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Optimal patch residence time in egg parasitoids: innate versus learned estimate of patch quality

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Abstract Charnov's marginal value theorem predicts that female parasitoids should exploit patches of their hosts until their instantaneous rate of fitness gain reaches a marginal value. The consequences of this are that: (1) better patches should be exploited for a longer time; (2) as travel time between patches increases, so does the patch residence time; and (3) all exploited patches should be reduced to the same level of profitability. Patch residence time was measured in an egg parasitoid *Anaphes victus* (Hymenoptera: Mymaridae) when patch quality and travel time, approximated here as an increased delay between emergence and patch exploitation, varied. As predicted, females stayed longer when patch quality and travel time increased. However, the marginal value of fitness gain when females left the patch increased with patch quality and decreased with travel time. *A. victus* females appear to base their patch quality estimate on the first patch encountered rather than on a fixed innate estimate, as was shown for another egg parasitoid *Trichogramma brassicae*. Such a strategy could be optimal when inter-generational variability in patch quality is high and within-generational variability is low.

Keywords Patch quality · Travel time · Egg parasitoid · Patch residence time · *Anaphes victus*

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Introduction

Optimal foraging theory (Stephens and Krebs 1986) assumes that animals adjust their behaviour to maximize their lifetime reproductive success under different ecological conditions. One of the challenges faced by animals is that resource distribution varies in space and time and the strategies used by mammals (Giraldeau and Kramer 1982), birds (Kacelnik 1984) and insects (van Alphen and Galis 1993) to exploit these resources optimally have been tested. The resources used by female insect parasitoids are hosts that can be dispersed in the habitat or aggregated in patches, and whose value varies according to the host species, its age, parasitism status and also to the time it takes to travel between patches. How long, and therefore to what limits, patches should be exploited is one of the key factors determining the foraging success of female parasitoids and is therefore a central question in the behavioural ecology of insect parasitoids.

The marginal value theorem (MVT) (Charnov 1976) proposes a model of optimal patch residence time that can be used for insect parasitoids. Females foraging in a patch experience a decreasing value of the patch, as hosts are progressively parasitized. Therefore, their instantaneous rate of fitness gain decreases. Under such conditions, the MVT predicts that females should exploit a patch until the instantaneous rate of fitness gain reaches a marginal value, which is the mean rate of fitness gain that can be achieved in all patches in the habitat. Such a threshold value depends on the average patch quality in the habitat and travel time between patches. Predictions of the MVT are: (1) the higher the patch quality, the longer a female should remain on the patch; (2) the longer the travel time between patches, the longer a female should stay in a patch; and (3) all exploited patches should be reduced to the same level of profitability when the female leaves the habitat. One of the important assumptions of the MVT is that females are “omniscient”, meaning that they have complete information on the quality of all patches in the habitat (Vos et al. 1998). Such “omniscient” females are unlikely in nature,

thus some mechanisms or rules are necessarily used to exploit patches optimally.

One such mechanism could be for the females to learn the average patch quality through sampling. In many species, females are assumed to modify their habitat quality estimate through experience (McNamara and Houston 1985; Bernstein et al. 1988). Depending on how fast females learn habitat quality and how variable the habitat is, females will eventually reach an acceptable habitat quality estimate (McNamara and Houston 1985; Bernstein et al. 1988). Such a learning ability should lead to results very similar to the MVT predictions (McNamara and Houston 1985). In species that have to learn the average value of the patch within a habitat, the marginal value reached upon leaving the habitat is the average of all patches visited. The degree to which species could adjust their estimates of patch quality based on previous experiences could vary and at the other end of the spectrum, species could have a fixed innate estimate of the habitat quality and base their patch exploitation on that estimate. Such a mechanism has been recently described by Wajnberg et al. (2000) for an egg parasitoid, *Trichogramma brassicae* Bezdenko (Hymenoptera: Trichogrammatidae). Females of this species have, upon their emergence, an innate estimate of habitat quality and exploit the first patch they encounter according to this estimate. In such species, even the first patch encountered is reduced to a marginal value determined by the fixed innate estimate. How good this strategy is depends on how close the female's estimate is to the true average patch quality in the habitat.

Besides learning the average patch quality in a habitat or having an innate estimate of that quality, several patch-leaving mechanistic rules have been studied theoretically and experimentally in parasitoids. Under particular environmental conditions, these patch-leaving rules can promote patch residence times that are in accordance with the optimal predictions of the MVT (Godfray 1994). In Waage's (1979) model, females enter a patch with an initial tendency to remain on it (i.e. responsiveness) and this tendency then decreases during patch exploitation time. Each host successfully attacked leads to an increase in the responsiveness, so that total patch residence time increases with the number of hosts attacked. This is the incremental model that has been shown to lead to patch residence times that are in accordance with the predictions of the MVT when there is a large variance in patches' quality in the environment (Iwasa et al. 1981). Such an incremental mechanism has been observed in several parasitoid species (van Alphen and Galis 1983; Cloutier and Bauduin 1990; Nelson and Roitberg 1995; van Alphen et al. 2003). A decremental mechanism, for which each host successfully attacked leads on the contrary to a decrement in the forager's responsiveness to the patch, has also been described for several other species (Strand and Vinson 1982; Wiskerke and Vet 1994; Driessen et al. 1995; Wajnberg et al. 2003). This decremental mechanistic rule has been shown to lead foraging females to optimal patch residence times when all available patches in the

habitat have the same quality (Iwasa et al. 1981; van Alphen et al. 2003).

In this paper, we describe variation in patch residence time in *Anaphes victus* Huber (Hymenoptera: Mymaridae) females in response to varying patch quality and travel time. We also discuss the conditions under which learned habitat evaluation is more adaptive than having an initial innate estimate. Testing variation in both patch quality and travel time simultaneously is realistic and typical for females experiencing variation in both parameters in the field and permits one to test for interactions between the two factors. These interactions will indicate if the mechanisms responsible for the response to these factors are linked or independent. The mechanistic rules associated with both host acceptance and rejection are determined using a Cox proportional hazards model. Results obtained are compared with the trends predicted by the MVT model, both in terms of patch residence times and marginal fitness gain when leaving. The ecological impact of the two strategies described in egg parasitoids is discussed in term of patch use in a variable environment.

Materials and methods

The mymarid *A. victus* is an egg parasitoid of Curculionidae, including *Listronotus oregonensis* (LeConte) (Coleoptera: Curculionidae), in northeastern North America. *A. victus* is a solitary species (Boivin and van Baaren 2000). It has been shown that supernumerary larvae are eliminated by physical fights between first-instar larvae when superparasitism occurs (Nénon et al. 1995). Female *A. victus* can discriminate between unparasitized hosts and hosts parasitized by either themselves or by another female (van Baaren et al. 1994; van Baaren and Boivin 1998a). When a female superparasitizes a host, its fitness gain is less than when it parasitizes a healthy host, and this fitness gain depends on the time interval between the two ovipositions (van Baaren et al. 1995). As such, females perceive an already exploited patch as a patch of lower quality. Under field conditions, partially exploited host patches are frequently found (G. B., unpublished data). *A. victus* females live for 4 days and have a lifetime fecundity of 40–50 eggs (van Baaren and Boivin 1998b). There are about ten generations per year (May–October) under northeastern North America conditions (Boivin 1999).

L. oregonensis oviposits on Apiaceae (Boivin 1999). The oviposition period lasts for 4–6 weeks in the field, and *A. victus* must exploit several host species throughout the season. On carrots, the average number of hosts per patch is approximately eight.

L. oregonensis and *A. victus* were reared in the laboratory (Boivin 1988) at 24±1°C and 18:6 h light:dark photoperiod. The females used were virgin and naive, as they had no previous contact with hosts.

The individual female parasitoids were isolated at emergence for either 3 h (short travel time) or 48 h (long travel time). These delays between emergence and patch exploitation were used to approximate variation in travel time. The females were then offered a patch of 16 *L. oregonensis* eggs on a wet filter paper on a grid 1.5 by 1.5 cm. The experiment was conducted under laboratory conditions (22–24°C and 40–60% relative humidity). The host eggs were 2–4 days old, the preferred developmental stage for female *Anaphes* (Picard et al. 1991). The behaviour of each female was video-recorded from the moment it entered the patch to the moment it left it for >60 s using a camera mounted on a binocular. Patch quality was allowed to vary by changing the proportion of eggs already parasitized by another female 3 h before the experiment. Proportions of host parasitized were 0%, 25%, 50%, 75% and 100% (only 0%,

50% and 100% for the long travel time). In patches with both unparasitized and parasitized eggs, the parasitized eggs alternated with unparasitized eggs in the patch. Each treatment was replicated 15 times.

The following behaviours were recorded: entering the patch, leaving the patch for >60 s, antennal drumming on a host, ovipositor insertion into the host, oviposition, antennal drumming on a host after oviposition, walking between hosts and resting. When a female left a host after initial antennal drumming, it was considered as an antennal rejection. When the host was rejected after insertion of the ovipositor, it was considered as an ovipositor rejection.

Data collected were first used to compute the total patch residence time under all conditions tested and the level of patch profitability before leaving. This last parameter should correspond to the rate of reproductive success just before leaving the patch and is usually estimated by the rate of encounters with hosts during the last minutes before the patch is abandoned (e.g. Cook and Hubbard 1977; Hubbard and Cook 1978; Waage 1979). In the present study, however, hosts encountered could be either healthy or previously attacked by the same female or by the previous one. Thus, all hosts attacked might not lead to the same level of reproductive success of the forager. We thus quantified patch profitability by an estimation of the actual rate of progeny production during the last minutes of patch exploitation before the patch is left. Since we were interested in estimating this parameter during only the last minutes of total patch residence time, we used the following Monte Carlo procedure. According to van Baaren and Boivin (1998a), attacking a healthy host should lead to an adult emergence with a probability nearly equal to 1.0. These authors also demonstrated that superparasitism of an already parasitized host results in an adult emergence with a probability of 0.5, providing that the time interval between the two attacks remains small (≤ 3 h). These conditions were met in our experiment, and we thus estimated that the two progeny developing within the host had an equal chance to win the competition. The Monte Carlo procedure permitted the estimation of the timing of increases in reproductive fitness on the patch. For each female studied, the number and times of each host attack was computed from the observation data and the progeny winning the competition was randomly drawn among all the attack times with equal probability. The timing of these successful events was used to compute the rate of reproductive success just before leaving the patch that represented the total number of progeny produced during the last 10 min before the patch was left. Such an arbitrary time period is commonly used in studies on patch residence time in parasitoids (Wajnberg et al. 2000). To verify whether this criterion had an effect on the results, all computations were also performed with a time limit of 5 min. The results led qualitatively to the same conclusions. For each female, this Monte Carlo procedure was repeated 100 times, and the average value was used as the estimate of patch profitability before leaving for that female.

Patch leaving mechanisms used by females in the different treatments were analysed by means of a Cox proportional hazards model (also called a Cox regression model) (Cox 1972; van Alphen et al. 2003). A thorough description of this model can be found in Kalbfleisch and Prentice (1980) or in Collett (1994). This model expresses the data in terms of patch leaving tendency (i.e. hazard rate), which is the probability per unit of time that a female leaves the patch, given that it is still on it. This model assumes that the leaving tendency is the product of an innate leaving tendency (i.e. baseline hazard) and an exponential factor (i.e. hazard ratio) representing the combined effect of all the explanatory variables (i.e. covariates) taken into account. The equation of the model is:

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

in which $h(t)$ is the hazard rate, $h_0(t)$ is the baseline hazard, t the time passed since the female entered the patch, and β_i the regression coefficients that give the relative contributions of P covariates z_i . A hazard ratio >1 will indicate an increasing effect on the females' patch leaving tendency, while a hazard ratio <1 will be interpreted in

the opposite way. Covariates can be time-dependent or fixed. The baseline hazard is the patch leaving tendency when all the covariates are equal to zero.

Nine time-dependent covariates were used to quantify the effect of attacking or rejecting a host on the females' patch leaving tendency: the number of successful attacks, antennal or ovipositor rejections of (1) a healthy host, (2) a host previously attacked by the same female, or (3) a host already attacked by the previous female. Both the initial quality of the patch and the waiting time for the females before being offered a patch were added as fixed categorical covariates. The case corresponding to a patch with 16 healthy hosts exploited after a short travel time was arbitrarily assumed to be the reference level corresponding to the baseline hazard with parameters set to zero. Finally, in order to check whether there was a change in the patch leaving mechanism with the quality of the patch or with the waiting time before reaching it, the interactions between all time-dependent covariates and fixed covariates were also added to the model. The parameters were estimated from the data by means of partial likelihood maximization (Cox 1975). The significant effects of the covariates were tested using a standard likelihood ratio test. In order to find the most significant parameters, the iterative procedure described in Wajnberg et al. (1999) was used. The adequacy of the final fitted model was assessed by making residual plots (see Wajnberg et al. 1999, for an example of such a plot). All computations were done in S-Plus (Venables and Ripley 1994).

Results

The time spent by *A. victus* on host patches decreased with a reduction in patch quality (Fig. 1), and this can be observed for both short and long delays (log-rank test, short travel time, $\chi^2=32.92$, $df=4$, $P<0.001$; long travel time, $\chi^2=29.49$, $df=2$, $P<0.001$). Moreover, patches were exploited for a longer period of time when the females had to wait a longer time interval before reaching them (log-rank test, $\chi^2=32.23$, $df=1$, $P<0.001$). These results indicate that the patch exploitation strategy adopted by *A. victus* appeared to be in accordance with some predictions of the MVT. However, another prediction of this model is that, whatever their quality, all patches should be reduced to the same level of profitability before being left. Rates of reproductive success just before leaving the patch were significantly smaller on patches of lower quality, and this reduction appears to be stronger when females have to wait a short period of time before reaching the patch (Kruskal-Wallis test, short travel time, $\chi^2=21.46$, $df=4$, $P<0.001$; long travel time, $\chi^2=5.06$, $df=2$, $P<0.08$) (Fig. 2). These marginal rates of fitness gain appeared also to be significantly lower when the females had to wait a longer time before the start of patch exploitation (Kruskal-Wallis test, $\chi^2=10.20$, $df=1$, $P<0.02$). Thus, our results do not support the prediction of Charnov's model of a constant rate of fitness gain when leaving patches for species with fixed innate estimates.

In order to understand these results better, the patch leaving mechanisms used by the females were studied by mean of a Cox regression model. Table 1 gives the estimated effect of all the covariates having a significant influence on the patch leaving tendency of the wasp females. The tendency of the females to leave was clearly related to the initial quality of the patch they were foraging on. The leaving tendency on a patch containing only hosts

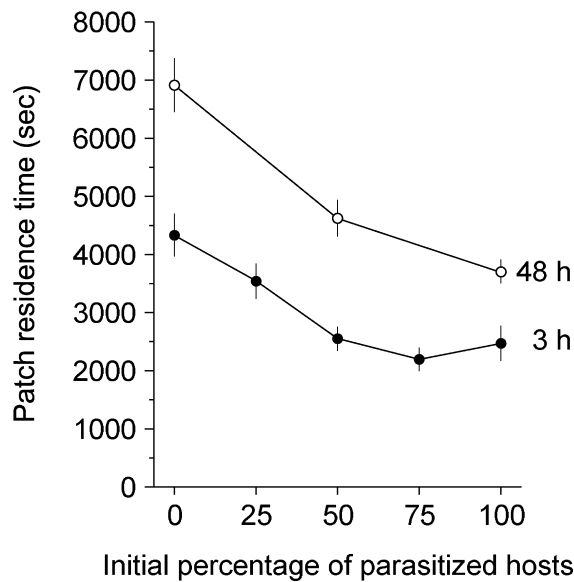


Fig. 1 Average (\pm SE) patch residence times (s) of female *Anaphes victus* after short (3 h) (●) or long (48 h) (○) travel times on patches of 16 hosts containing different initial percentages of parasitized hosts. Both averages and SEs are computed from the Kaplan-Meier estimator of the corresponding survivor functions

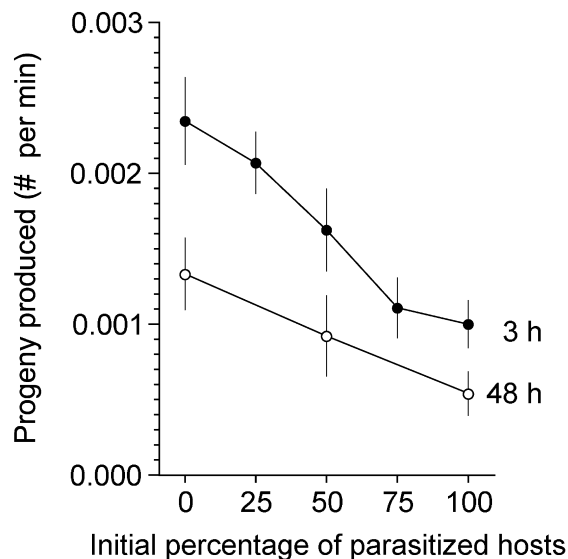


Fig. 2 Average (\pm SE) number of progeny produced per minute during the terminal 10-min period by female *A. victus* after short (3 h) (●) or long (48 h) (○) travel times on patches of 16 hosts containing different percentages of parasitized hosts

already attacked by a previous female was 25.58 times higher than on a patch containing only healthy hosts. Moreover, the tendency to leave was reduced by a factor of 0.45 when females had to wait a longer time before starting to exploit the patch they were offered, and there were no interactions between patch quality and the time spent by the females before encountering the patch ($P > 0.05$; see Fig. 3).

Furthermore, each successful oviposition on a healthy host increased the patch leaving tendency by a factor of 1.43 while ovipositing in a host already attacked by

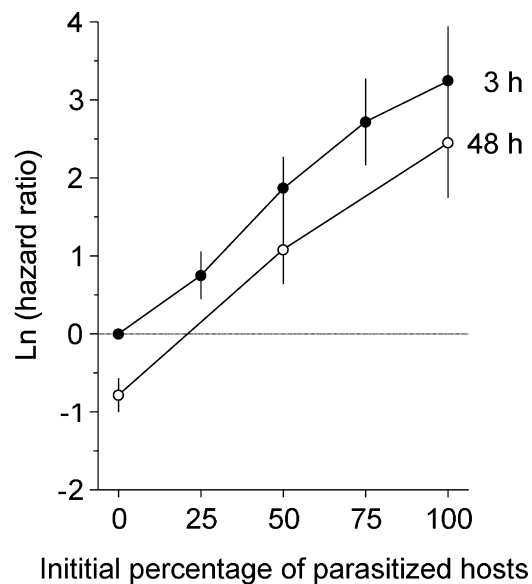


Fig. 3 Log of the hazard ratio (\pm SE) for females after short (●) and long (○) travel times on patches of 16 hosts containing different initial percentages of parasitized hosts

another female increased it by a factor of 1.15. Rejecting a healthy host after inserting its ovipositor and antennal or ovipositor rejection of a host that was attacked previously by another female were also significant variables with a hazard ratio > 1 (Table 1). All the other time-dependent covariates tested (i.e. ovipositing in a host already attacked by the same female, antennal rejection of a healthy host or a host previously attacked by the same female, ovipositor rejection of a host previously attacked by the same female) did not show any significant effect (all P -values > 0.05). Finally, no significant interactions were observed between all the decremental mechanisms observed and the effect of the patch quality or the delay between emergence and patch exploitation (all χ^2 at $P > 0.05$). Therefore, the patch leaving mechanisms discussed so far did not change according to the quality of the patch exploited by the females or the time they had to wait before exploiting it.

Discussion

The patch residence time strategy of *A. victus* is in broad accordance with the predictions of Charnov's MVT model. As predicted, females stayed longer on better quality patches when the quality was changed by increasing the initial proportion of already parasitized hosts. The capacity of *A. victus* females to discriminate between unparasitized and parasitized hosts has already been documented along with their capacity to detect the genetic relatedness between themselves and females that previously parasitized a host (van Baaren et al. 1994; van Baaren and Boivin 1998a). Delay between emergence and patch encounter was used here to mimic increasing travel time between patches. Increasing this travel time from 3 to 48 h significantly increased patch residence time for all patch qualities tested. The number of eggs deposited per patch,

Table 1 Estimated regression coefficient (β), SEs and hazard ratio [$\exp(\beta)$] for only those covariates that had a significant effect ($P < 0.05$) on the patch leaving tendency of *Anaphes victus* females. χ^2 correspond to the likelihood ratio tests. All of them were computed with all the other significant terms present in the model. Patches of 16 unparasitized hosts exploited after a short travel time were assumed to be the reference level (i.e. baseline hazard with a coefficient set to zero)

	β	SE	$\exp(\beta)$	$\chi^2(df)$	P-value
Patches with 0% of already parasitized hosts	0.00	—	1.00	30.42 (4)	<0.001
Patches with 25% of already parasitized hosts	0.75	0.31	2.12		
Patches with 50% of already parasitized hosts	1.87	0.40	6.49		
Patches with 75% of already parasitized hosts	2.72	0.56	15.13		
Patches with 100% of already parasitized hosts	3.24	0.70	25.58		
Oviposition in a healthy host	0.36	0.06	1.43	35.54 (1)	<0.001
Oviposition in a host attacked by another female	0.14	0.07	1.15	4.45 (1)	0.035
Antennal rejection of a host attacked by another female	0.05	0.02	1.05	4.79 (1)	0.029
Ovipositional rejection of a healthy host	0.20	0.07	1.22	6.17 (1)	0.013
Ovipositional rejection of a host attacked by another female	0.11	0.02	1.11	21.60 (1)	<0.001
Travel time	-0.79	0.22	0.45	13.33 (1)	<0.001

and therefore their patch residence time, also increased in *Anagrus sophiae* as the distance travelled increased (Cronin and Strong 1999). However, female *A. victus* experiencing long travel time were tested at an older age (48 h) than females with short travel time (3 h). It is known that life expectancy can influence reproduction (Roitberg et al. 1993b), and part of our results may be explained also by that factor. The fact that females stayed longer in a patch when the delay between emergence and patch exploitation increased, indicates that dispersal in *A. victus* could lead to a greater level of patch exploitation in situations where host patches are dispersed (Cronin and Strong 1999). The increase in patch residence time with longer travel time implies that isolated patches will be parasitized more than aggregated patches. This would improve the colonization success of a parasitoid by increasing mate availability to its offspring (Cronin 2003). Recolonization of host patches after winter mortality is likely to be an important ecological constraint in egg parasitoids in temperate regions (Boivin 1994).

However, the prediction of Charnov's model, that a female should leave patches at the same marginal rate of fitness gain, was not supported by our data. Female *A. victus* left the patches at a lower rate of fitness gain when patch quality decreased and/or when travel time increased. These results are contrary to what is expected for omniscient females and to what has been found in another egg parasitoid species, *T. brassicae*, when the effect of patch quality was tested (Wajnberg et al. 2000).

In order to explain these results, the proximate patch leaving rules used by *A. victus* females were studied by means of a Cox's regression model. The results obtained show that each oviposition in a host—healthy or already attacked—leads to an increase in the tendency of the female to leave the patch. This suggests that, as far as ovipositing in a host is concerned, *A. victus* is using a decremental mechanism similar to the countdown mechanism described by Driessen et al. (1995). Such a mechanism has been shown to lead to optimal patch residence time when the variance in patch quality is low in the environment (van Alphen et al. 2003), which is likely to be the case for the species studied here (Boivin 1999). Such a decremental mechanism is also observed when a healthy host is rejected after antennal inspection, or when

an already attacked host is rejected, either after antennal or ovipositor inspection. The rate of encounter with parasitized hosts informs the female of the decreasing value of the quality of the patch it is foraging on and the fact that it increases its patch-leaving tendency is thus considered in this case to be adaptive (van Alphen and Vet 1996).

The results of the Cox's regression model also show that the patch leaving tendency is higher when females are foraging on lower quality patches and when they experience a shorter travel time before reaching the patch. According to the incremental mechanistic model proposed by Waage (1979), such changes in patch residence time could be explained by the fact that: (1) females have a higher initial level of responsiveness when they enter a better quality patch and when they travel for a longer time before reaching the patch; (2) the patch responsiveness might decrease at a lower rate during foraging on better quality patch and after a longer travel time; (3) the different decremental effects observed might be of a lower intensity on better patches and after a longer travel time; or (4) any combination of these three potential explanations. Results obtained showed that the third hypothesis does not apply as there was no significant interaction between all the decremental effects observed (see Table 1) and both the quality of the patch and the time needed to reach it (all P -values > 0.05). Therefore, the results observed are likely the consequence of a higher initial tendency to remain on the patch and/or a lower rate of decline of this tendency during patch exploitation for females foraging on a higher quality patch and with a shorter travel time. In the experiment conducted here, these females were also older than those that were offered a patch immediately upon emergence. Due to physiological modifications during the ageing process, these females could also show a slower decline in their level of responsiveness during their patch foraging time. For example, it is possible that the efficiency of females' sensillae that are used to detect and identify stimuli coming from each host encountered, thus triggering the decision to attack or to reject it, would be modified in the course of time, leading older females to experience a slower decline in their patch responsiveness.

In a series of field experiments with the Mymaridae *Anagrus columbi*, Cronin (2003) found that isolation of host patches increased per capita oviposition and patch

residence time. He concluded that the distance-dependent oviposition response by this species could be due either to heterogeneity in individual oviposition rates (the individuals dispersing farther being those with the highest oviposition rates) or to an optimal foraging response to dispersal distance. Our results with *A. victus* support the optimal foraging response hypothesis as individuals that experienced a long delay between emergence and patch encounter showed a longer patch residence time.

Variations in the marginal rate of fitness gain reached upon leaving a patch could be related to the mechanistic rule used by female parasitoids (Wajnberg et al. 2000). These authors found that, when an incremental rule is used by a species, the quality of the first patch visited has no effect on the marginal rate of gain reached when the patch is left. On the contrary, when a decremental effect is used, the quality of the first patch exploited will affect the marginal rate of fitness gain when leaving (Wajnberg et al. 2000). *A. victus* females showed such decremental effects associated with both oviposition and rejection following insertion of the ovipositor when either short or long travel times were tested and, as suggested by the simulation model of Wajnberg et al. (2000), left patches at different marginal rates of fitness gain as patch quality changed. Such variations in the marginal rate of fitness gain is contrary to the prediction of the MVT model that foraging females should reduce all patches exploited to the same level of profitability, whatever their quality. This prediction is implicitly based on the fact that females should be omniscient. More realistically, species responding to the MVT model are likely to use an innate estimate selected to be close to the average patch quality of the habitat. Long-lived species, where females exploit a large number of patches, can estimate the average value of the habitat from all patches sampled. However, this is less likely for short-lived species, such as egg parasitoids, that exploit only a small number of patches in their lives. In the experiment described here, patch residence time was measured on the first patch ever encountered by the females. The females thus have either to use an innate estimate of the optimal marginal rate of fitness gain, in which case we would expect a relatively constant rate of gain when leaving patches of different qualities, or to base their estimation on the patches they are exploiting. In this last case, naive females would base their first estimate on the first patch they encountered.

Figure 4 gives a graphical representation of Charnov's MVT model. It shows optimal residence times on the first patch encountered for naive females without an innate estimate of the quality of the habitat (i.e. for foragers that are not omniscient). Even on the first patch encountered, females should stay longer on a better quality patch and/or when the time needed to reach it increases. However, contrary to what is expected from omniscient animals, upon leaving the first visited patch marginal rates of fitness gain will be higher if the patch is of a better quality and/or if the female found it after a shorter travel time (Fig. 4). This corresponds to the results obtained here (see Fig. 2) and may be due to the fact that the females used in

the experiment were naive, thus without any knowledge of the quality of the patches they have to exploit. It can also be predicted that the difference in optimal patch residence time between females experiencing short or long travel times will decrease as patch quality decreases (Fig. 4). Such a reduction in patch residence time was also observed experimentally (see Fig. 2).

Strategies used by insect parasitoids to adjust their residence time on patches of their hosts appear to vary greatly, even between species sharing similar lifestyles like egg parasitoids. Such strong inter-specific differences are likely the consequence of important variation in the constraints imposed by habitat variability, and thus in the ability for a species to predict upon adult emergence the average quality of patches that will be exploited. Females without an innate estimate of patches' quality have to sample their habitat while foraging (Li et al. 1993). Doing so, they are predicted to gradually improve their estimate of the mean rate of fitness gain that can be achieved in the environment (McNamara and Houston 1985). Wajnberg et al. (2000) showed that females of the egg parasitoid *T. brassicae* left the first patch they encountered with a marginal rate of fitness gain that did not depend on the quality of the patch exploited. From this result, these authors suggested that, upon emergence, females have an innate estimate of the average quality of all patches available in the environment. On the contrary, the results obtained here suggest that *A. victus* females do not have such an innate estimate or their innate estimate can be rapidly adjusted, leading them to leave the first patch they exploited with different marginal rates of fitness gain when

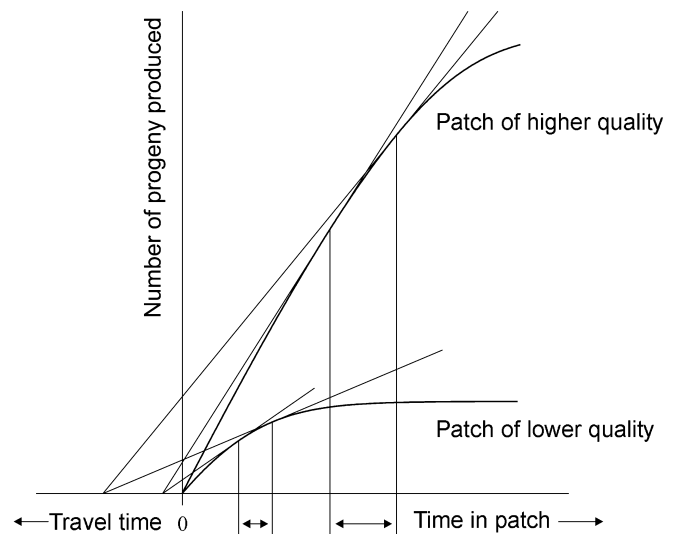


Fig. 4 Graphic representation of Charnov's model showing optimal residence times on the first patch encountered for naive females without an innate estimate of the quality of the habitat (i.e. for foragers that are not omniscient). For a given travel time, the time spent in a patch is longer when patch quality increases (lower vs. higher rate of fitness gain curve). As travel time between patches increases (to the left of the vertical axis) so does the patch residence time. Note that the difference in patch residence time when travel time varies is larger for high-quality patches than for low-quality patches

quality and travel times varied. The strategy used by *A. victus* females is thus that they are likely to use the first patch encountered to estimate the quality of their habitat and to adjust this estimate as they gain more experience on the following encountered patches. The two strategies, using an innate estimate as in *T. brassicae* or using a learned estimate as in *A. victus*, should converge to the real value of the average marginal rate of fitness gain as females forage in an habitat (McNamara and Houston 1985).

These two strategies, innate estimate (i.e. *T. brassicae*-like) and learned estimate (i.e. *A. victus*-like), could lead to optimal patch residence time in different “universes” (Fig. 5). When there is no or little variability both within and between generations, we expect both strategies to perform optimally. In the innate estimate strategy, natural selection will probably select an estimate that is close to the average value of patch quality and, in the course of generations, females will use a marginal rate of fitness gain that will lead to optimal patch residence time. In the learned estimate strategy, the females base their estimate on the first few encountered patches and, because there is little variation in this universe, their estimate will rapidly and always be close to the true average value of the habitat. If the variability between generations remains low but variability within a generation increases (Fig. 5, line A), the innate estimate strategy becomes rapidly more advantageous as the females using this strategy will always be close to the habitat average although variance in patch quality will be higher. Females using the learned estimate strategy will use their first few patch encounters to estimate the average value of the habitat but, as the intra-generation variance increases, the accuracy of their estimate decreases. Indeed, when the value of the first patches encountered happens to be far from the habitat average, females using the learned estimate strategy will use a patch residence time that is far from the optimum for this habitat. When the inter-generational variability

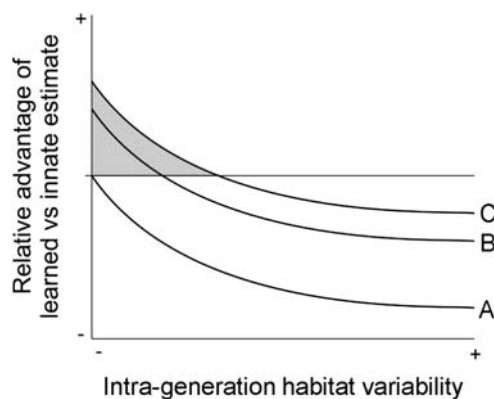


Fig. 5 Conditions under which a strategy with no innate knowledge of the habitat is advantageous. As variability within generations increases, the learned estimate strategy is less and less advantageous when the between generation variability is low (line A). However, as variability between generations increases (lines B, C), in cases where variability within generations is low, the learned estimate strategy becomes advantageous (shaded zone)

increases (Fig. 5, lines B and C), the females using the innate estimate strategy will face an increased risk of using an estimate that is far from the true average value of the habitat. On the contrary, females using the learned estimate strategy will base their estimate on the first few encounters and will therefore be at an advantage as their estimate will be closer to the habitat average for this generation. The advantage of the learned estimate strategy will decrease as the within-generational variability increases for the same reasons discussed above. In short, the learned estimate strategy should perform better in situations of low within-generation variability but at medium to large between-generation variability. In all other situations, using an innate estimate should lead to more optimal patch residence times. Using dynamic programming, Roitberg et al. (1993a) showed that learning could be an advantageous strategy when memory units were long enough. A short memory remembering only the last encounter for example, was the least favoured strategy with lower fitness gain than no memory at all. Patch residence time of the encyrtid *Leptomastix dactylopii* was predicted by a model using limited memory of the last seven hosts encountered in a patch (Pierre et al. 2003).

The hosts of *A. victus* are eggs of Curculionidae that are typically found in small egg clutches and therefore variability in patch quality in a given generation is probably low. This can be contrasted with *T. brassicae* that attacks Lepidoptera eggs found in clutches varying from one to several hundred eggs. In northeastern North America *A. victus* has about ten generations per year in the period covering May–October. This period is longer than the oviposition period of any of its hosts and this species must therefore change hosts several times per season. *A. victus* can thus experience high variability in patch quality between generations reflecting differences in the oviposition behaviour of different species of Curculionidae. These conditions are what are expected to be optimal for females using a learned estimate strategy. The conditions under which a learned estimate strategy should be optimal, i.e. low within-generational variability coupled with high between-generational variability, are the same conditions proposed by Stephens (1993) to facilitate the evolution of learning. Learning of individual marking pheromones has already been shown in *A. victus* females as they evaluate host quality (van Baaren and Boivin 1998a). Thus, parasitoid species evolving in such a universe could exploit optimally patch resources without being omniscient or using a fixed estimate.

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