Optimal patch-leaving behaviour: a case study using the parasitoid *Cotesia rubecula*

BRIGITTE TENHUMBERG*, MIKE A. KELLER,
HUGH P. POSSINGHAM* and ANDREW J. TYRE*
Department of Applied and Molecular Ecology, University of Adelaide, Waite Campus, Private Bag 1, Glen Osmond,

Summary

1. Parasitoids are predicted to spend longer in patches with more hosts, but previous work on *Cotesia rubecula* (Marshall) has not upheld this prediction. Tests of theoretical predictions may be affected by the definition of patch leaving behaviour, which is often ambiguous.

2. In this study whole plants were considered as patches and assumed that wasps move within patches by means of walking or flying. Within-patch and between-patch flights were distinguished based on flight distance. The quality of this classification was tested statistically by examination of log-survivor curves of flight times.

3. Wasps remained longer in patches with higher host densities, which is consistent with predictions of the marginal value theorem (Charnov 1976). Under the assumption that each flight indicates a patch departure, there is no relationship between host density and leaving tendency.

4. Oviposition influences the patch leaving behaviour of wasps in a count down fashion (Driessen *et al*. 1995), as predicted by an optimal foraging model (Tenhumberg, Keller & Possingham 2001).

5. Wasps spend significantly longer in the first patch encountered following release, resulting in an increased rate of superparasitism.

Key-words: Cox's proportional hazards model, host density, oviposition.

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Introduction

The optimal exploitation of patchily distributed resources has attracted considerable attention from behavioural ecologists and a large body of theory has been amassed (Stephens & Krebs 1986; Perry & Pianka 1997). The most basic prediction is that a consumer should leave a patch when the rate of return in that patch drops below the average rate of return elsewhere in the environment (Charnov's marginal value theorem; Charnov 1976). Therefore, consumers are predicted to stay longer on patches with higher prey density. Patch use by *Cotesia rubecula* (Marshall) (Hymenoptera: Braconidae), a solitary larval parasitoid of the cabbage butterfly, *Pieris rapae* (L.) (Lepidoptera: Pieridae), was examined in this paper.

One important assumption of Charnov's model is that fitness returns from foraging in a patch decrease

*Present address: Department of Zoology and Entomology, University of Queensland, St. Lucia, QLD, 4072
Correspondence: Dr Brigitte Tenhumberg, Department of Zoology and Entomology, University of Queensland, St. Lucia, QLD, 4072. Tel: + 61 73365 3539, Fax: + 61 73365 1655. E-mail: btenhumberg@zen.uq.edu.au

over time. However, the underlying process for this decreasing patch profitability differs between predators and parasitoids. In predators prey consumption results in a decreased encounter rate with the remaining prey, while in parasitoids parasitism in a patch results in more time wasting inspecting and rejecting, or parasitizing already parasitized hosts (= avoiding or engaging in superparasitism). Some parasitoid species may not be able to detect the difference between parasitized and unparasitized hosts (host discrimination), thus increasing the risk of superparasitism. The benefit of superparasitism is generally expected to be low (Visser, van Alphen & Nell 1992), although this varies among species and with time interval since previous parasitism (Field, Keller & Calbert 1997). In addition, parasitoid foraging behaviour can be influenced by limited egg supply (Minkenberg, Tatar & Rosenheim 1992). Hence, the patch leaving behaviour of parasitoids is expected to be influenced by both host density and the total number of ovipositions (e.g. van Alphen & Vet 1986; Godfray 1994). Thus, the rate of return as a function of time for parasitoids is likely to be much more complicated than for predators.

The boundaries of theoretical patches are unambiguous. In reality, patch boundaries may be ambiguous because they depend on the forager's perception of the environment (Ayal 1987). What is considered to be a patch by an observer may not necessarily agree with what is considered to be a patch by a forager. A further complication arises when patches have a hierarchical structure and foraging behaviour changes between patch levels (Kotliar & Wiens 1990; Keller & Tenhumberg, in press). The patch hierarchy for *C. rubecula* could range from fields of host plants, down to individual host plants, single leaves on host plants and, finally, down to individual hosts on leaves. For all these reasons, it is important and often difficult to correctly match the scale of the observation unit to the scale of the theoretical model (Addicott *et al.* 1987; Ayal 1987; Godfray 1987). Identifying appropriate patch boundaries is critical to rigorously testing theoretical predictions. In agricultural contexts, we expect female *C. rubecula* to spend most of their life within a single cabbage field and optimize their offspring production among cabbage plants (M. Keller, personal observation). To explore this hypothesis patch leaving behaviour was studied in an array of several cabbage plants (= single patches) each bearing different numbers of host insects.

After defining a particular area as a patch and choosing an appropriate study unit, it can also be difficult to determine when a forager actually leaves each patch. Some parasitoids, such as *C. rubecula*, often take flight immediately after attacking a host caterpillar, but subsequently return to the same plant (Nealis 1986). Such revisits also occurred without a host having been attacked. The high frequency and variable duration of these short flights raises the question of how to distinguish between inter- and intra-patch flights. Landing on another plant is not a reasonable criterion for defining the end of a patch visit, because in a limited experimental habitat wasps will sometimes return to the same plant by chance, even after having 'left'. Intra- and inter-patch flights were distinguished quantitatively using a statistical method designed for behavioural data analysis – log survivor curves (Scherer & Ekman 1982; Haccou & Meelis 1994).

In this paper, identifying the correct cut-off point for intra-patch flights was crucial for detecting the influence of host density and oviposition on patch leaving behaviour. As expected from the marginal value theorem (Charnov 1976), the leaving tendency of *C. rubecula* was negatively correlated with host density. Leaving tendency was increased by high oviposition rates, suggesting that *C. rubecula* uses a countdown rule (Driessen *et al.* 1995). In addition, wasps spent much longer on the first patch after release compared to subsequent patch visits. This study of the patch leaving behaviour of *C. rubecula* is unique because the wasps were observed under field conditions. Our conclusions highlight the importance of correctly identifying patch-leaving behaviour.

Materials and methods

INSECTS AND PLANTS

Parasitic wasps, *C. rubecula*, and their hosts the cabbage white butterfly, *P. rapae*, were collected from gardens near Adelaide, South Australia. The rearing methods for these insects were described elsewhere (Keller 1990). Cabbage plants with 8–10 fully expanded leaves were infested with 2–4-day-old larval *P. rapae* 1 day before the experiment. Mated *C. rubecula* were marked with a dot of coloured enamel paint (Testor Corp., Rockford, Illinois) on the thorax to allow individual identification in the field. The wasps were held overnight in 150-mm Petri dishes with honey, a cabbage leaf and eight host larvae. This ensured that the wasps were not hungry, and had experience with hosts and host-associated kairomones.

EXPERIMENTAL DESIGN AND IMPLEMENTATION

The experiment was carried out in the Waite Campus Arboretum in summer 1988, 1989 and 1990. On the day of the experiment cabbage plants infested with 0, 1, 2 and 5 host larvae, which had fed on the plant for 1 day, were arranged randomly in a Latin square design marked by gridlines on the ground (Fig. 1). A new arrangement was used for each experiment. Prior to release, wasps were exposed in a 150-mm Petri dish to a cabbage leaf with feeding damage of *P. rapae* for two min. The tendency of wasps to fly away when handled was overcome by this exposure. Wasps were released from a 15×50-mm vial supported 50 mm above the ground by a wooden block ($n = 3$ wasps in 1988, $n = 13$ wasps in 1989, and $n = 2$ wasps in 1990). As soon as a wasp flew
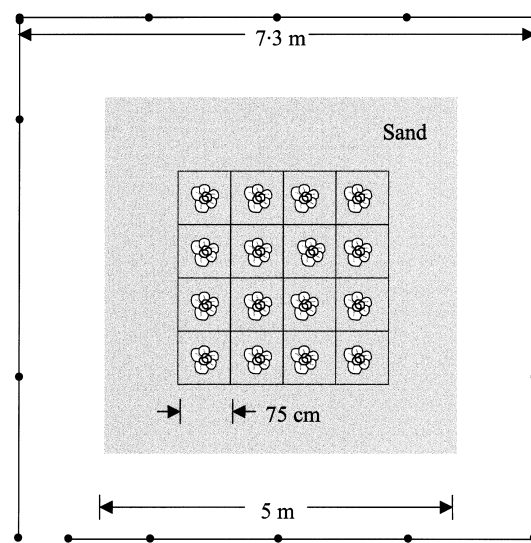

Fig. 1. Layout of field plot showing the positions of cabbages and grid lines. Potted cabbage plants were placed into buried pots so that the soil level was flush with the ground. Wasps were released in the centre of the grid. Light sand was spread on the ground to facilitate observations. Shade cloth around the perimeter (dotted line) minimized wind gusts.

from the release vial, her behaviour was recorded by two observers on a cassette recorder. The behaviour, position within the experimental arena and leaf number visited was transcribed with event recording software accurate to 1 s. Plants on which a larva was parasitized during an observation were replaced with fresh plants before the release of the next wasp.

DEFINITION OF PATCH DEPARTURE

An entire cabbage plant was defined as a 'patch'. A patch-leaving event could be identified by several characteristics including onset of flight, flight destination (landing on a different plant), flight duration or flight distance. Wasps leave a patch when they fly off a plant in search of another patch. However, wasps in this study frequently returned to the same plant. There are two possibilities for flights that lead back to the same plant. First, the wasps could be actually 'leaving', and simply end up back on the same plant either by chance or because there are no 'better' plants around. In this case all flight events should be treated as patch departures and subsequent searches treated as new patch visits. The second possibility is that wasps could be flying simply as a more efficient means of reaching another part of the plant and not actually leaving to move to another plant. In this case, return visits are part of the same patch visit. In the first case, all flights represent a single behavioural category, patch departure, while in the second case flights off a plant represent a mixture of two behaviours, within patch movements and patch departures.

Flights that returned the wasp to the same plant varied in length from 1 to 222 s, while flights between two different plants varied from 1 to 254 s. Clearly, neither the destination nor the duration can be used to distinguish between 'leaving' and 'remaining' flights. *C. rubecula* usually changed leaves on a plant by flying. Therefore, short distance flights could mainly be associated with searching all over a plant for hosts. To test this hypothesis the data set was split into short distance and long distance flights, based on whether wasps flew over a grid cell line (see Fig. 1). Note that a wasp could return to the same plant and be considered as 'leaving' the patch. The shortest duration of those flights was 1 s and returns to the same plant after crossing a grid cell line accounted for 36% of flights.

The two possible definitions of patch leaving (flying off a plant and flying over a grid cell line) were examined using ln – survivor curves. It is commonly assumed that a single 'behaviour' should have a constant probability of terminating, leading to an exponential distribution of behaviour durations (Haccou & Meelis 1994). This assumption can be tested graphically by plotting the logarithm of the 'survivor function

$$S(x) = \frac{j}{n} \qquad \text{eqn 1}$$

where n is the total number of observations, and j is the number of observations with a duration greater than or

equal to x. $Ln[S(x)]$ is a straight line with a slope of $-\lambda$ for an exponential distribution with parameter λ. If a set of observations consists of a mixture of different behaviour categories, i.e. a mixture of within and between patch flights, $Ln[S(x)]$ will be concave upward. The set of all flight times was tested for the presence of mixtures of exponential distributions with Darling's test for mixtures (Haccou & Meelis 1994). After splitting the flight records into within patch and between patch flights based on the distance travelled, the flight record subsets were tested for exponentiality against undetermined alternatives using Kolmogorov–Smirnov tests. We further assessed the fit visually by examining the estimated survival curves for the points at which the expected straight line was outside the 95% confidence limits of the survival curve. To demonstrate the effect of patch definition on the interpretation of a wasp's behaviour, the data were analysed assuming either that a wasp leaves a patch as soon as she takes flight or that some short distance flights represent within patch movements.

COVARIATES

Three covariates were included in the Cox's proportional hazards model: host density, oviposition, and whether a wasp was foraging on the first patch after release or a later patch. The last covariate was chosen to compensate for acclimatization behaviour of wasps because unpublished data by Mike Keller indicated atypical behaviour of wasps directly after their release.

The first two covariates were included because there is a range of theoretical and empirical evidence that host density and oviposition influences the patch leaving behaviour of foraging parasitoids (Driessen & Bernstein 1999). Depending on the parasitoid species each oviposition either increases (countdown mechanism) or decreases this leaving tendency (count-up mechanism; Driessen & Bernstein 1999).

In general, foragers are expected to stay longer on patches with higher resource density. According to the marginal value theorem (Charnov 1976), a forager should leave a patch when the rate of return in a patch drops below the average rate of return elsewhere in the environment. A parasitoid wasp reaches this leaving threshold later in patches with higher host density. In wild populations cabbage plants usually contain between zero and two *P. rapae* hosts (Harcourt 1961; Kobayashi 1966; Jones 1977). Three common host densities (0, 1 or 2 hosts per plant) and a very high density of 5 hosts per plant were chosen for this experiment.

Most wasps left a patch either without ovipositing or after one oviposition. As a consequence, there was not enough data for the Cox's proportional hazard model to test the effect of the number of previous ovipositions. Hence, the effect of the oviposition rate, the reciprocal of the time before the previous oviposition, was included in the model instead. We used the whole data set to calculate the oviposition rate, instead of splitting the data according to the number of ovipositions.

COX'S PROPORTIONAL HAZARDS MODEL

The patch departure behaviour of the wasps was modelled with methods from survival analysis, by assuming there is some baseline rate at which wasps switch from searching within patches for hosts to searching between patches for new patches, and that this patch departure rate is influenced by variables such as the host density within patches or the number of previous ovipositions (Haccou *et al*. 1991; Haccou & Hemerik 1985).

The patch departure rate is assumed to be a function of time, and certain events, called 'renewal points', reset the patch departure rate to its initial value. In the simplest case the amount of time spent searching in a patch is the time between two renewal points (Haccou *et al*. 1991; Hemerik, Driessen & Haccou 1993). The basic renewal points for the analysis were landing in and departing from a patch. Oviposition events were defined as renewal points, because if oviposition is important, the transition rate will be different following an oviposition.

One important feature of the analysis of behavioural durations is censoring, which occurs if the start or finish of a behavioural event was not observed (Haccou & Meelis 1994). Including these records in the analysis is important because they contain the information that the behaviour lasted at least for the observation time. If censored records were excluded, then the analysis would be biased in favour of shorter behavioural records. Three censoring events were found in the data: (1) experiment ended before wasp left the plant; (2) a wasp inadvertently slipped off the plant; and (3) oviposition. Oviposition was a censoring event because the wasp might have left at a different time if no oviposition had occurred.

The effect of covariates on patch departure rates was examined using Cox's proportional hazards model. The cumulative patch departure rate, or 'leaving hazard' in survival analysis terminology, was estimated as $-Ln[S(x)]$ (Haccou & Meelis 1994). The survivor function [$S(x)$, equation 1] is estimated by patch leaving or 'failure' events. We used the Kaplan–Meier estimator to calculate $S(x)$ (Cox & Oakes 1984), because it accounts for censoring. The steeper the slope of $-Ln[S(x)]$, the higher the patch leaving rate.

In Cox's proportional hazards model, the observed hazard rate is the product of a baseline hazard and a factor that gives the joint effect of a set of covariates $z_1, \ldots, z_p$. The effect of a covariate is assumed to be proportional across the full range of the baseline hazard (the 'proportionality assumption'). The general form of the model is:

$$h(t,z) = \lambda_0(t)\exp\sum_{i=1}^{p}(\beta_i z_i),\qquad \text{eqn 2}$$

where $h(t,z)$ denotes the observed hazard rate, $\lambda_0(t)$ the baseline hazard, t is the time since the last renewal point, and $\beta_1, \ldots \beta_p$ are the relative contributions of the covariates. The form of $\lambda_0(t)$ is left unspecified. $\lambda_0(t)$ and $\beta_1, \ldots \beta_p$ are estimated by likelihood maximization (Cox & Oakes 1984; Kalbfleisch & Prentice 1990;

Haccou & Meelis 1994). The significance of the model was tested with likelihood ratio tests and the proportionality assumption using the asymptotic χ^2 test statistic T(G) (Grambsch & Therneau 1994). In this test, significant non-proportionality is indicated by statistically significant *P*-values. The survival analysis was performed in S-PLUS, version 4·5 (MathSoft, Inc., Bagshot Surrey, UK).

Results

PATCH LEAVING EVENT

In 25–46% of cases *C. rubecula* returned to a plant without landing somewhere else (Fig. 2). The frequency of one or more return visits tended to be higher on plants with 2 or more hosts compared to 0 or 1 host per plant. This is consistent with wasps being more likely to land on plants with higher host densities. Moreover, wasps that returned at least once were also more likely to return multiple times on plants with more hosts.

The two different patch-leaving criteria were tested first. A patch-leaving event was characterized by either (1) taking flight or (2) by flying longer distances (crossing at least one grid cell line). The ln-survivor curve of all flight times was concave, consistent with a mixture of 'within-patch' flights and 'patch-leaving' flights (Darling's $K_n = 37437$, $P < 10^{-6}$, Fig. 3a). However, undertaking long flights was also not a perfect discriminator of patch-leaving events. The hypotheses that durations of flights within one grid cell (Fig. 3b; Komolgorov–Smirnov $D = 0·0868$, $P = 0·0003$) and flights that included at least one grid cell change (Fig. 3c; Komolgorov–Smirnov $D = 0·134$, $P = 0·003$) were distributed exponentially have to be rejected. However, the fit of the data to the exponential distribution within each component was drastically improved by
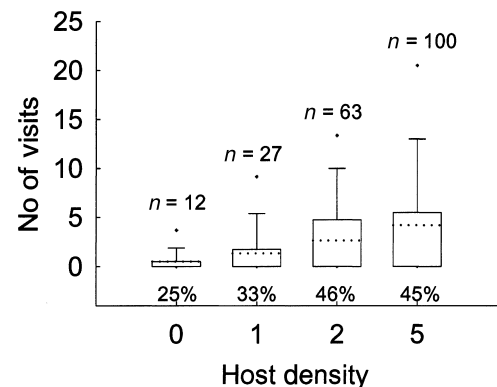

Fig. 2. Box and whisker plots of the number of return visits to a plant before landing on a different plant (18 wasps). The median number of returns was 0 in all cases. The box plots indicate the mean (dotted line), 75th percentile (top of box), 90th percentile (whisker) and the 95th percentile (dot). The percentage values below the box refer to how often wasps returned to land on the same plant one or more times after taking flight. The sample sizes indicate the number of initial visits to plants at each host density.
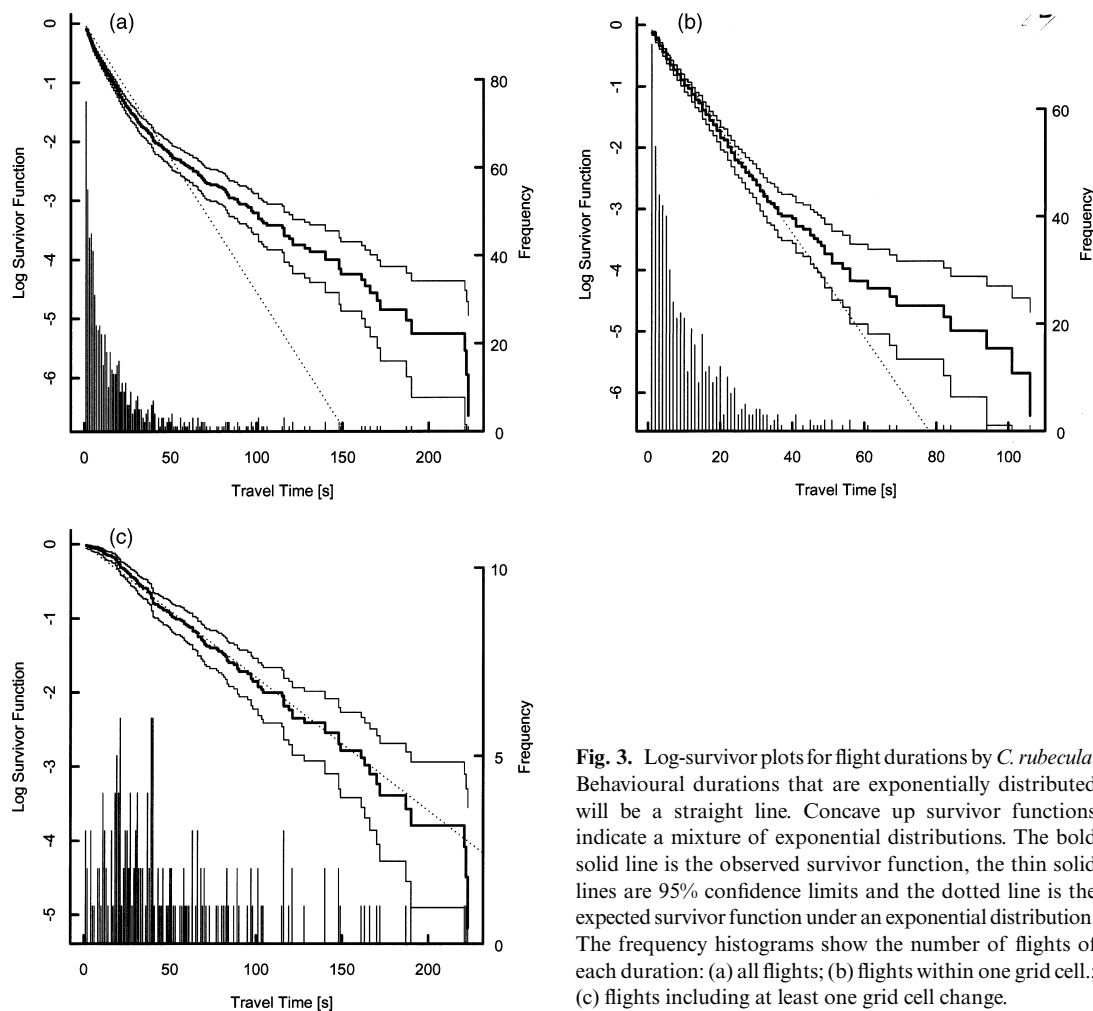
Fig. 3. Log-survivor plots for flight durations by *C. rubecula*. Behavioural durations that are exponentially distributed will be a straight line. Concave up survivor functions indicate a mixture of exponential distributions. The bold solid line is the observed survivor function, the thin solid lines are 95% confidence limits and the dotted line is the expected survivor function under an exponential distribution. The frequency histograms show the number of flights of each duration: (a) all flights; (b) flights within one grid cell.; (c) flights including at least one grid cell change.

breaking the distribution into two components. For within grid cell flights, deviations from an exponential distribution occur primarily in very long lasting flights (< 2% of 589 flights) and this excess of long flights could represent true patch departures misclassified as within-patch flights by our criterion. For between grid cell flights the deviations are primarily in very brief flights (< 16% of 178 flights) and this excess could be true within-patch flights misclassified as patch-leaving events. The overall percentage of misclassification of patch leaving or staying was small (< 5% of 767 flights), so a wasp was considered to have left a patch as soon as she crossed a grid cell line.

OVIPOSITION BEHAVIOUR

C. rubecula often left plants without finding hosts, and also superparasitized hosts during the experiment. Wasps left a plant without encountering a host 78% of the time. Female wasps sometimes laid more than one egg at higher host densities, however, there was no significant effect of host density on the relative frequency of 0, 1, or 2 or more ovipositions (test of independence, $G = 6.55$, $P = 0.47$, d.f. = 7; Table 1). Even though most wasps did not lay more eggs than there were hosts

Table 1. Distribution of ovipositions on plants with different host densities. Entries in bold highlight cases where wasps laid more eggs than there were hosts available, and superparasitism certainly occurred

	Number of ovipositions					
Host density	0	1	2	3	4	9
1	26	6	**1**	0	0	0
2	54	8	3	0	0	0
5	98	16	10	4	1	**2**

available, 30% of all ovipositions resulted in superparasitism (The percentage of hosts that contained 1, 2, 3 or 4 eggs per host was 70, 19, 6 and 5%, respectively). This suggests that some hosts were more attractive, easier to detect or more accessible than others.

LEAVING TENDENCY

The effect of (1) host density, (2) oviposition rate, and (3) whether or not the wasp was searching on the first patch on leaving tendency of *C. rubecula* were estimated with a Cox's proportional hazards model. The proportionality assumption was fulfilled for all covariates

Table 2. Summary of the model selection procedure for the Cox's proportional hazards model

Initial model	Deviance	ΔD	d.f.	Covariate tested	P
Baseline hazard only	611·6	12·4	3	Density, oviposition rate, and first patch	< 0·0001
		6·9	1	Density	0·0002
		3·5	1	Oviposition rate	0·008
		1·6	1	First patch	0·08
Baseline + Density	604·7	3·6	1	Oviposition rate	0·009
		2·2	1	First patch	0·037
Baseline + Density + Oviposition rate	601·1	2	1	First Patch	0·042

Table 3. Final coefficients for each of the three covariates

	β	SE(β)	Z	P
Host density	−0·1995	0·0509	−3·92	< 0·0001
Oviposition (rate/min)	0·0678	0·0182	3·74	0·0002
1st Patch	−0·5983	0·3180	−1·88	0.06

(host density: $\chi^2 = 0.05688$, $P = 0.8115$; oviposition: $\chi^2 = 0.05141$, $P = 0.8206$; 1st patch: $\chi^2 = 0.86404$, $P = 0.3526$). The results are summarized in Tables 2 and 3. A decreasing leaving tendency is indicated by a negative β-value resulting in longer patch times.

1. Host density had a negative effect on leaving tendency of *C. rubecula* (negative β-value). For example, the leaving tendency was 20% smaller [exp(−0·1995) = 0·8] on plants with one host compared to plants with no host. For wasps that left a plant without laying an egg, this resulted in longer average patch residence times on plants with higher host densities (33, 48, 95 and 115 s on plants with 0, 1, 2 and 5 hosts, respectively).

2. The effect of oviposition rate was opposite to that of host density (positive β-value). So, if wasps had two ovipositions per minute the leaving tendency increased by 7% compared to one oviposition per minute [exp(0·0678) = 1·07].

3. Whether or not a wasp was in the first patch (first patch covariate) did not significantly reduce the deviance on its own, but was a marginal contributor when the other two covariates were included. The leaving tendency of wasps during the first patch visit was 45% smaller [exp(−0·5983)] than the leaving tendency on patches visited later.

Under the assumption that all flights, either within or between grid cells, are patch-leaving events, there was no significant influence of host density on leaving tendency (Likelihood Ratio statistic 0·73, d.f. = 1, $P = 0.39$).

Discussion

Studying patch leaving behaviour of parasitoids is important because it improves our understanding of the underlying mechanisms of behaviour, and the impact of predators and parasitoids in controlling pest populations. In this study, the influence of oviposition and host density on the patch leaving behaviour of *C. rubecula* was examined. There is a large body of evidence amassed that both factors strongly influence the foraging behaviour of parasitoids in the laboratory. This study is unique because our experiments were set up in the field. In addition, our study highlights the importance of correctly defining patch-leaving behaviour and identifies acclimatization behaviour in *C. rubecula* for the first time.

Field observations of behaviour are important in elucidating interactions between parasitoids and their hosts. Even though there are difficulties associated with tracking small, freely flying insects, observations in the field can reveal how changes in weather, the seasonal characteristics of plants, and the availability of hosts affect the foraging behaviour and success of parasitic wasps (Casas *et al.* 1993). Also, behaviour observed in laboratory arenas may not reflect what happens in the field. For example, the braconid wasp *Diaeretiella rapae* (McIntosh) responds to odours associated with brassicaceous host plants in a Y-tube olfactometer (Read, Feeney & Root 1970). However, this was not observed in field experiments, possibly because the laboratory arena did not take into account the distance over which attraction occurs (Sheehan & Shelton 1989).

OPTIMAL PATCH LEAVING

Optimal foraging theory assumes that an animal's behaviour is shaped by natural selection and, as a consequence, animals may have evolved to follow certain rules of thumb that result in behaviour close to the optimal behaviour. This paper focuses on the role of host density, and oviposition or oviposition rate on the patch-leaving behaviour of *C. rubecula*. Our results suggest that the initial leaving tendency of *C. rubecula* decreases with increasing host density. Wasps may estimate the host density by means of the kairomone concentration, which has been demonstrated for other parasitoid species (Waage 1978, 1979; Galis & van Alphen 1981; Dicke *et al.* 1985; Geervliet *et al.* 1998; Thomsen 1999). The effect of host density on the leaving tendency broadly follows from the marginal value theorem and general rate-maximizing theory (Charnov 1976). The higher the host density, the higher is the potential offspring

production in the current patch relative to the environmental average, consequently wasps should exploit patches with higher host densities more thoroughly.

Waage (1979) proposed a model connecting the influence of host density and oviposition. He suggested that a parasitoid leaves a patch when her 'responsiveness' to the patch drops below a critical value. The leaving tendency calculated in this paper would be the inverse of the responsiveness. The initial responsiveness is determined by the concentration of kairomones in the patch, i.e. the parasitoid's estimate of the host density (patch quality). If nothing else happens the wasp leaves after a fixed giving-up time. If a host is encountered the responsiveness can either increase (incremental mechanism; Waage 1979) or decrease (count down mechanism; Driessen *et al*. 1995). If the estimate of patch quality is poor, the incremental mechanism will ensure that a patch with lots of hosts is not abandoned too early or that females do not waste too much time on low quality patches. Alternatively, if a forager's estimate of patch quality is very good, e.g. because hosts are uniformly distributed among patches (Iwasa, Higashi & Yamamura 1981; Driessen *et al*. 1995), a decremental mechanism is more advantageous. In the literature, there is evidence for both mechanism (see review in Driessen & Bernstein 1999).

C. rubecula females frequently left patches after laying a single egg, and a high oviposition rate increased the leaving tendency. Both results are consistent with a countdown mechanism, and qualitatively match the predictions made by Tenhumberg *et al*. (2001). Both the host distribution and a high risk of self-superparasitism can promote a countdown mechanism. In the field, cabbage plants rarely contain more than two hosts (Harcourt 1961; Kobayashi 1966; Jones 1977). On plants with two hosts, females have a 50% chance that the second host encountered already contains an egg. As *C. rubecula* seem not to discriminate between healthy and parasitized hosts, females run a high risk of superparasitism if they do not leave after the first oviposition. *P. rapae* larvae tend to avoid each other by moving to a different leaf or to a distant area of the same leaf. So, for two ovipositions to occur very close together in time (high oviposition rate), the wasp most likely encountered the same host twice.

Tenhumberg *et al*. (2001) constructed a stochastic dynamic programming model of the patch leaving behaviour of *C. rubecula*. The influence of the number of eggs laid in the current patch, and the distribution of hosts among plants was included in the model. This model predicted both a positive response to host density and a countdown response to oviposition as a consequence of the basic biology of the system. The assumption that females are unable to discriminate between parasitized and healthy hosts is crucial for these predictions. Rosenheim & Mangel (1994) demonstrated the sufficiency of the cost of self-superparasitism to promote early departure from incompletely exploited patches.

The results presented in this paper contradict recently published experiments on the patch leaving behaviour of *C. rubecula* at the scale of a single leaf (Vos, Hemerik & Vet Louise 1998). The authors report a lower tendency to leave infested leaves compared to uninfested leaves, but there was no difference in the tendency to leave leaves of different host densities. Host encounters increased the patch residence time suggesting an incremental mechanism. It is possible that there are genetic differences in patch leaving rules between wasps from Australian and European populations. Differences between strains in patch leaving responses following oviposition have been reported for the parasitoid *Venturia canscens* (Gravenhorst) (Waage 1979; Driessen *et al*. 1995).

IMPORTANT CONSIDERATIONS FOR THE
DESIGN OF FORAGING EXPERIMENTS

In our study we identified two factors influencing the interpretation of the results: (1) definition of patch leaving, and (2) acclimatization behaviour. We discuss each of these factors in turn.

Correctly identifying the cut-off point for a patch visit was crucial for detecting the effect of host density on the patch-leaving behaviour predicted by optimal foraging theory. This highlights the importance of correctly defining patch-leaving behaviour. According to Waage (1978, 1979) crossing a patch boundary elicits a change in behaviour. In the simplest case transition to leaving a patch is identified by taking flight. Recognizing a change in behaviour is more difficult for animals, such as *C. rubecula* that fly both within and between patches. We used log-survivor curves to test whether our distinction between within and between patch flights based on flight distance was correct. Although our distinction was not perfect, the percentage of misclassifications was low. A wasp's patch leaving behaviour was consistent with optimal foraging theory only when departing flights were distinguished from flights within the same patch.

We found that *C. rubecula* needs time to settle in a new environment. This acclimatization behaviour is expressed in an extended patch time resulting in twice as many ovipositions in the first patch when compared to subsequent patches. This results in correspondingly higher superparasitism rates. The acclimatization behaviour did not interfere with the detection of the effects of oviposition rate and host density. However, for other questions, such as addressing the efficiency of parasitoids as biocontrol agents, it might be better to exclude any acclimatization behaviour from the experiment. For applied research questions it is important to know the exploitation rate or what percentage of hosts escape parasitism. Both parameters will be influenced by acclimatization behaviour. An unusually long patch residence time will reduce the percentage of hosts escaping parasitism, as well as the foraging efficiency of parasitoids as they waste

more time superparasitizing, or inspecting and rejecting already parasitized hosts.

Acknowledgements

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