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Genetic variation in patch time allocation in a parasitic wasp

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Summary

1. The intra-patch experience acquired by foraging parasitoid females has often been considered to have a strong influence on their tendency to leave a patch, and thus on their total patch residence time. Most studies that have been performed on this subject suggest that the patch-leaving rules observed are adaptive because they enable the females to adjust their patch residence time to local environmental conditions.

2. Considering a behavioural rule as being adaptive supposes that it has been progressively settled by natural selection, and thus that there is, in the population, genetic variation on which the natural selection could act.

3. Therefore, this study aimed to discover whether there was indeed genetic variability in the patch-leaving decision rules in a population of the egg parasitoid species *Telenomus busseolae*, which attacks patches of its hosts, the eggs of *Sesamia nonagrioides*. Different wasp families were compared using the isofemale lines method, and the behavioural records were analysed by means of a modified version of the Cox's proportional hazards model proposed by Haccou *et al.* (1991) and Hemerik, Driessen & Haccou (1993).

4. The results obtained show that *T. busseolae* females increase their tendency to leave the patch after each successful oviposition. Each host rejection also led to an increase in the tendency to leave the patch, but this effect was smaller when host rejections were observed between two ovipositions occurring in rapid succession. Subsequent visits to the patch also increased the patch-leaving tendency.

5. Genetic variability was found in both the global patch-leaving tendency and in the effect that successful ovipositions and host rejections have on this tendency.

6. The adaptive and evolutionary consequences of these results are discussed.

Key-words: Cox's regression model, genetic variability, parasitoids, patch time allocation, *Telenomus busseolae*.

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Introduction

Patch time allocation in parasitoids (and predators) has been the focus of considerable theoretical and experimental work in the last few decades, and has progressively become one of the main subjects in behavioural ecology and optimal foraging theory (see Stephens & Krebs 1986, for a review). The starting point is that hosts (or prey) usually occur in discrete patches (Godfray 1994), and foraging females are usually time limited in the sense that they are unable to find enough hosts in which to lay all their eggs during their life time (Nelson & Roitberg 1995). Therefore, the time allocated to each patch can be an important factor in the reproductive success of a parasitoid, and can thus be the target of strong selective pressures.

A number of theoretical models have been proposed to predict the optimal residence time a female should allocate to each visited patch. The most well-known one is Charnov's (1976) marginal value theorem. This theoretical approach, and most of the subsequent ones, make the implicit assumption that foragers

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know exactly the distribution and the quality of the patches within the habitat (Waage 1979; McNair 1982; van Alphen & Vet 1986; Godfray 1994). Such an assumption is obviously unrealistic, especially in a stochastic, unpredictable environment (Oaten 1977; Green 1980; McNamara 1982; Green 1984). In order to circumvent this problem, it has been repeatedly proposed that animals, while foraging on a patch, are, in fact, continuously sampling their environment in order to obtain the information needed to trigger the patch-leaving decision (McNamara 1982; Green 1984; van Alphen & Vet 1986; Yamada 1988; Li, Roitberg & Mackauer 1993).

Simple patch-leaving decision rules, based on intra-patch experience, have been proposed; for example, Waage (1979) has suggested that female parasitoids enter a patch with a certain level of responsiveness that is determined by the concentration of contact kairomones, and thus by the number of hosts available. Afterwards, females are supposed to exhibit a turning response each time they encounter the edge of the patch (Waage 1978). When no hosts are encountered, the level of responsiveness is assumed to decrease over time down to a threshold value at which the turning response is no longer elicited, and the patch is left. When a host is attacked, the responsiveness to the patch edge is increased by a given increment. The size of the increment depends on the time elapsed since the preceding oviposition. Such an incremental effect in response to each oviposition has been observed in several parasitoid species; on the phycitid moth parasitoid *Venturia canescens* (Gravenhorst) Waage (1978, 1979), on several *Drosophila* parasitoids (van Lenteren & Bakker 1978; van Alphen & Galis 1983; Hemerik, Driessen & Haccou 1993), on an aphid parasitoid (Cloutier & Bauduin 1990), on a leafminer parasitoid (Nelson & Roitberg 1995) and on a whitefly parasitoid (van Roermund, Hemerik & van Lenteren 1994). Using a mathematical approach, Iwasa, Higashi & Yamamura (1981) showed that this mechanism can lead to a result that closely approximates the optimal strategy when the hosts exhibit a clumped distribution (i.e. with a large variance in patch density). Therefore, under some particular conditions, such a patch-leaving decision rule is considered to be adaptive (van Alphen & Vet 1986).

In some cases, successful ovipositions have been shown to have a decremental effect on patch residence time. The most striking example has been observed on *Cardiochiles nigriceps* Vierick, a parasitoid of the tobacco budworm, which immediately leaves the patch after a single oviposition (Strand & Vinson 1982). Such a decremental effect, sometimes called a 'count-down' mechanism (Driessen *et al.* 1995), has also been observed on a Lepidopterous larval parasitoid (Wiskerke & Vet 1994), on an aphid parasitoid (van Steenis *et al.* 1996), and on *Venturia canescens* (Driessen *et al.* 1995). This patch-leaving mechanism is supposed to be adaptive when host patches are small (Strand & Vinson 1982) or when hosts are uniformly distributed (Iwasa *et al.* 1981; Driessen *et al.* 1995).

The general idea behind these patch-leaving decision rules is that an encounter with a healthy host provides, not only a suitable place to lay an egg, but also information. In the case of an incremental effect, the information may be that the patch is richer than had first appeared and therefore it is worthwhile to spend an additional amount of time foraging on it. In the case of a decremental effect, the information may be that the patch resources are depleting and it is becoming less and less interesting to remain on it. The encountering of an already attacked host will also provide the forager with some information regarding the level of patch exploitation. Thus, encounters with parasitized hosts should have a decremental effect on patch residence time (van Alphen & Vet 1986; van Alphen 1993). Indeed, this has been verified for several *Drosophila* parasitoids (van Alphen & Galis 1983; van Alphen & Vet 1986; Bakker & van Alphen 1988; van Lenteren 1991; Hemerik *et al.* 1993) and for an aphid parasitoid (van Steenis *et al.* 1996). However, on other parasitoid species, some investigations failed to show any effect (Waage 1979; van Roermund, Hemerik & van Lenteren 1994), or even showed the opposite effect (Nelson & Roitberg 1995).

The different patch-leaving rules discussed so far are *a priori* hypotheses that have to be investigated using laboratory experiments. However, the analysis of experimental data based on these simple models has generally been considered to be problematic (Haccou *et al.* 1991; Hemerik *et al.* 1993). An alternative approach has been proposed in order to deduce the effect of females' intra-patch experience on their patch-leaving decision, from experimental data with minimal prior assumptions. The method used for this is a transposition to ecological problems of a statistical method widely used to analyse survival data in medical research; i.e. Cox's (1972) proportional hazards model (Haccou *et al.* 1991; van Alphen 1993; Hemerik *et al.* 1993). This model has the advantage of being stochastic, in the sense that the deduced behavioural mechanisms are phrased in terms of probabilities instead of fixed rules, like those proposed by Charnov's (1976) or Waage's (1979) models, and this appears to be more appropriate to analyse data on time allocation (van Roermund *et al.* 1994). Moreover, it can be used to detect time-dependant mechanisms and thus, the timing of the different events that occur during patch exploitation can be taken into account. Supposedly, such time-dependant processes have a strong effect on patch-leaving decisions (Waage 1979; van Alphen 1993). Therefore, this model seems appropriate to analyse the fact that a female parasitoid may experience a continuous decrease in contact with healthy hosts on a depleting patch and must continually re-assess the changing value of the patch, based on only its previous experience (Cowie & Krebs 1979; McNamara & Houston 1985; Li *et al.* 1993).

Finally, the use of this model permits the testing of any interactions between different behavioural mechanisms that are involved in the determination of patch residence time; for example, this model can be used to quantify the fact that the effect of encountering healthy hosts on patch-leaving decisions could change according to the number of hosts found that are already attacked. Such interaction mechanisms are expected to affect patch-leaving decisions (Nelson & Roitberg 1995).

The use of this statistical approach has shown that female parasitoids are managing their patch residence time according to the experience they acquire while foraging on the patch. At least qualitatively, most of the patterns that have been revealed are usually in agreement with the prediction of optimal foraging theory (Haccou *et al.* 1991; Hemerik *et al.* 1993; Godfray 1994), and are thus thought to be adaptive. Therefore, behaviours have probably been progressively settled by natural selection over the course of generations (Iwasa *et al.* 1981; Pyke 1984). This is conceivable only if the biological traits of the wasp that are involved are genetically determined and if there is variation on which natural selection could act. However, such genetic variation has never been demonstrated. The aim of the present study is thus to look for genetic (i.e. polygenic) variability in the effect of intra-patch experience on patch time allocation by females of *Telenomus busseolae* Gahan (Hym.; Scelionidae), which attack patches of one of their hosts, the eggs of *Sesamia nonagrioides* Lefebvre (Lep.; Noctuidae). To achieve this, the results obtained on different wasp families were compared using the isofemale lines method (Parsons 1980; Hoffmann & Parsons 1988). Experimental data were analysed using a modified version of the Cox's proportional hazards model that was used by Haccou *et al.* (1991) and Hemerik *et al.* (1993). First, the results have given a comprehensive insight into the mechanisms used by *T. busseolae* females to manage their patch time allocation. Then, an analysis of the inter-family variation was used to identify strong genetic variability in these mechanisms in the population analysed. The evolutionary consequences of these results are discussed.

Material and methods

PARASITOIDS AND HOSTS

Telenomus busseolae is a solitary egg parasitoid of various lepidopteran species belonging to Noctuidae and Pyralidae (Polaszek, Ubeku & Bosque-Perez 1993). Its geographical distribution covers several African countries, the middle East and India. In Europe, it has been found only in Greece (Polaszek *et al.* 1993) and in Portugal (C. Meierosse, unpublished data). Host egg-masses attacked by this species can vary greatly in size, both within a species (e.g. the egg-mass size of the Noctuidae *Sesamia nonagrioides* can range from about 20 eggs to more than 160 eggs) and between species (from a few hosts up to several tens of eggs per egg-mass). Moreover, the hosts of *T. busseolae* are often present in the same period of the year in the field.

The *T. busseolae* strain used in this experiment was reared from ≈ 10 parasitized egg-masses of *S. nonagrioides*, provided by Dr S. Kornosor (University of Çukurova, Adana, Turkey). These egg-masses were collected from corn fields located in Adana in September 1994. From the time of capture onwards, the strain was maintained on *S. nonagrioides* under laboratory conditions for ≈ 30–32 generations, at 26 ± 1 °C, 65 ± 5% RH, L : D 16 : 8 h (see Colazza, Rosi & Clemente 1997). The *S. nonagrioides* strain, originating from pupae collected in central Italy, was reared on a diet based on milled corn stalks and cobs as described by Giacometti (1995), and was maintained under the same laboratory conditions. Adult moths were kept in an oviposition cage with a wet cardboard cylinder covered spiralwise with parafilm strips to provide suitable oviposition sites (Giacometti 1995). The moth colony has been refreshed, at irregular intervals, by wild material collected from corn fields.

EXPERIMENTAL SET-UP

Ten mated *T. busseolae* females, taken at random from the mass-reared population, were used to establish 10 isofemale lines (i.e. families). All of these females were reared under highly standardized conditions, some of them even developed in the same vial. Furthermore, the host eggs that were used for rearing these females (and also those used for the experiment) originated from several *S. nonagrioides* females and were randomly distributed over the 10 families compared. Thus, any variation that may be observed between families cannot be explained by variation in the environmental conditions of the developing founding mothers. Experiments were performed on the next generation. On average 8·3 (range: 6–10) daughters were observed per family and were randomly distributed over all the days of the experiment. Therefore, a total of 83 females was analysed. The statistical test of the variation observed between families indicates whether or not the behavioural mechanisms studied can be considered to be family features. If this is the case, this would indicate the existence of a significant genetic variation in the patch-leaving decision mechanisms that were identified (i.e. isofemale lines method, Parsons 1980; Falconer 1981; Hoffmann & Parsons 1988). It should be noted that the isofemale lines method that was used here provides information on broad sense genetic variability, that is to say, it does not distinguish between additive and non-additive components of the genetic variation observed. Any kind of genetic determinism, including dominance and maternal effect, may also be revealed. A thorough analysis of the genetic variation in the behavioural traits studied, using the isofemale lines method, would have necessitated the design of some accurate way to avoid the effect of environmental influence on the variation observed (e.g. by splitting each family and rearing them in independent replicates, and/or by repeating the experiment over successive generations). However, this design would have resulted in an experiment that would have been too large to handle. So, all sources of variation (e.g. rearing vials, host eggs used for rearing and experiments, etc.) were randomly distributed over all the 10 families compared.

Freshly emerged *T. busseolae* females were kept with males for 24 h for mating. They were then individually isolated with a drop of honey solution and used in experiments when they were 2–3 days old. Experiments were carried out during the daytime at 26 ± 1 °C and 60 ± 5% RH. At the beginning of each replicate, a single female was introduced into an arena (diameter: 18 mm, height: 4 mm) with a circular patch of five freshly laid *S. nonagrioides* eggs in the middle. Females were not allowed to contact any hosts before the experiment (i.e. inexperienced females) and were used only once. Attacked hosts were not replaced, so the patch suffered a continuous depletion.

As soon as the female was introduced into the arena, she exhibited a succession of patch-entering and -leaving behaviours. While foraging on the patch and as soon as a suitable host was encountered, she adopted a characteristic oviposition posture and started to drill the egg chorion with her ovipositor. This behaviour lasted, on average, (± SD) 80·9 ± 36·5 s. Then, after a successful oviposition, the female adopted a typical marking behaviour, sweeping the surface of the host several times with her ovipositor. This marking behaviour, which lasted, on average, 6·9 ± 2·4 s, probably corresponds to the deposition of a chemical compound that indicates to other females and to herself that the host has already been attacked. When an unsuitable host was encountered, the female adopted the oviposition posture, but did not show any marking behaviour thereafter. This event was considered to be a so-called host rejection behaviour.

In order to increase the number of replicates per unit of time, six females, each on a separate arena with a single host patch, were simultaneously videotaped, leading to a cumulative video recording of continuous observation of more than 31 h. The videotapes were then analysed with an event recorder and, for each female, the beginning and the end of the following behaviours were recorded with an accuracy of 0·1 s: (i) entering or (ii) leaving the patch; (iii) adopting an oviposition posture or (iv) showing a marking behaviour; (v) standing still or (vi) preening. Patch entering was considered to be the point when the female had at least four legs on the egg mass, and patch leaving was recorded when the female had all her legs on the substrate. Observations started as soon as the female entered the patch for the first time and stopped when she left the patch for more than 60 s.

After analysing all the videotapes, it appeared that the preening behaviour was observed only when the female was off the patch. Therefore, since only intra-patch residence time was studied, the duration of this behaviour was not taken into account. The behaviour of 'standing still' was also mostly observed when the female was off the patch. In this case, it was also not taken into account. In only six out of 392 patch visits studied, was this behaviour observed while the female was on the patch, but its duration was only about 2·5% of the corresponding patch residence time. Thus, in these cases, the duration of this behaviour was included in the total intra-patch foraging time.

On some occasions, the female left the patch and walked a few millimetres away for a short excursion before returning to the hosts. The patch was thus considered to be left when the female spent at least 1·0 s off the patch. Such an arbitrary criterion is commonly used in studies on patch time allocation by parasitic wasps (Waage 1978, 1979; Driessen *et al.* 1995). However, to check whether the criterion had any artefactual effect on the results, all computations were also performed with a threshold value of 5·0 s. The results led qualitatively to the same conclusion in both cases.

In order to have a sufficient number of replicates, the females were confined within the experimental arena. Despite the fact that the patch/arena surface ratio was less than 0·013, these experimental conditions may induce an increase in the patch-returning tendency of the females. Therefore, in order to reduce the possibility of this artefact, only the patch-leaving tendency was studied, and only the first five visits to the patch were taken into account. However, when the data were available, computations were also made with the first 10 or 15 visits to the patch. The results obtained led qualitatively to the same conclusion in all cases. Therefore, confining the females does not seem to have any effect on the results obtained.

DESCRIPTION OF THE MODEL

The data were analysed using a Cox's proportional hazards model, also called a Cox's regression model. A detailed description of this model can be found in the literature on survival analysis (e.g. Kalbfleisch & Prentice 1980; Collett 1994). Such a model enables the correct handling of censored data (see Bressers *et al.* 1991; Haccou & Meelis 1992, for a discussion on this). It is formulated in terms of hazard rate, which is the probability per unit of time that a female leaves the patch, given that she is still on it. Thus, this represents the tendency for a female to leave the patch. In survival analysis terminology, entering the patch corresponds to a renewal point and leaving the patch to a failure. It is assumed that the hazard rate function is the product of a basic tendency to leave the patch (baseline hazard), which is reset after each renewal point, and a so-called hazard ratio, which gives the joint effect of all the explanatory variables taken into account (covariates). The general form of the model is:

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

where $h(t)$ is the hazard rate, $h_0(t)$ the baseline hazard, t the time since the latest renewal point, and β_i the coefficients that give the relative contribution of p covariates. These coefficients can be interpreted through the hazard ratio, which is the exponential term. A joint effect of the covariates leading to a hazard ratio greater than one will be interpreted as having an increasing effect on patch-leaving tendency, while a hazard ratio lower than one will be interpreted in the opposite way. Covariates can be time-dependent or fixed. The baseline hazard, which is the hazard rate when all the covariates are equal to zero, is left unspecified.

All observable behavioural events that occur during the exploitation of a patch cannot be considered because the resulting data set would be too large. Therefore, optimality theory can be used to restrict the set of relevant features of intra-patch experience that should be taken into account (Haccou *et al.* 1991; Hemerik *et al.* 1993). The model that was used was derived from the one proposed by Haccou *et al.* (1991) and Hemerik *et al.* (1993). As in their model, in the present study first the number of successful ovipositions that were observed during the current patch visit was considered. The analysis of the corresponding hazard ratio will indicate whether each oviposition had an incremental or decremental effect on patch residence time. The number of host rejections during the current patch visit was also added, because they could also have an effect on the leaving tendency. Moreover, whereas Haccou *et al.* (1991) and Hemerik *et al.* (1993) considered the instantaneous oviposition and host rejection rates up to eight or four ovipositions backwards in time, the present study only looked at these rates up to the three preceding ovipositions in order to reduce the number of parameters to estimate (see below). These rates, expressed in time^{-1}, were assumed to change with patch depletion and their study allowed the analysis of the corresponding consequence of this on the patch-leaving tendency of females. All these covariates were time-dependent. In addition to this, two fixed covariates were also considered: the rank of subsequent visits to the patch and the family to which each female belonged. The rank of visits to the patch can also be considered to be the number of times females were off the patch (as in Haccou *et al.* 1991; Hemerik *et al.* 1993), or, equally, the number of times females cross the edge of the patch. Finally, in order to quantify the genetic variability in each of the behavioural mechanisms studied, the interaction between the 'family' effect and all the relevant covariates was also considered. Table 1 gives a list of all of these covariates with their dimensions.

To fit the model with a categorical covariate (i.e. a factor), such as the 'family' effect, the first family was arbitrarily assumed to be the reference level corresponding to the baseline hazard with a parameter set to zero. Thus, only nine parameters need to be estimated for this factor. The same procedure was used for all the corresponding interactions (see McCullagh & Nelder 1989; Collett 1994, for a detailed explanation). Parameters were estimated from the data by the maximization of the 'partial likelihood' function proposed by Cox (1975). The procedure gives the estimated coefficients of the model with their estimated variance–covariance matrix, which, in turn, can be used to compute confidence intervals of hazard ratios (see Appendix 2). All computations were carried out in S-Plus, using the package developed by T. Therneau (Venables & Ripley 1994).

Several statistical procedures are available for testing the significant effect of the covariates, all of which take into account the existence of possible correlations between the corresponding parameters. In general, a Wald-test has been used (Haccou *et al.* 1991; Hemerik *et al.* 1993; van Roermund *et al.* 1994; Ormel, Gort & van Alebeek 1995), however, for the study reported here, a standard likelihood ratio test was preferred (Collett 1994; see McCullagh & Nelder 1989, for a general description of this test). The procedure that was used to fit the model is described in Appendix 1.

The name 'proportional hazards model' stems from the assumption that, for different values of a fixed covariate, the hazard rates described in eqn 1 are proportional (Kalbfleisch & Prentice 1980; Collett 1994). The most simple and efficient method to test this assumption is to plot the log-cumulative hazard, log[-log S(t)], against log(t), where t is the patch time duration and S(t) is the Kaplan–Meier estimate of the survivor function, for each value of the fixed covariates (Andersen 1982; Collett 1994). If the curves can be taken to be parallel, the proportional assumption is justified. Figure 1 gives the log-cumulative hazard plots for the two fixed covariates studied.

Hazard rates for the first visit to the patch do not appear to be proportional to those obtained for the subsequent visits. In this case, the model can still be fitted by means of stratification between the first and the subsequent visits to the patch, leading to a new model with different baseline hazard functions. For the isofemale lines, however, the proportional assumption appears to be justified.

Finally, the adequacy of the fitted model can be assessed by making residuals plots. The most commonly used residuals in the analysis of survival data are those proposed by Cox & Snell (1968) (e.g. Hemerik *et al.* 1993; van Roermund *et al.* 1994). For the present study, it was preferred to use the deviance residuals proposed by Therneau, Grambsch & Flem-

Table 1. List of the explanatory covariates used in the Cox's regression model. The indicated dimensions correspond to the number of parameters that should be estimated to test them (see text)

Covariates	Dimension	Time-dependant
Number of successful ovipositions during the visit to the patch	1	Yes
Number of host rejections during the visit to the patch	1	Yes
Oviposition rates up to the three preceding ovipositions	3	Yes
Rejection rates up to the three preceding ovipositions	3	Yes
Rank of successive visits to the patch	1	No
Family each female belongs to (i.e. female's genotype)	9	No
Interaction 'family'–'number of ovipositions'	9	Yes
Interaction 'family'–'number of host rejections'	9	Yes
Interaction 'family'–'oviposition rates, three steps backwards'	27	Yes
Interaction 'family'–'rejection rates, three steps backwards'	27	Yes
Interaction 'family'–'rank of visit to the patch'	9	No

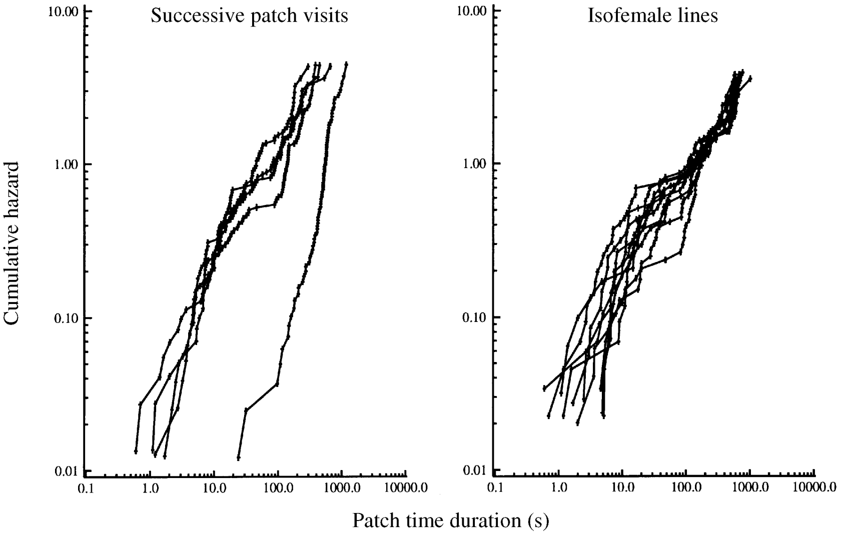

Fig. 1. Log-cumulative hazard plots for the two fixed covariates used in the Cox's regression model. The curve on the right in the left panel (successive visits to the patch) corresponds to the first patch visit. Both axes are in log scale.

ing (1990), because they have the same properties of residuals used to check the adequacy of linear models and are thus easiest to interpret. Indeed, they are uncorrelated with one another and are symmetrically distributed around zero with an expected value of zero, when the fitted model is correct. Figure 2, which gives the corresponding plot for the final model fitted, shows that nothing is amiss. Therefore, the final model seems properly to describe the patch-leaving tendency of *T. busseolae* females.

Results

The fitting procedure, described in Appendix 1, has led to a final model with 32 parameters. Table 2 gives the estimated effect of all the covariates that have a significant influence on the patch-leaving tendency of *T. busseolae* females.

Each successful oviposition significantly increased the patch-leaving tendency by a factor of 4·16. This result indicates that *T. busseolae* females are using a decremental mechanism to manage their residence time on patches of five *S. nonagrioides* eggs. Furthermore, the rejection of a host also led to an increase in the patch-leaving tendency (here, by a factor of 2·37). Despite these highly significant effects, the instantaneous oviposition rates, up to the three preceding ovipositions, have not shown any effect on the patch-leaving tendency (all χ^2 at $P > 0{\cdot}05$). However, there was a significant effect of the rejection rates up to two ovipositions backwards in time. The corresponding hazard ratios were both less than unity, suggesting that they have a decreasing effect on the patch-leaving tendency. Therefore, when host rejections appeared between two ovipositions that were in rapid succession, and this up to two ovipositions

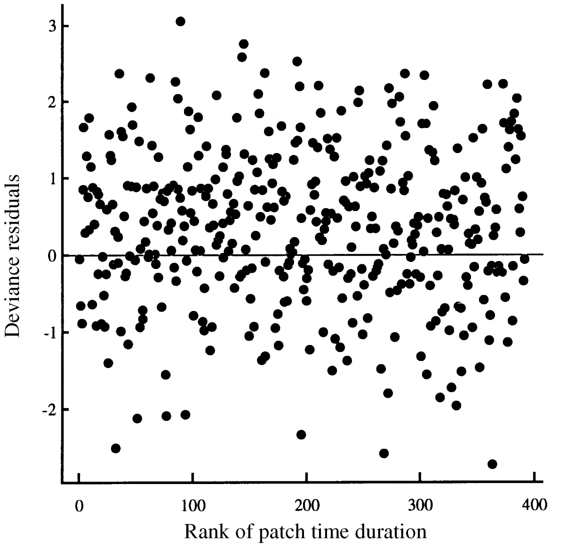

Fig. 2. Plot of the deviance residuals against the rank order of patch time duration. These residuals were computed after the final model had been fitted to the data (see text).

backwards in time, the corresponding rejection rates increased and the effect of each host rejected on the patch-leaving tendency is reduced or possibly reversed. In fact, according to eqn 1, and taking into account the host rejection rate r_1 only one step backwards in time, the hazard ratio after one host rejection was exp (0·86–85·64 r_1). Thus, the increasing tendency to leave the patch after each host is rejected will be cancelled or reversed as soon as $r_1 > 1{\cdot}004 \times 10^{-2}$ (i.e. as soon as the hazard ratio decreases below unity). Only nine out of 987 (i.e. 0·9%) rejection rates estimated were over this threshold value. Therefore, the host rejection rate one step backwards in time only had a reducing, but not reversing, effect on the increasing tendency to leave the patch that was induced by each host rejected. The same conclusion was obtained when the host rejection rate two steps backwards in time was considered, but in this case, the effect was less significant.

As can be seen in Fig. 3, the first visit to the patch was always much longer than the subsequent ones. Up to 60% of all the successful ovipositions were observed during this first patch visit. Afterwards, the patch-leaving tendency significantly increased by a factor of 1·21 for each subsequent visit, leading to a decrease in the corresponding average residence time (see Table 2). Finally, no significant interactions were observed between the rank of patch visit and the effect of each successful oviposition, host rejection and rejection rates up to two steps backwards in time (all χ^2 at $P > 0{\cdot}05$). Thus, the patch-leaving rules that have been discussed so far (e.g. decremental effect of each oviposition, etc.) seem to remain constant over the successive visits to the patch.

The results also have shown that there is a significant variation in the patch-leaving tendency between the isofemale lines that were compared (see Table 2). Within the *T. busseolae* population that was studied, some families showed a significantly stronger patch-leaving tendency than others. This suggests that the variation in the behavioural traits involved may be under genetic control. The genetic variation quantified in this manner can either be transmitted to the following generation according to Mendelian mechanisms or can be maternally inherited. Both mechanisms can have an important ecological meaning and can be the target of strong selective pressures, leading the females to adapt their patch-residence time to local environmental conditions. Besides this global genetic variation, there was also a significant interaction between the isofemale lines and the effect of each oviposition. As can be seen from Fig. 4a, each oviposition has led, globally, to hazard ratios above unity, confirming the associated decremental effect on the patch-residence time described above. However, the present results indicate that this effect is not the same among the different lines compared. This suggests the existence, within the population, of significant genetic variation in the intensity of the decremental effect on the patch residence time. Finally, a significant interaction was observed between the isofemale lines and the effect of each host rejected (see Table 2 and Fig. 4b). Within the

Table 2. Estimated regression coefficients (β), standard errors (SE) and hazard ratios [exp(β)] for only those covariates that had a significant effect ($P < 0{\cdot}05$) on the patch-leaving tendency of *T. busseolae* females. χ^2 corresponds to the likelihood ratio tests. All of them were computed with all other significant terms present in the model. For each covariate including the 'isofemale lines' effect, nine parameters were estimated. They are not provided here

	β	SE	exp(β)	χ^2(d.f.)	P-value
Ovipositions (1)	1·43	0·17	4·16	179·06 (1)	< 0·001
Host rejections (2)	0·86	0·30	2·37	21·52 (1)	< 0·001
Rejection rate one step backwards	–85·64	34·02	$6{\cdot}43 \times 10^{-38}$	7·10 (1)	0·008
Rejection rate two steps backwards	–90·16	47·22	$6{\cdot}95 \times 10^{-40}$	4·04 (1)	0·044
Rank of patch visit	0·19	0·05	1·21	12·81 (1)	< 0·001
Isofemale lines (3)	–	–	–	17·91 (9)	0·036
Interaction (1) × (3)	–	–	–	21·52 (9)	0·011
Interaction (2) × (3)	–	–	–	25·52 (9)	0·002

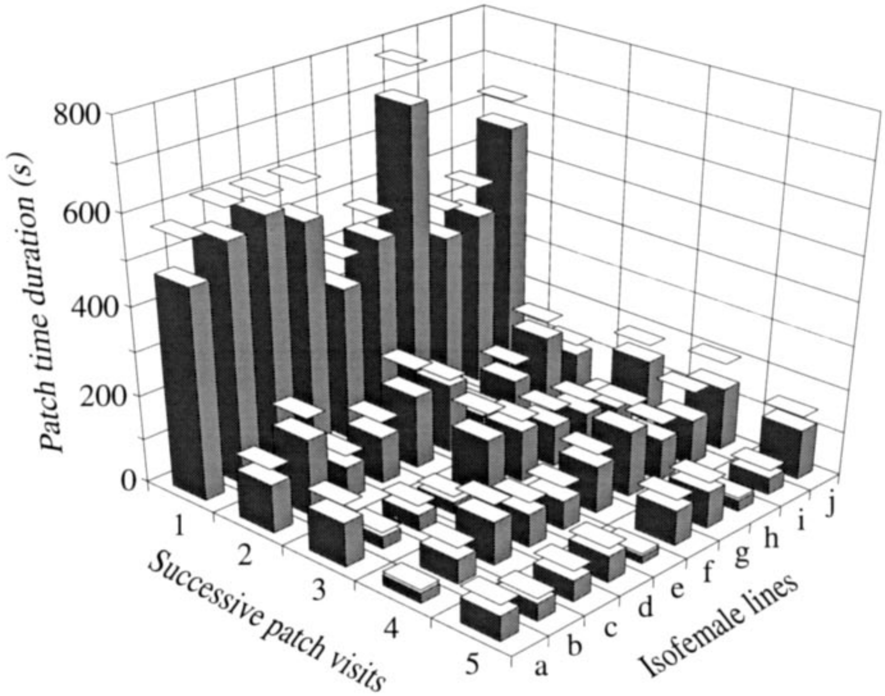

Fig. 3. Average patch residence times for each isofemale line and for each visit to the patch. Additional upper limits correspond to standard errors. Both averages and standard errors are computed from the Kaplan–Meier estimator of the corresponding survivor functions.

population analysed, the decremental effect of each host rejected on the patch-residence time also appears to be a family feature. This result suggests that this variation is also genetically determined.

Discussion

As pointed out by Haccou *et al.* (1991), the use of a Cox's regression model to describe patch-leaving strategies has the advantage of providing quantitative results that indicate the importance of each tested effect on the patch-leaving tendency of females. Using this method, the results presented have revealed that the intra-patch experience of *T. busseolae* females which attack eggs of *S. nonagrioides*, has a strong influence on their decision to leave the patch. The effect of several behavioural events that appeared during the intra-patch foraging process were quantified. Most of them were shown to have a significant influence on the tendency of females to leave the patch, and thus on their patch-residence time.

The strongest effect was related to successful ovipositions, each of them leading to a significant increase in the patch-leaving tendency. This indicates that *T. busseolae* females were using a decremental mechanism similar to the 'count-down' mechanism proposed by Driessen *et al.* (1995) for the larval parasitoid *Venturia canescens*. As stated by these authors, such a mechanism, also observed on other parasitoid species (Strand & Vinson 1982; Wiskerke & Vet 1994; van Steenis *et al.* 1996), may be adaptive when hosts are uniformly distributed across patches (Iwasa *et al.* 1981) or host patches are small (Strand & Vinson 1982). In both cases, each host that is attacked will provide information regarding the loss of the future value of the patch and may thus promote readiness to leave. In the present study, patches of five hosts were offered to the females and these patches were much smaller than those usually encountered under natural situations. This could be the reason why each oviposition was found to have a decremental effect on patch-residence time. In order to verify this hypothesis, complementary experiments were performed using the same experimental set-up, but with patches of 10 (18 females) or 15 (21 females) hosts. In both cases, a Cox's regression model led to the same conclusion: each successful oviposition significantly increased the patch-leaving tendency by a factor of 1·86 (on patches of 10 hosts) or 2·49 (on patches of 15 hosts). Thus, the decremental mechanism appears to be a fixed rule which does not seem to depend on the size of the host patch. This mechanism is probably an adaptive behaviour for females that attack hosts which are uniformly distributed across patches in the prospected environment.

Each successful oviposition was followed by a typical marking behaviour, which probably corresponds to the deposition of a contact pheromone on the attacked host. Therefore, the decremental effect associated with each oviposition may be related to the increase in the amount of pheromone deposited and this may lead to a stepwise decrease in the respon-

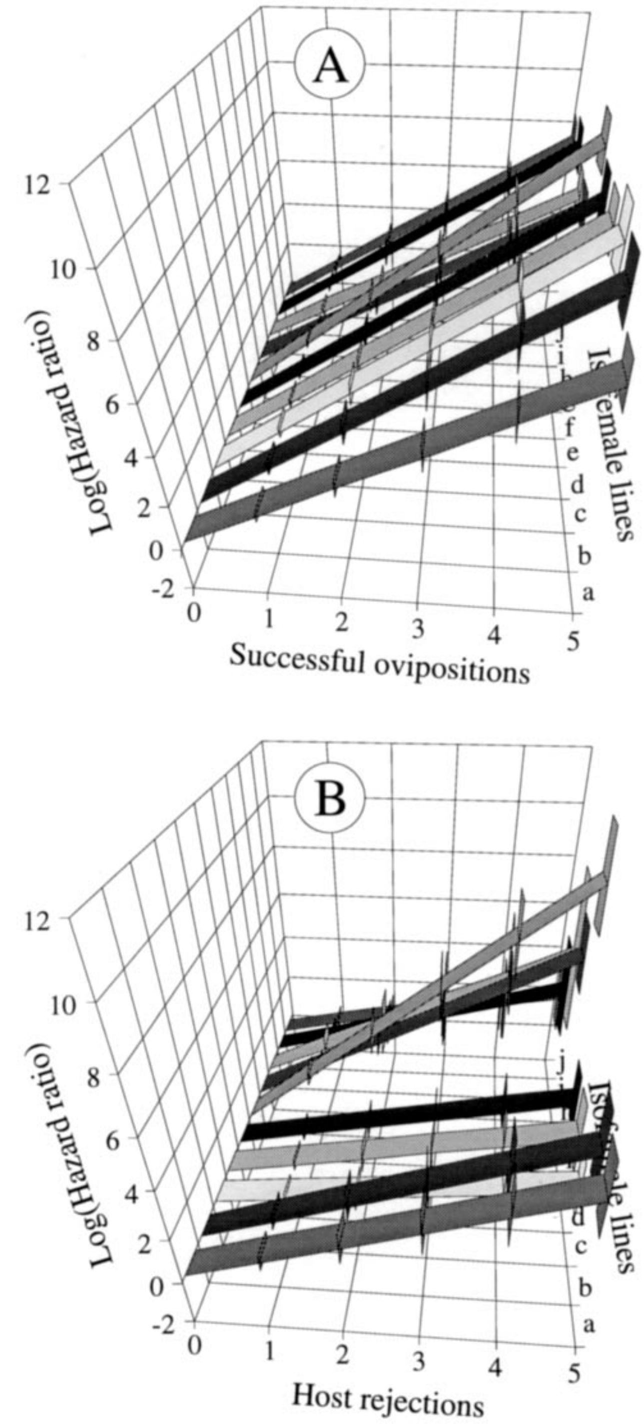

Fig. 4. Graphical representation of the interaction between the isofemale lines and the effect of (a) each successful oviposition or (b) host rejection. Hazard ratios (± SE) are computed according to the explanation provided in Appendix 2. Isofemale lines are labelled as in Fig. 3.

siveness of females to the patch. This mechanism appears to be similar to the one described for several leaf-miner parasitoids by Sugimoto and his colleagues (Sugimoto, Murakami & Yamazaki 1987; Sugimoto & Tsujimoto 1988; Sugimoto *et al.* 1990). Using a mathematical approach, these authors have shown that, while searching for host larvae on a leaf, foraging females deposit a marking chemical compound. They found that a patch-leaving decision was triggered as soon as the amount of this marking cue reached a critical threshold. In the results presented here, however, the marking pheromone was only deposited at particular discrete time intervals, i.e. when hosts were successfully attacked.

Each host rejection also led to a significant increase in the patch-leaving tendency. As stated by van Alphen & Vet (1986), van Lenteren (1991) and van Alphen (1993), such a mechanism could be adaptive because the rejection of a host provides the female with some information regarding the decreasing value of the patch on which she is currently foraging. Besides this, instantaneous oviposition rates, up to three preceding ovipositions, do not have any significant effect. A similar result was obtained on the *Drosophila* larval parasitoid *Leptopilina clavipes* (Hemerik *et al.* 1993), whereas *L. heterotoma* appears to react to these rates more significantly (Haccou *et al.* 1991). In this case, the most recently experienced oviposition rates were shown to have the strongest effect. These instantaneous oviposition rates are likely to change as a result of patch depletion. Therefore, the results obtained here suggest that *T. busseolae* females are not using the rate of patch depletion as a way to decide when the patch should be left. On the other hand, there was a significant effect of the host rejection rates, up to two ovipositions backwards in time. These rates have a reducing effect on the increasing tendency to leave the patch associated with each host rejection. These rejection rates can only be estimated if host rejections are followed by at least one successful oviposition. Thus, this result suggests that any successful oviposition that occurs after one or several host rejections will restore, to a certain extent, the wasp's motivation to remain on the patch, and this mechanism will be all the stronger as this new successful oviposition occurs rapidly after the previous one. In such a case, the wasp acquires new information, indicating that healthy hosts are still available on the patch and it therefore becomes worthwhile to remain on it for an additional amount of time. Thus, this mechanism may be considered to be adaptive.

Finally, there was significant variation in the patch-leaving tendency between subsequent visits to the patch. In particular, the first visit was always much longer than the subsequent ones. A similar result has been observed for several other parasitoid species (e.g. van Lenteren & Bakker 1978; Waage 1979; Strand & Vinson 1982; Haccou *et al.* 1991). Furthermore, Haccou *et al.* (1991) demonstrated that, after the patch has been visited once, the patch-leaving tendency of *L. heterotoma* females increases, but in a non-monotonic way. Here, the patch-leaving tendency was also found to increase with each subsequent visit to the patch, but this effect was considered to be linear. The fact that the fitted model appeared to describe correctly the observed data seems to confirm such a hypothesis. Several mechanisms can be proposed to explain this result. First, it may be possible that foraging females have used their past experience, acquired during preceding visits to the patch, to adjust their current patch-residence time. Such a mechanism could explain why the first visit was much longer than the subsequent ones, because females were only naive in the first case when they have to discover a new environment. Second, after the patch has been visited once, females may recognize some landmarks or patch marking, or may experience a reduced motivation to search because of egg depletion, habituation or tiredness (van Alphen & Galis 1983). Under such a hypothesis, the most important mechanism would be the recognition of a marking pheromone that is deposited after each successful oviposition. A third hypothesis can be related to the rate of patch depletion and thus, indirectly, to the rate of superparasitism (i.e. oviposition in a host that has already been attacked). Indeed, under the experimental conditions used here, some cases of superparasitism did occur; for example, in two out of 83 (i.e. 2·4%) first visits to the patch that was studied, six or seven successful ovipositions were observed on the patch of five hosts. Even though the timing of such events was not recorded, their frequency would be likely to increase during subsequent visits to the patch. This, in turn, could lead to a corresponding increase in the patch-leaving tendency.

In all theoretical and experimental studies performed on patch time allocation, the patch-leaving decision rules, under a given environment, have always been considered to be fixed species-specific mechanisms (Driessen *et al.* 1995). However, the results obtained by the present study indicate that there was strong genetic variability in the corresponding mechanisms, within the population studied. Using the isofemale lines method, different genetic variations were observed and quantified. First of all, there was a significant global genetic variation in the patch-leaving tendency between the different families compared. This indicates that, within the studied population, some genotypes result in females remaining on the patch for a longer period of time than others. According to Waage's (1979) model, the patch residence time will depend on: (i) the initial degree of responsiveness to the patch edge, which is assumed to be related to the number of hosts available; and (ii) the decreasing rate of this responsiveness during the foraging process, leading to a decreasing tendency to exhibit a turning response each time the patch edge is encountered (Waage 1978, 1979). Thus, the inter-family variability observed in this study could be the consequence of genetic variation in the initial response to the number of hosts available in the patch and/or in the rate of habituation to the patch edge. Irrespective of the mechanism involved, such genetic variation is likely to be the characteristic of a polyphagous species like *T. busseolae*, which is known to attack, over successive generations, several host species showing strong differences in patch size, quality and distribution.

Aside from the global genetic variability, there was also, within the analysed population, significant genetic variation in the intensity of the decremental effect of each oviposition on the patch-residence time (see

Fig. 4a). The decremental (or even incremental) effect of each oviposition has always been considered to depend only on the time between successive ovipositions (Waage 1979) or on the number of past ovipositions (Driessen *et al.* 1995). The results presented here show that it also depends on the genotype of the females. As suggested above, the observed decremental effect may be related to the response to a deposited pheromone on each successfully attacked host. Therefore, the genetic variability in the intensity of this decremental effect may correspond to genetic variation in the amount of pheromone deposited and/or in the response level to such a marking cue. A decremental effect is usually considered to be an adaptive behaviour for females which attack hosts with a uniform distribution across patches (Iwasa *et al.* 1981). The observed genetic variability in the intensity of the decremental effect could thus be considered to be a characteristic of a wasp population that consists of females which experience some variation in the distribution pattern of their hosts.

Finally, there was also significant genetic variability in the intensity of the decremental effect associated with each host rejection (see Fig. 4b). For some families, each host rejection led to a strong increase in the patch-leaving tendency, while for others, the increase appears to be less pronounced. As stated by van Alphen & Vet (1986), encounters with parasitized hosts, and thus host rejections, could affect patch time, either because they impart information to the parasitoid about the decreasing value of the patch or because they decrease the forager's host-searching motivation. The genetic variation observed in the intensity of the decremental effect associated with each host rejected could thus correspond to genetic variability in the quality of the information acquired on the decreasing value of the patch, and/or in the associated decreasing level of the host searching motivation of females.

The genetic variation observed in the intensity of the decremental effect associated with each oviposition or host rejection indicates that there is, within the analysed population, genetic variability in the response to the information acquired by the foraging females during their intra-patch foraging experience. Patch time allocation is considered to have a strong influence on the spatial distribution of parasitoids, and thus on the population dynamics of parasitoid–host systems (van Alphen 1993). Thus, it would be interesting to include such an inter-individual genetic variability in models that take into account individual behavioural decisions in order to estimate its consequence in terms of population dynamics. To accomplish this, the models developed by Bernstein, Kacelnik & Krebs (1988, 1991) and Krivan (1997) could provide a good starting point. Finally, patch-residence time is known to be influenced by the number of females foraging on a patch (Visser, van Alphen & Nell 1990; Visser & Driessen 1991). Therefore, experiments are now being performed in order to see whether there is some interference between *T. busseolae* females foraging on a patch and if, within the population studied, there is genetic variability in this behavioural mechanism.

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Appendix 1

Usually, all the parameters of a Cox's regression model are estimated and tested simultaneously. However, if we consider the 99 parameters listed in Table 1 and the possible pairwise interactions between all the covariates, except for the 'family' effect, the model presented here can have more than 130 parameters that need to be estimated and cannot be fitted that way. Therefore, the fit of the model was performed using the iterative procedure described in the following steps (Collett 1994).

1. The model was first fitted with only one of the covariates (except the 'family' effect) at a time.
2. All the covariates that gave a significant likelihood ratio test at the preceding step were fitted together. In the presence of certain covariates, others may cease to be important. So, the effect of each covariate was tested again by sequentially omitting each of them from the set. Only those that still showed a significant effect were retained in the model. Once a covariate was dropped, the effect of omitting each of the remaining ones in turn was re-examined.
3. Covariates which were not important on their own, and so were not under consideration in the previous step, may become important in the presence of others. Thus, they were added to the model built in step 2 one at a time, and those leading to a significant effect were retained in the model. This process may result in some terms in the model that was built in step 2 ceasing to be significant. In this case, the terms were removed and the process was resumed at step 2 above.
4. A final check was made to ensure that all covariates in the model were significant by omitting and testing them one at a time, and that any covariate which was not included did not have a significant effect once it was added.
5. Finally, the 'family' effect was added and tested with the corresponding interactions. The total covariates selection procedure was performed with a significance level of 10%, in order to avoid rejecting an effect that would appear to be significant in the following steps.

Appendix 2

The fitting procedure of the model leads to the estimation of coefficients with their estimated variance–covariance matrix. In return, these different parameters can be used to estimate specific hazard ratios with their standard error. Let us consider the result shown in Fig. 4a that presents the interaction between the isofemale lines and the effect of each oviposition in terms of hazard ratios and their standard error. For these effects only, the model contains 10 parameters, α_i, $i = 1, 2, \ldots, 10$, with $\alpha_1 = 0$ (i.e. baseline hazard) and nine estimated parameters corresponding to the isofemale lines compared; one term, δ, corresponding to the effect of each oviposition, and 10 parameters, γ_i, $i = 1, 2, \ldots, 10$ (with $\gamma_1 = 0$), corresponding to the interaction between these two effects. Thus, the hazard function for a female belonging to family i, and that has already attacked j hosts is:

$$h(t) = h_0(t) \exp\{\alpha_i + j(\delta + \gamma_i)\}. \qquad \text{eqn A1}$$

So, the hazard ratio for this female, relative to a female of the same family that has not yet shown any oviposition is:

$$[\exp\{\alpha_i + j(\delta + \gamma_i)\}]/[\exp\{\alpha_i\}] \qquad \text{eqn A2}$$

which reduces to $\exp\{j\,(\delta + \gamma_i)\}$. The standard error of the log-hazard ratio is thus:

$$j\surd[\mathrm{var}(\delta) + \mathrm{var}(\gamma_i) + 2\,\mathrm{cov}\{\delta,\gamma_i\}] \qquad \text{eqn A3}$$

For the first family, both α_1 and γ_1 are set to zero, and the standard error of the log-hazard ratio is modified accordingly. The same procedure is used for the interaction between the family effect and the number of host rejections (Fig. 4b).