondly, the incremental effect of attacks decreased with increasing aphid density (Fig. 2). A possible explanation for this is

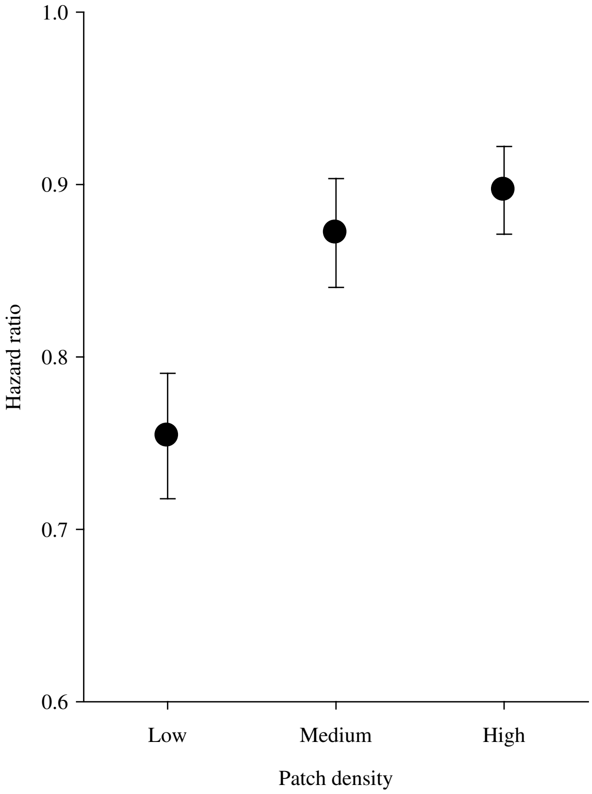

Fig. 2. Estimated hazard ratios (± SE) corresponding to the effect of each host attack on patch-leaving tendency for the three aphid densities. The closer the hazard ratio to one, the weaker the associated incremental effect.

that the first attack has a stronger incremental effect than subsequent ones. Because there are fewer attacks on low density patches, the proportion of first attacks in these patches is greater and the average effect of attacks should therefore be stronger than on more dense patches. From a functional point of view, a strong incremental effect of first attack makes sense when prior information on patch quality is unreliable because a first successful attack indicates unambiguously the presence of hosts in the patch.

The aim of this study was more to understand which proximate information aphid parasitoids use to assess patch quality, than to test whether their behaviour on a patch is optimal. The results show that parasitoids use the herbivore-induced response of plants and direct encounters with hosts to assess patch quality and adjust their patch residence time. More experiments will be necessary to understand how parasitoids allocate their time in more complex environments, with several plants and several patches.

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