

Habitat assessment by parasitoids: mechanisms for patch use behavior

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Animals foraging for patchily distributed resources may optimize their foraging decisions concerning the patches they encounter, provided that they base these decisions on reliable information about the profitability of the habitat as a whole. Females of the parasitoid *Lysiphlebus testaceipes* exploit aphid hosts, which typically aggregate in discrete colonies. We show here how between-colony travel time and the number of aphids in previously visited colonies affect parasitoid foraging behavior. We first assumed that parasitoids use travel time and previous colony size to estimate a mean rate of fitness gain in the habitat and derived quantitative predictions concerning the effect of these two variables on patch residence time and patch-leaving rate of attack. We then tested these theoretical predictions in laboratory experiments in which female parasitoids were allowed to visit two successive colonies. As predicted, the observed residence time in the second colony increased with increasing travel time and decreasing size of the first colony. Patch-leaving rate of attack decreased with increasing travel time but was not affected by previous colony size. These results suggest that parasitoids use these two variables to assess habitat quality. However, discrepancies between the data obtained and quantitative predictions show that the effect of travel time on patch use may be more complex than assumed in our model. *Key words:* learning, *Lysiphlebus testaceipes*, marginal value theorem, optimal foraging theory, patch size, travel time. [*Behav Ecol*]

Animals that estimate habitat quality are able to adapt their behavior accordingly. In habitats in which resources are patchily distributed, foragers that estimate habitat quality accurately can optimize the time spent on each patch (Charnov 1976). The optimization of individual behavior in this way leads to a stable distribution of the forager population among the patches of the habitat (Bernstein et al. 1988, companion paper). The decision to stay on a patch or to leave it requires knowledge of the maximal average rate of fitness gain in the habitat. One of the predictions of the marginal value theorem (MVT; Charnov 1976) is that increases in maximal average rate of fitness gain (i.e., habitat profitability) should lead to decreases in the time of residence on a patch with a given resource level. Although foragers are unlikely to be able to measure maximal average rate of fitness gain directly, they can estimate this parameter from past experience, through a learning mechanism. A version of the MVT based on learning predicts that a forager can reach the optimum if it estimates its own average rate of gain in the habitat and leaves patches when its instantaneous rate of gain equals its estimate of average rate (McNamara and Houston 1985).

What information do foragers use to estimate the average rate of gain in the habitat? Two factors provide foragers with reliable information for this estimation: 1) time traveled between previously visited patches and 2) resource levels in previously visited patches. The average rate of gain is the ratio between the sum of gains on all patches and the sum of travel times and residence times (Charnov 1976). From this defini-

tion of the average rate, increasing the time required to travel between patches and decreasing the size of previous patches should decrease estimates of average rate and increase residence time on a patch of a given size. Travel time has been shown to affect patch residence time primarily in vertebrates such as pigeons (Todd and Kacelnik 1993), starlings (Kacelnik 1984; Cuthill et al. 1990; Brunner et al. 1992), and guinea pigs (Cassini et al. 1990). Several studies have demonstrated an effect of the size of alternative patches on residence time on a given patch (Stephens and Krebs 1986; Nonacs 2001), but none has clearly shown how the number of items in a patch affect residence time on the following patch. A recent study showed that *Asobara tabida* females increase their residence time on host patches in response to an increase in travel time (Thiel and Hoffmeister 2004), but the effect of the number of hosts on the previous patch remains to be studied.

In this study, we used the aphid parasitoid *Lysiphlebus testaceipes* Cresson (Hymenoptera: Braconidae) and its host, *Aphis gossypii* Glover (Hemiptera: Aphididae), to investigate whether parasitoids use time traveled between host patches and number of hosts in previous patches to assess habitat quality and to optimize their patch use behavior (i.e., maximize their average rate of gain). We first derived a set of quantitative predictions concerning the effect of travel time and size of previous patch on parasitoid patch use. The predictions rely on hypotheses of the MVT based on learning. We then experimentally tested these predictions with *L. testaceipes*. We manipulated the number of aphids on a patch or the travel time between two patches and observed the foraging behavior of the parasitoids on the second patch.

A number of features of the *A. gossypii*–*L. testaceipes* system make it particularly suitable for testing the predictions of the MVT based on learning. First, aphid larvae aggregate around their mothers in colonies, which form discrete patches of variable density on plants. Female parasitoids visit several colonies during their lifetime and have to decide how much time to allocate to each colony. Second, *L. testaceipes* females

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lay a mean of 180 eggs during the 2.56 days of their life (measured in the laboratory at 25°C; van Steenis 1994). In the field, such a large number of eggs to be laid in such a short life span may result in time limitation—an assumption underlying the MVT and other rate-maximizing models (Sevenster et al. 1998). Third and most importantly in the context of learning, aphid populations show some of the highest rates of population increase known in animals. For example, the intrinsic rate of increase of *A. gossypii* in cucumber greenhouses is $r = 0.35 \text{ day}^{-1}$ (Rochat 1997). This implies that before the carrying capacity of the environment is reached, the number of host aphids can increase by a factor of 25 between two successive generations of *L. testaceipes* (9.5 days for females at 25°C; van Steenis 1994). This extremely high level of variation in habitat quality is known to favor the evolution of learning because a fixed response to average profitability over evolutionary time would almost never be adaptive (Stephens 1991).

THEORETICAL PREDICTIONS

Let us consider a forager that searches randomly on depleting patches. The cumulative gain on a patch may be defined as an increasing function with negative acceleration (Stephens and Krebs 1986). Based on a Poisson distribution, such a function takes the form:

$$g(t) = K \left[1 - \exp\left(\frac{-t}{KTh}\right) \right], \quad (1)$$

where $g(t)$ is the cumulative gain at time t , K is the maximum number of attacks by the forager within the patch, and Th is the handling time, that is, the time taken by the forager to attack a host (or prey) (for previous use of this function see Cowie 1977; Ollason 1980; Charnov and Parker 1995). With such a function, the instantaneous gain rate is easily calculated as the derivative of $g(t)$ with respect to t ,

$$g'(t) = \frac{1}{Th} \exp\left(\frac{-t}{KTh}\right). \quad (2)$$

According to the MVT based on learning, foragers should leave patches when the instantaneous rate of gain decreases to their estimate of habitat-wide maximal average rate, when $g'(t) = \gamma$. Replacing $g'(t)$ by its corresponding function gives the optimal patch residence time:

$$t^* = -KTh \ln(\gamma Th). \quad (3)$$

Hence, an increase in the estimated average rate of gain γ , for a given type of patch, should result in an increase in patch-leaving rate of gain, $g'(t^*)$, and decreasing patch residence time, t^* . A verbal interpretation of this simple mathematical argument is that foragers are likely to assess a given patch as less profitable if they have previously experienced a rich section of the habitat than if they have experienced a poor section. This results in foragers leaving the patch earlier, when the instantaneous rate of gain is still high.

Long travel times between patches should indicate a low average rate of gain. In particular, Dusenberry (1989) showed that when foragers search patches by random walk, the time taken to detect a patch is inversely proportional to the density of patches in the habitat. The forager's estimate of the maximum average rate of gain can be expressed as follows:

$$\gamma = \frac{1}{a\tau}, \quad (4)$$

where a is the searching efficiency of the forager and τ is the travel time between the two patches. Thus, the optimal

patch-leaving rate of gain and the optimal patch residence time become:

$$g'(t^*) = \frac{1}{a\tau} \quad (5)$$

and

$$t^* = -KTh \ln \frac{Th}{a\tau}, \text{ respectively.} \quad (6)$$

The predictions of Equations 5 and 6 are represented graphically in Figure 1A,C.

The estimate of average rate of gain increases with the resource level of the previous patch. It is both realistic and simple to suppose that an increase in the density of resources in every patch leads to a proportional increase in the estimate of maximum average attack rate. The forager's estimate of the maximum average rate of gain may therefore be expressed as:

$$\gamma = bd + c, \quad (7)$$

with $b \neq 0$, where d is the density of resources on the previous patch, b is the slope of the relationship, and c is a residual estimation in the absence of a previous patch. The optimal patch-leaving rate of gain and the optimal patch residence time therefore become:

$$g'(t^*) = bd + c \quad (8)$$

and

$$t^* = -KTh \ln [Th(bd + c)], \text{ respectively.} \quad (9)$$

Figure 1B,D represents graphically the predictions of Equations 8 and 9.

MATERIALS AND METHODS

We carried out two experiments to test the predictions derived above concerning the effect of travel time and size of previous patch on residence time and patch-leaving rate of gain. The aim was to quantify the foraging behavior of *L. testaceipes* females on a standard colony of *A. gossypii* (the test patch) after they had visited the first colony (the conditioning patch). A patch consisted of an *A. gossypii* colony developed on a leaf of cucumber (*Cucumis sativa*, var. Serit). To simulate a natural aphid aggregation, each patch was created by releasing a single 24-h-old virginoparous adult female under one leaf of the plant. The female was allowed to reproduce for a controlled period of time, depending on the desired patch size. Tested parasitoids were young (<24 h) virgin *L. testaceipes* females. They came from a strain initially founded from 10 individuals emerging from mummies of *A. gossypii* collected on hibiscus in Lisbon, Portugal. Before the experiments, this parasitoid strain was mass reared for about 200 generations on *A. gossypii* as a host insect and *C. sativa* (var. Carmen) as a host plant. Tested individuals were initially kept naive by isolating them, at the mummy stage of the parasitized host, in different glass vials before emergence. After emergence, adults were fed on honey.

We manipulated either the travel time between the conditioning patch and the test patch or the size of the conditioning patch. The foraging behavior of females on the test patch was quantified by recording the temporal ordinate of three behavioral items: arrival at the patch, exit from the patch, and attack of an aphid. Attacks were defined as the stinging of an aphid for about 1 s in a frontal position, with the abdomen bent between the legs. This excluded shorter stings (<1 s), which usually precede the stings recorded and are thought to

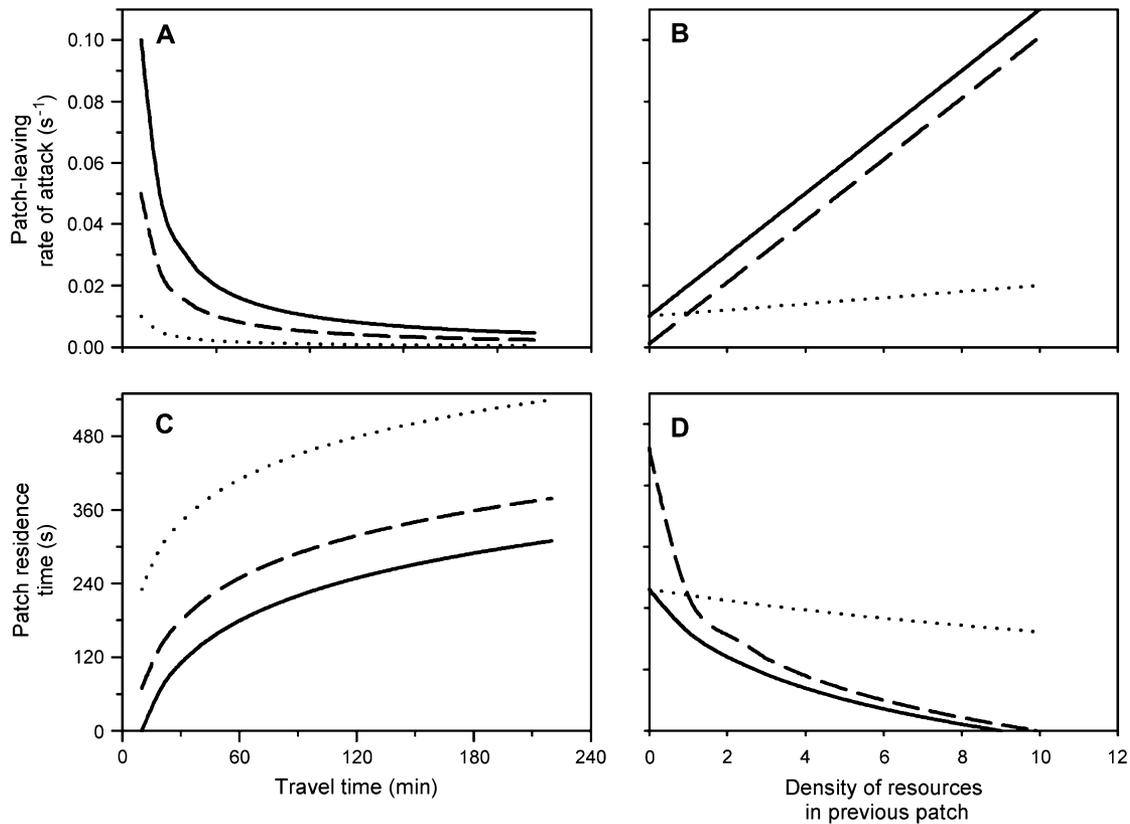


Figure 1

Theoretical predictions about the effect of travel time (A, C) and density of resources in the previous patch (B, D) on patch-leaving rate of attack (A, B) and patch residence time (C, D). Graphs A and C represent Equations 5 and 6, respectively, with $a = 1$ (solid line), $a = 5$ (dashed line), and $a = 10$ (dotted line). Graphs B and D represent Equations 8 and 9, respectively, with $b = c = 0.01$ (solid line), $b = 0.01$ and $c = 0.001$ (dashed line), and $b = 0.001$ and $c = 0.01$ (dotted line).

be used for probing. Consistent with previous field observations (C Tentelier, unpublished data), the parasitoid was considered to have left the patch when it had remained for more than 1 min at a distance of at least 1 cm from the closest aphid. Behavior was recorded with an accuracy of 0.1 s on a computer running event-recorder software, making it possible to time each attack precisely and to check the shape of gain functions. Both experiments (manipulation of travel time and manipulation of colony size) were based on a randomized block design, with all levels of treatment occurring at least once in a random order on each day of the experiment (21 days with one replicate per day in the first experiment and 10 days with three replicates per day in the second experiment).

In the first experiment, the travel time was defined as the time between leaving the conditioning patch and entering the test patch. Five different travel times were tested, from 29 to 207 min (Table 1). During this “travel” time, parasitoids were kept individually in small vials and provided with a droplet of honey. Parasitoids moved very little within the vials, so time was the most variable element of treatment (as opposed to other variables, such as distance to aphids, energy reserves, etc). We controlled for the confounding effects of time and aging by testing all parasitoids at the same age, about 244 min (Table 1). This required precise manipulation of the handling time between emergence and exposure to the conditioning patch, as well as of travel time. With this procedure, the

Table 1
Design of the experiment testing the effect of travel time between two colonies on foraging behavior

Treatment level	Time between emergence and conditioning patch	Travel time between first and second patch	Age at testing
1	31 [29–32]	206 [202–210]	240 [237–244]
2	60 [59–62]	180 [176–183]	244 [241–247]
3	121 [120–123]	119 [114–124]	244 [240–249]
4	181 [179–183]	58 [54–62]	244 [241–248]
5	210 [208–211]	28 [26–31]	242 [240–245]

Numbers are means and 95% confidence limits of times in minutes. The age at testing is equal to the time between emergence and exposure to the conditioning patch + the residence time on the conditioning patch + the travel time between the conditioning patch and the test patch.

arithmetic mean of time to exposure to the conditioning patch was the same for all levels of treatment (120 min). We therefore assumed that parasitoid behavior on the test patch was affected only by the most recent travel time (i.e., the time between the first and second patches), rather than by average travel time. This is consistent with the parasitoid having a short memory window or placing more weight on recent than on older information. Such a weighting of information has been shown to be adaptive in a changing habitat and is assumed in most optimal foraging models based on the acquisition of information (e.g., Kacelnik and Krebs 1985; McNamara and Houston 1987; Bernstein et al. 1988; Valone 1992; Hirvonen et al. 1999). We assessed the correlation between the number of stings and the number of offspring by rearing the aphids of the test patches for 10 more days in a controlled environment chamber (20°C and 16:8 light:dark) after being exposed to parasitoids. We counted the aphids transformed into mummies.

In the second experiment, we manipulated the size of the conditioning patch by manipulating the age of aphid colonies (i.e., the time between the founding of the colonies and tests with parasitoids). We used four levels of treatment for conditioning patches (Table 2), from 1 day (10 aphids) to 7 days (48 aphids). Each parasitoid was first exposed for 1 h to the conditioning patch and then released for test on a standard patch with a 3-day-old colony (22 aphids). For conditioning, parasitoids were enclosed under an inverted Petri dish covering the cut leaf supporting the patch. During this step, parasitoids might have laid more eggs in larger colonies than in smaller ones. This would result in differences in the number of eggs remaining in the ovaries between treatments that might have influenced foraging behavior on the test patch. We could not control egg load, but the parasitoids tested were dissected immediately after the test to count the eggs remaining in one of their ovaries.

Two dependent variables were used to quantify parasitoid foraging behavior: the patch-leaving instantaneous attack rate, defined as the number of stings made in the last 2 min before the parasitoid left the patch (as done by e.g., Hubbard and Cook 1978; Wajnberg et al. 2000), and patch residence time. These two variables violate the assumptions of normality (both are positive by definition) and homoscedasticity underlying standard parametric statistics. We thus used generalized linear models based on a log link function and either a Poisson distribution (for patch-leaving rate of attack) or a gamma distribution (for patch residence time). Analyses were carried out with the GENMOD procedure in version 8.0 of the SAS statistical package (SAS Institute Inc. 1999). The validity of the two models was assessed by checking plots of residuals versus predicted values. Analyses based on likelihood ratio statistics were performed to test the main effects of treatment and day. Under the null hypothesis, these statistics converge toward

Table 2
Design of the experiment testing the effect of the number of aphids in the conditioning patch on foraging behavior in the test patch

Treatment level	Age of the conditioning patch (<i>d</i>)	Number of aphids	Age of the test patch (<i>d</i>)	Number of aphids
1	1	10 [9–11]	3	22 [20–23]
2	3	21 [20–23]	3	21 [19–22]
3	5	35 [32–37]	3	22 [19–24]
4	7	48 [46–50]	3	20 [19–22]

Number of aphids is expressed as the mean and 95% confidence limits per treatment level. The number of aphids in the test patch is the same for the different treatment levels ($df = 3$; $\chi^2 = 1.78$; $P = 0.62$).

a chi-square distribution. GENMOD therefore uses Pearson's chi square to test the validity of generalized linear models. Egg load was used as a continuous variable in analysis of the second experiment. We also used nonlinear regression (NLIN procedure in SAS) to assess the fit of data to quantitative predictions.

RESULTS

In both experiments, the cumulative number of stings increased steadily with random searching within a patch (Equation 1; Figure 2). Both travel time and the size of the conditioning patch affected the foraging behavior of *L. testaceipes*. In the first experiment, travel time affected both the patch-leaving rate of attack (degrees of freedom [df] = 4; $\chi^2 = 40.24$; $P < 0.0001$) and patch residence time ($df = 4$; $\chi^2 = 27.87$; $P < 0.0001$). Consistent with the qualitative predictions of the MVT with learning, increasing travel time was associated with decreasing patch-leaving attack rates and increasing patch residence times (Figure 3). However, the experimental data obtained did not fit quantitative predictions based on an inverse relationship between travel time and γ (Figure 3).

In the second experiment, the size of the conditioning patch did not affect patch-leaving attack rate ($df = 3$; $\chi^2 = 6.51$;

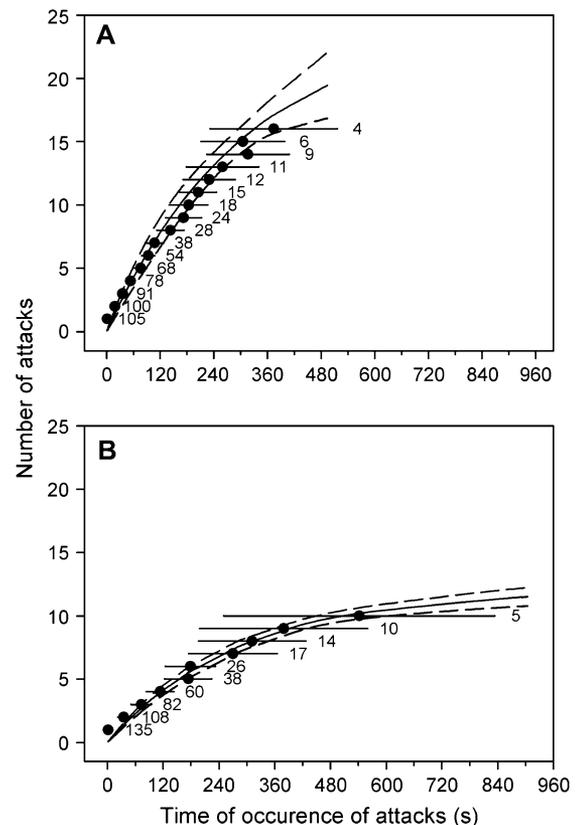


Figure 2
Gain functions for "travel time" (A) and "patch size" (B) experiments. Points and error bars represent means and 95% confidence intervals of the time of occurrence of each attack calculated across all observations. Numbers next to error bars indicate sample size. Lines represent the mean (solid line) and 95% confidence interval (dashed lines) for the nonlinear model of Equation 1 fitted by the least squares method. The best fit to data was obtained with $K = 24.42$ [15.55–33.29] and $Th = 12.71$ [9.55–15.87] for the travel time experiment, and $K = 11.95$ [10.95–12.95] and $Th = 23.62$ [20.60–26.64] for the patch size experiment.

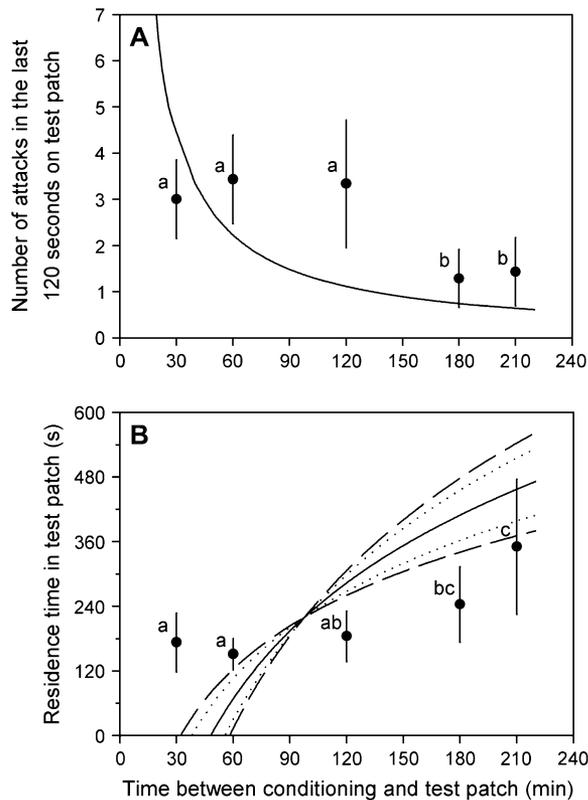


Figure 3

Mean and 95% confidence interval for patch-leaving attack rate (A) and residence time in the test patch (B) versus travel time between the conditioning patch and the test patch. Different letters indicate significantly different means (pairwise comparisons of least square means using Bonferroni correction for P values). Solid lines in panels A and B represent the nonlinear models of Equations 5 and 6, fitted by the least squares method. The values of K and Th were found by fitting the cumulative gain function (i.e., $K = 24.41$ and $Th = 12.71$). Estimates of a equal 0.0001 for Equation 5 and 0.004 for Equation 6. In panel (B), dashed lines and dotted lines represent the predictions for the 95% confidence interval limits of estimates of K and Th , respectively.

$P = 0.0893$) but did affect patch residence time ($df = 3$; $\chi^2 = 39.31$; $P < 0.0001$). The relationship between residence time and conditioning patch size (Figure 4) fitted MVT quantitative predictions based on learning and a Poisson distribution of attacks, assuming that the average rate of gain is positively and linearly correlated with conditioning patch size. In addition to being affected by past foraging experience, patch-leaving attack rates and residence times were significantly affected by day but with no clear pattern evident.

The precise recording of aphid exploitation by parasitoids enabled us to test some of the underlying hypotheses of the MVT. First, the number of attacks observed during patch exploitation by female parasitoids was positively correlated with the number of aphid hosts that subsequently became mummies ($r = 0.90$; $P < 0.0001$)—a good indicator of parasitoid fitness. The regression line fitting these data had a slope of 0.78, so, on average, 78% of the attacks yielded mummies. Second, in the patch size experiment, parasitoids were not egg limited. Females left the test patches with a mean of 88 [84–93] eggs per ovary, whatever the size of the conditioning patch ($df = 3$; $\chi^2 = 4.34$; $P = 0.23$). The lack of effect of patch size does not necessarily mean that wasps laid similar numbers of eggs in rich and poor conditioning patches. Instead, it indicates that patch size accounts for a smaller proportion

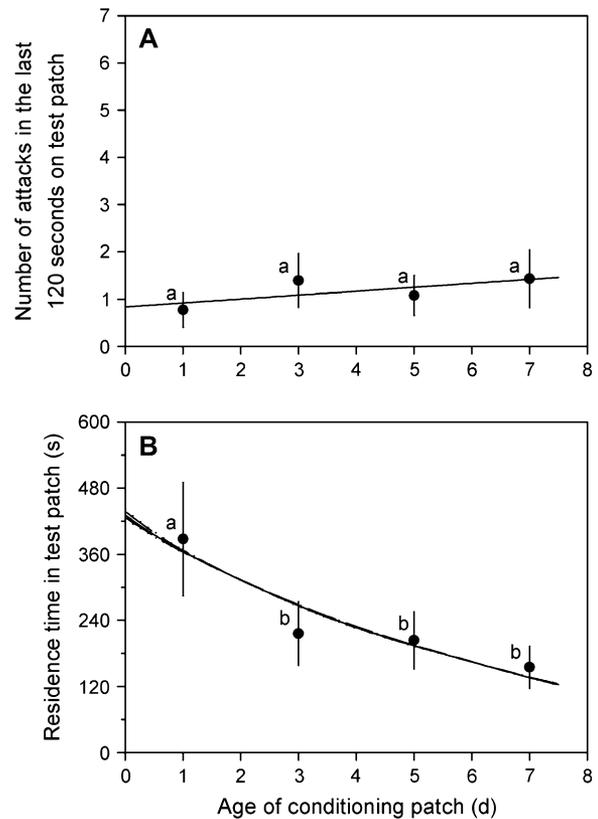


Figure 4

Mean and 95% confidence interval for patch-leaving attack rate (A) and residence time in the test patch (B) versus age of the conditioning patch. Different letters indicate significantly different means (pairwise comparisons of least square means, using Bonferroni correction for P values). Solid lines in panels A and B represent the nonlinear models of Equations 8 and 9, fitted by the least squares method. The values of K and Th were found by fitting the cumulative gain function (i.e., $K = 24.41$ and $Th = 12.71$). For Equation 8, $b = 0.0127$ and $c = 0.8$. For Equation 9, $b = 0.0004$ and $c = 0.008$. In panel (B), dashed lines and dotted lines represent the predictions for the 95% confidence interval limits of estimates of K and Th , respectively.

of total variance in egg load than other factors, maybe because the total number of eggs laid in both patches is very small compared to the huge egg load of females. Further evidence that egg load did not influence the results is provided by the finding that the introduction of egg load as a covariate in statistical models affected neither the patch-leaving attack rate ($df = 1$; $\chi^2 = 0.48$; $P = 0.49$) nor patch residence time ($df = 1$; $\chi^2 = 2.88$; $P = 0.09$).

DISCUSSION

Qualitative predictions

The predicted qualitative effect of travel time and previous patch size on current patch use by female *L. testaceipes* was partly supported by our experimental results. Longer travel times led to longer residence times and lower patch-leaving rates of attack; larger conditioning colonies led to shorter residence times but not to higher patch-leaving rates of attack. The qualitative effects of the manipulated variables on patch time allocation by parasitoids suggests that these variables provided information about environment-wide profitability.

The design of the travel time experiment highlighted the role of time as proximate information for parasitoids to adjust

patch use. We tested all individuals four hours after emergence, so the observed effect cannot be confounded with the age of the parasitoids (as in Boivin et al. 2004), a variable known to affect patch use behavior (Mangel 1987; Weisser 1994; Ventura Garcia et al. 2001). Moreover, parasitoids covered only negligible distances and energy losses, which can also influence patch use (Sirot and Bernstein 1996; Casas et al. 2003), were limited by ad libitum feeding. Travel time therefore actually consisted of a waiting time, as in the work of Kacelnik and Todd on pigeons (Kacelnik and Todd 1992; Todd and Kacelnik 1993). In this case, time seems to be the cue used by *L. testaceipes* females. In most previous studies showing an effect of travel between patches on patch exploitation, the variable manipulated was the distance traveled by foragers between patches (Zimmerman 1981; Cassini et al. 1990; Cuthill et al. 1990; Brunner et al. 1992, 1996; Cronin and Strong 1999). Hence, travel time and energy costs also increased with travel distance, making it hard to determine which of these variables really had a proximate effect on the behavior of foragers.

The effect of previous patch size on residence time was due to learning, rather than to a difference in egg load due to the exploitation of conditioning patches. The attack rate of parasitoids is influenced by egg load (Driessen and Hemerik 1992; Casas et al. 2000), and spending time on a rich conditioning patch could have led to egg limitation. In our experiment, a large number of eggs remained in the ovaries after the parasitoid had visited the test patch, and no difference was observed between treatments, maybe because female *L. testaceipes* are able to mature eggs during their adult life (Le Ralec 1991). Egg load also had no effect on parasitoid behavior in the test patch. We were therefore able to rule out the hypothesis of an effect of egg load. The precise cue used by *L. testaceipes* females remains unknown. It may be direct contact with aphids, perception of host-derived stimuli such as honeydew (Budenberg 1990; Shaltiel and Ayal 1998), or quantitative response of infested plants (Du et al. 1998).

In a recent study, Thiel and Hoffmeister (2004) showed that time between patches is used by females of the *Drosophila* parasitoid *A. tabida* to assess environment-wide profitability. They suggested that a mechanism of sensitization/desensitization to chemicals associated with host patches is responsible for the effect of travel time. They concluded that the sensitivity of parasitoids to chemicals decreases during the exploitation of a patch and increases when the parasitoid is traveling between patches. Our results are consistent with such a mechanism of sensitization/desensitization. After visiting a rich patch, female *L. testaceipes* may be desensitized to chemicals associated with hosts, and their motivation to stay on subsequent patches may be reduced. This motivation would increase with the duration of travel time between patches. Models and data on the dynamics of odor molecules in the peripheral olfactory system of insects are also consistent with the sensitization/desensitization hypothesis (Kaissling 2001). The saturation of odor-binding proteins may account for desensitization during patch use, and the degradation of odor molecules may increase sensitization during travel, until a limit where no odor molecule remain in the lymph.

Quantitative predictions

The model developed in the introduction of this paper provided quantitative predictions, which did not fit the data very well. Only the observed effect of previous patch size on residence time was consistent with the predictions of the model. Hypotheses concerning the link between the manipulated variables and the parasitoids' estimate of habitat-wide profitability γ may account for these discrepancies.

An inverse relationship between travel time and the value of γ was assumed because, in the case of random search, travel time between patches is an inverse function of the density of patches in the environment (Dusenberry 1989). However, it is possible that an increase in travel time does not actually mean an inverse variation in environment-wide profitability. There are two nonmutually exclusive reasons for this. First, the pattern of searching between patches may not be completely random because of the capacity of parasitoids to detect host patches at a distance based on plant provided cues (Turlings et al. 1995; Dicke and Vet 1999). If parasitoids can precisely locate patches from afar, they will fly directly from patch to patch, and travel time becomes a linear function of the distance between patches. The ability of female *L. testaceipes* to locate host patches in the field is unknown, but studies conducted in wind tunnel showed that this parasitoid is attracted to host plants, whether aphid infested or not (Schuster and Starks 1974; Lo Pinto et al. 2004). This parasitoid therefore probably directs its search to host plants and, therefore, does not search at random. Interestingly, the results presented in the companion paper concerning the aggregation of parasitoids on host patches also suggest nonrandom searching. Second, travel time can provide information about different aspects of the environment that may influence patch use behavior. For example, travel time is also time spent alone, so that the duration of travel time may provide the parasitoid with information about the probability of encountering another insect of the same species, a variable known to influence sex ratio (Strand 1988), superparasitism (Visser 1995; Hoffmeister et al. 2000), and patch residence time (Visser et al. 1992). In this case, long travel times indicate low densities of parasitoids of the same species, which means relatively good environments. Thus, the inverse relationship between travel time and the density of patches may be only part of a more complex relationship between travel time and the parasitoid's estimate of environment-wide profitability.

The assumed linear relationship between the size of the conditioning patch and the parasitoids' estimate of environment-wide profitability fitted the patch residence time data well. The fit to the data concerning patch-leaving rate of attack was also good, but the slope of the regression was not significantly different from zero. This result is consistent with the prediction of Equation 8, with a very small b (Figure 1). In this case, achieving the statistical power needed to differentiate the slope parameter from zero (i.e., to detect an effect of patch size) would require much more data than we have collected. Consistently, fitting the model to the data for patch residence time also gave a small value for the slope parameter b . Such a small value suggests that variation in patch size affected the estimates of habitat quality slightly, but significantly. The apparently weak effect of the size of previous patch on current patch use may be an artifact of our experimental design. Variation in the size of the conditioning patch accounted for only a small proportion of the size variation existing in the field (from 1 foundress to 9000 individuals per cucumber leaf; R Boll, personal communication). The behavior of parasitoids on the test patch might have been more strongly affected if we had used more contrasted levels of conditioning patch infestation.

The MVT based on learning forms the basis of more complex models on the distribution of foragers in their habitat (the first of which is Bernstein et al. 1988). These models make several additional hypotheses about the behavior of foragers, making experimental results hard to interpret (Tregenza 1995). In this paper, we show that the learning hypothesis is credible for *L. testaceipes*. Thus, this parasitoid is a good biological model for testing predictions about population distribution, which is the scope of the companion paper.

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