Journal of Theoretical Biology 313 (2012) 1–11

Contents lists available at SciVerse ScienceDirect

Journal of Theoretical Biology

journal homepage: www.elsevier.com/locate/yjtbi

Patch leaving rules: A stochastic version of a well-known deterministic motivational model

Jean-Sebastien Pierre[a], Jean-Pierre Masson[b], Eric Wajnberg[c,*]

[a] Unité Mixte de Recherche CNRS, Université de Rennes 1 n 6553, "Ecologie-Biodiversité-Evolution", Campus de Beaulieu, Bâtiment 14A, 35042 Rennes Cedex, France
[b] Agrocampus Rennes, 65 rue de St Brieuc, 35042, Rennes-Cedex, France
[c] INRA, 400 Route des Chappes, BP 167, 06903 Sophia Antipolis Cedex, France

HIGHLIGHTS

- ► We developed a stochastic model describing patch-leaving rules in animals foraging for resources.
- ► For this, we give a quasi close form expression for the distribution of patch residence times.
- ► We also present statistical procedures to estimate the corresponding parameters.
- ► As examples, the model is fitted on two independent experimental data sets.
- ► The model provides a stochastic interpretation of motivation leading foragers to optimality.

ARTICLE INFO

Article history:
Received 2 January 2012
Received in revised form
31 July 2012
Accepted 2 August 2012
Available online 13 August 2012

Keywords:
Patch models
Departure rules
Optimal foraging
Motivation
Stochastic models

ABSTRACT

A famous motivational model proposed for insect parasitoids by Waage (1979) provides a candidate mechanism for patch-leaving decision rules in foragers. In this model, the animal is supposed to enter a patch of resources with an initial tendency to stay in it, which then regularly decreases. Every encounter with a resource item increases or decreases this tendency, and the forager is supposed to leave the patch when this tendency or motivation falls below a given threshold. Evidence of such increases and drops in this tendency to stay were often obtained by analyzing experimental data with a Cox (1972) proportional hazards model. The Waage (1979) model is purely deterministic and predicts a fixed departure time for a fixed set of encounters with foraging items. On the other hand, empirical data show a large variability of departure times under fixed conditions. We present a fully stochastic version which overcomes this problem and gives a quasi close form expression for the distribution of patch residence times as well as a statistical procedure to estimate its parameters. Two examples of the model fitting on experimental data sets are provided. This novel model, although more complicated than Waage (1979) model, improves its realism and provides a stochastic interpretation of motivation as a proximal mechanism leading foragers to optimality.

1. Introduction

Most animal species exploit resources that are distributed in discrete patches in the environment (Stephens and Krebs, 1986; van Alphen et al., 2003; Wajnberg, 2006). This is the reason why there have been, in the last few decades, a lot of theoretical and experimental studies which have tried to understand how animals should optimally allocate their foraging time in each patch they are exploiting in order to maximize their rate of progeny production (Charnov, 1976; Stephens and Krebs, 1986; Wajnberg, 2006). A large number of the results published were obtained on insect parasitoids foraging for patchily distributed hosts (Godfray, 1994; Wajnberg, 2006). Besides the fact that these animals are usually easy to rear and to study, most species are usually unable to find enough hosts in which to lay all their eggs during their lifetime (Driessen and Hemerik, 1992; Sevenster et al., 1998; Rosenheim, 1999). They are thus likely under strong selective pressures to develop efficient patch time allocation strategies, hence to use elaborated patch leaving decision rules (Godfray, 1994; Wajnberg et al., 1999, 2004; Wajnberg, 2006). Moreover, the foraging behavior of solitary insect parasitoids is directly related to their fitness since each attack of a potential host will give the opportunity to obtain (at most) one offspring.

The question of the optimal time foragers should allocate to each patch they are exploiting was answered early within the

---

* Corresponding author. Tel.: +33 49 238 6447; fax: +33 49 238 6557.
E-mail addresses: jean-sebastien.pierre@univ-rennes1.fr (J.-S. Pierre), jeanpierre.masson@me.com (J.-P. Masson), wajberg@sophia.inra.fr (E. Wajnberg).

0022-5193/$ - see front matter © 2012 Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.jtbi.2012.08.003

framework of the Marginal Value Theorem (MVT) (Charnov, 1976). This framework predicts that each patch should be exploited until the rate of gain within the patch has decreased to a marginal value. This rate, measured in energy intake units for predators or herbivores and directly in fitness units for parasitoids, is the mean rate of gain that can be achieved in all the available patches in the environment. Several examples of animal species that are following the prediction of this theoretical model have been published in the literature (*e.g.*, Hassell, 1978; Hubbard and Cook, 1978; Waage, 1979; Wajnberg et al., 2000).

This theoretical approach and all those that were developed afterwards make the implicit assumption that foragers know exactly the distribution and the quality of all available patches in the habitat (Waage, 1979; McNair, 1982; Godfray, 1994; Wajnberg, 2006). Such an assumption is obviously unrealistic and the underlying proximate mechanisms used by foraging animals to reach optimal patch time strategies are not always known (Godfray, 1994; Wajnberg et al., 1999, 2000; van Alphen et al., 2003; Wajnberg, 2006). This is how simple patch leaving rules, so-called rules of thumb, were initially proposed by several authors. Three simple rules were successively proposed: the forager should leave the patch after (1) finding and attacking a fixed number of hosts (Gibb, 1962), (2) a fixed time has elapsed (Krebs, 1973), or (3) no hosts have been found for a fixed amount of time (fixed giving-up time; Hassell and May, 1974, Murdoch and Oaten, 1975). Some of these rules, when adopted by a forager, lead to patch residence times that closely approximated optimal strategies (see Wajnberg, 2006 for a review). Waage (1979), who performed some empirical work on the parasitic wasp *Nemeritis canescens* (Gravenhorst), proposed a more elaborate process. He defined a new class of processes that is both motivational and mechanistic; which is based on a latent variable called motivation that the author interpreted as the tendency to stay in the patch and to continue to forage in it. In the Waage (1979) model, the forager enters the patch with an initial motivation linked with its expectation of patch profitability. This initial motivation is noted aP where P is the number of potential hosts in the patch and a a constant linking the number of hosts to the concentration of kairomones they produced, a cue that is perceived by the forager. After entering the patch, the initial motivation monotonously decreases with time in the absence of any encounter with a host: a linear decrease of the form $-bt$ is proposed where the constant b is the rate of decrease and t is the time spent on the patch. Every host encountered and attacked raises instantaneously the motivation level by a given quantity. Waage (1979) described the following equation for total patch residence time T:

$$T=\left(aP+\sum I_i-r^*\right)/b \tag{1}$$

where r* is the critical level of responsiveness below which the patch should be left, and I_i the change in the level of responsiveness due to the ith discovery of an item. Deliberately forgetting additional sophistications, we shall consider I as a constant. The so-called motivation or tendency to stay, $m(t)$ at any time t after the parasitoid entered the patch is then given by the equation:

$$m(t)=aP-bt+n(t)I \tag{2}$$

where $n(t)$ is the number of hosts attacked up to time t. This equation is easily deduced from the Waage (1979) model of patch residence time (1) and an example is provided in Fig. 1.

In this model, the patch is left when the motivation $m(t)$ falls below a given threshold r^* that will be set to zero in what follows without loss of generality. Such a model is called incremental, since each new host attack increases the motivation level, thereby increasing the time spent in the patch by a fixed quantity I/b. The process shows a strong analogy with the concept of the patch richness estimator proposed by Iwasa et al. (1981). In the model of Iwasa et al. (1981), the motivational arousals of the Waage (1979) mechanism would correspond to a sudden increase in the forager's estimation of the number of resource items remaining in the patch.

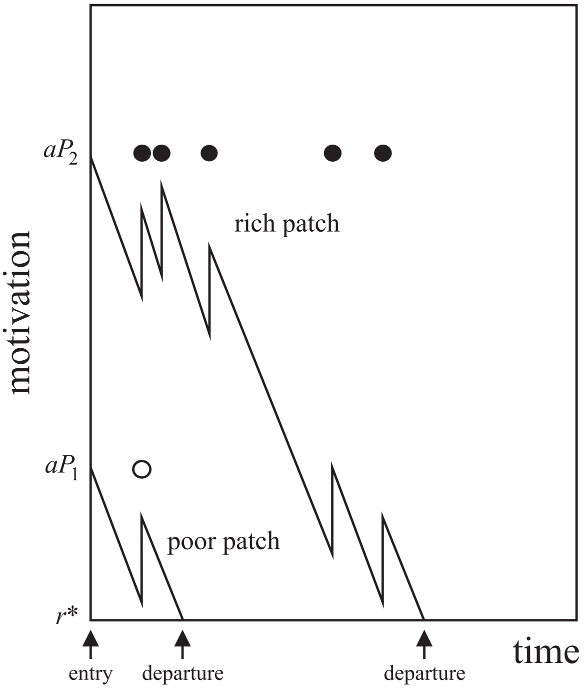

Fig. 1. Graphical representation of the Waage (1979) incremental model. Lines represent the evolution of motivation (or responsiveness) of the forager in the course of the patch residence time. Two cases are represented: a poor patch in which the forager enters with motivation aP_1 and a rich patch in which the initial motivation is aP_2. After entering the patch, the motivation decreases linearly except when a host is met and attacked (close circles in the rich patch, open circle in the poor patch). At each attack, the motivation increases by a quantity I. The departure is obtained when the motivation level falls below a given threshold r^*.

Several variations of such a mechanistic model were proposed. The most well-known one was suggested by Driessen et al. (1995) in which the idea of a monotonous decrease in motivation is preserved while the animal is foraging on the patch, but the effects of each host attack is decremental instead of being incremental. Following Iwasa et al. (1981), such a decremental effect was demonstrated to be adaptive when all patches contain a relatively uniform number of hosts. Although based on inverse mechanisms, both incremental and decremental approaches belong clearly to the same class of processes. van Alphen (1993) was the first to propose a model combining both incremental and decremental processes in which the attack of a healthy host increases the motivation level, while rejecting a parasitized host decreases it. Such a combined mechanism was verified for different parasitoid species (van Alphen, 1993; Wajnberg et al., 1999, 2000, 2003, see Wajnberg, 2006 for a review). Finally, based on observations on *Leptomastix dactylopii*, Pierre et al. (2003) proposed to replace the monotonous decrease in forager's motivation to remain on the patch by a logarithmic decay over time.

Unfortunately, the motivation level corresponds to a latent variable and, as such, can only be appreciated through its indirect effects on the time spent on a patch. Therefore, identifying incremental/decremental effects implies that one must record both the total time spent on a patch and the set of behavioral events occurring in it, e.g., the successive times of encounters with hosts. The analysis of such survival data, eventually with time-dependant covariates (see Wajnberg, 2006 for a review) can be performed with a Cox (1972) regression analysis. This analysis was shown to be very efficient and is now widely used (Haccou et al., 1991; van Alphen, 1993; Hemerik et al., 1993; Vos et al., 1998; Driessen and Bernstein, 1999; Wajnberg et al., 1999, 2000, 2003; van Alphen et al., 2003; Wajnberg, 2006, 2012). In this paper, we show that the deterministic shape of the mechanistic, motivational model initially proposed by Waage (1979), and of the subsequent ones, can raise several methodological problems. We address these different problems and propose a fully stochastic version of the Waage (1979) model that describes more accurately patch time allocation and patch-leaving decision rules used by animal foragers. We finally propose a statistical method to adjust such a stochastic patch time allocation model to data collected experimentally.

2. Discrepancies between the Waage (1979) model and the Cox regression analysis

2.1. Evenly distributed patch leaving events

The basic feature of the Waage (1979) model is deterministic. The only random part arises from the discoveries of hosts in the patch. Such a random component may be considered as a Poisson process with constant intensity (i.e., very large patches, negligible depletion) or of decreasing intensity (i.e., with depletion). Hence, conditionally to a given set of host discoveries, the time spent in the patch is fixed and can be easily obtained using the following equations:

If no host is found:

$$t_0 = \frac{aP}{b} \tag{3}$$

If n hosts are found:

$$t_n = \frac{1}{b}(aP + nI) \tag{4}$$

According to this simple model, if no host is found the distribution of the patch residence times is a Dirac. This means that residence times end at t_0 with probability 1 as defined in (3). If a random number of n hosts are found, the distribution is the product of a “Dirac comb” by a discrete distribution that may be derived analytically (but this will not be developed here). Fig. 2 gives an example of such a distribution. As far as we know, such distributions, or any approaching distributions, were never mentioned in the literature nor observed in real animal experiments.

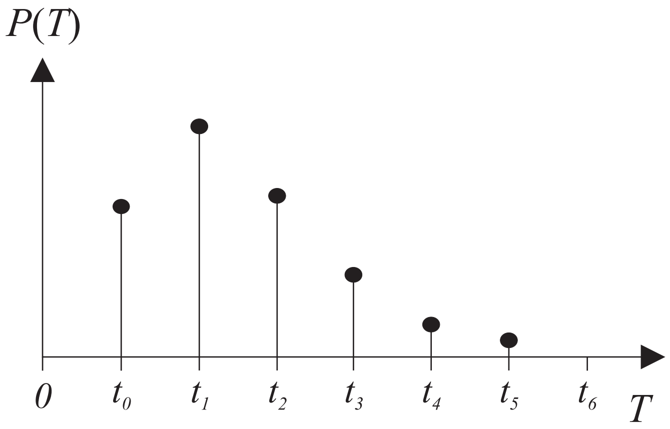

Fig. 2. Probability distribution of patch residence times in the Waage (1979) model. If host encounters follow a Poisson process, the residence times should be distributed as a “Dirac comb”. Departure can only occur at evenly distributed times spaced by a length of I/b. Departures from the patch occur exactly at times $t_0, t_1, \ldots, t_n$ with probabilities given by the vertical axes.

2.2. Identifiability

Consider the two cases where $n=0$ and $n=1$ for two different individuals. Eqs. (3) and (4) provide the expected patch residence time for these two individuals. Therefore, there are only two independent equations to estimate three parameters: aP (considered as a single parameter), b and I. This generalizes obviously when $n>1$, showing that the model is not estimable. One of its three parameters must be set as a scaling factor, $b=1$ for instance.

2.3. Lack of stochasticity: between and within individual variation

The only source of stochasticity in the Waage (1979) model lies in the random discovery and attacks of the hosts. The same sequence of host attacks is supposed to produce the same time departures. In the true world, however, under identical conditions, individuals generally differ in their state parameters aP, I and b. How should the three parameters vary from one patch to another in the life of a single individual and how should they vary between individuals? These problems are different, and this probably explains why no attempt has been made to estimate directly the parameters of a Waage (1979) model from experimental data. Obviously, some source of stochasticity is needed.

2.4. No link with the Cox proportional hazards model

2.4.1. A shift in the hazard rate and not a proportional variation

Since residence times are usually analyzed with Cox's regression models (Wajnberg, 2006), through the use of the hazard rates function which corresponds to the ratio of the probability density function of the residence times to the survivor function at time t (see Haccou and Meelis, 1992; Collett, 1994; Kalbfleisch and Prentice, 2002; Zens and Peart, 2003), it would be useful to interpret the Waage (1979) model in terms of hazard rates and to find out what should be the hazard rate function with or without some random variation in the model's parameters. In the case where no host is encountered and without any random variation, the time spent in the patch by a forager is fixed and given by Eq. (3) above. The probability density function of patch residence times is then a Dirac distribution $\delta(t-aP/b)$ as we have seen before (see Fig. 3e). The corresponding cumulative distribution function is thus a Heaviside function switching from 0 to 1 at $t=aP/b$. The survivor function $S(t)$, is thus the complementary Heaviside function switching from 1 to 0 at the same time coordinate (Fig. 3c). The hazard rate function is null for every $t<aP/b$, infinite for $t_0=aP/b$, null again for $aP/b<t<(aP+I)/b$ and undefined for $t>(aP+I)/b$. When two or more host encounters occur, the hazard rate function is a Dirac comb (Fig. 2) and the survivor function becomes a weighted sum of complementary Heaviside functions. The hazard rate function can be used as a measure of the tendency of the parasitoid to leave the patch. This point contrasts slightly with Waage (1979), and separates two concepts: the motivation to stay on the patch, which corresponds to the responsiveness in Waage (1979), and the tendency to leave it which is null until the motivation falls to zero. Under the Waage (1979) model, it seems perfectly correct to say that the tendency to leave the patch is null until the animal really leaves it. The motivation, on the other hand, is the latent variable which triggers the tendency to leave.

2.4.2. Introducing a normal random noise in Waage's model

Let us introduce a random component in the Waage (1979) model by assuming a normal distribution for the ratio aP/b, and rescaling the time in such a way that $t_0=0$ and the variance in

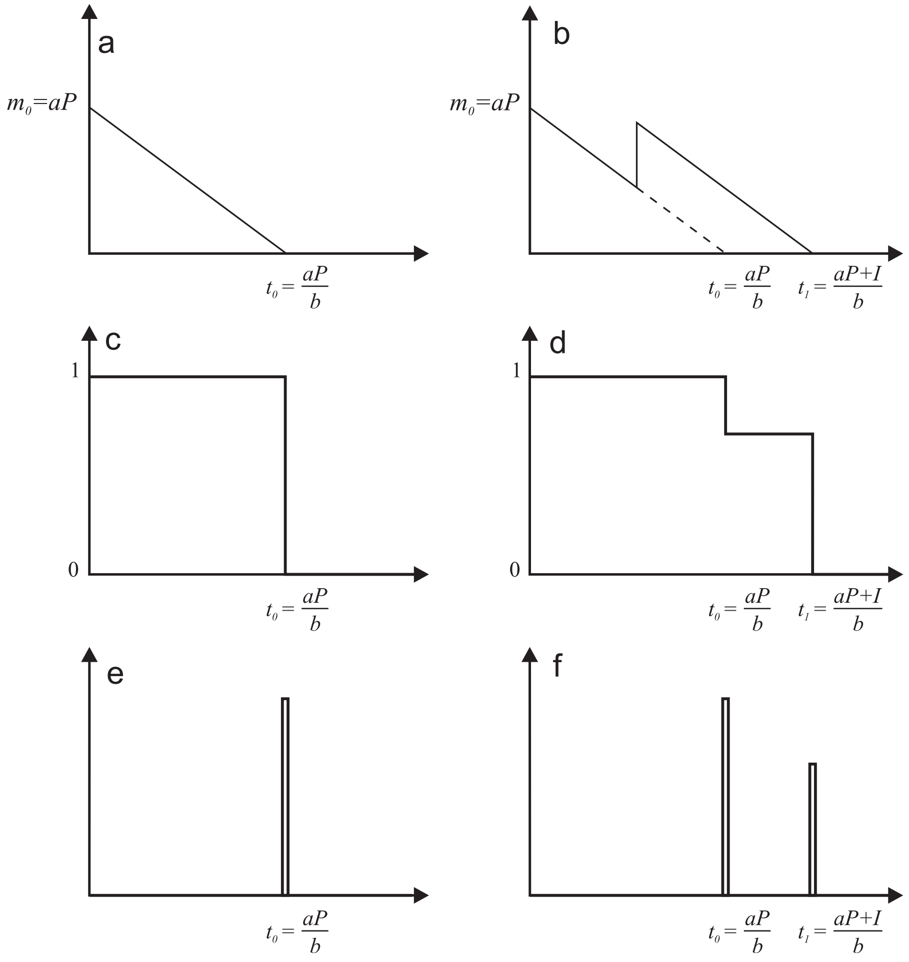

Fig. 3. Graphical representation of the Waage (1979) processes (a and b) with the corresponding survivor functions (c and d) and probability density functions (e and f) in the hypothesis of no host being attacked (left column) or of either zero or one host randomly attacked (right column). Without any attack, the departure time is strictly equal to t_0 (a). With zero or one attack, the departure time can take only two values t_0 and t_1, separated between each other by I/b (b). Correspondingly, without any attack, the survivor function is the complementary Heaviside function, switching from 1 to 0 at t_0 (c). With zero or one attack, the survivor function switches at t_0 from 1 to the probability of no attack since t_0 and then to zero at t_1 (d). Panels (e) and (f) are attempts to represent the corresponding probability density functions, respectively consisting in a single impulse when no attack occurs before time t_0 and of two impulses if one attack occurs.

patch residence time is 1. Doing this, and considering a situation in which no hosts are encountered, the hazard rate function simplifies into:

$$h_0(t)=\frac{f(t)}{1-F(t)}=\frac{\exp\,(-(t^2/2))}{\int_t^{+\infty}\exp\,(-(s^2/2))ds} \tag{5}$$

which plays the role of the "baseline hazard function" in proportional hazards models.

Let us now assume that each encounter with a suitable host leads to a fixed increment I of the tendency to stay. Then, each host encounter results in a simple translation to the right of the hazard function $h(t)$ by a factor of I/b. The corresponding density, log-survivor and hazard rate functions are given in Fig. 4a, b and c, respectively. Driessen and Bernstein (1999) and Tenhumberg et al. (2001a) showed two examples where similar albeit different survivor functions were proposed.

The general form of the a Cox (1972) regression model, also called a proportional hazards model (Collett, 1994; Kalbfleisch and Prentice, 2002), is:

$$h(t)=h_0(t)\exp\left(\sum\beta_i z_i\right) \tag{6}$$

where $h(t)$ is the hazard rate function, the z_i are explanatory covariates, either quantitative or qualitative (factor levels), and the β_i are regression coefficients estimated from the data and affecting the baseline hazard rate $h_0(t)$.

Starting from (5), we rescale it in such a way that

$$t\rightarrow T-\frac{aP}{b}. \tag{7}$$

The effect of a single host encounter is then to delay the patch residence time by a time lag of I/b, leading to the computation of the corresponding hazard rate function as follows:

After one host encounter, the mean departure time is

$$T-\frac{aP}{b}=\frac{I}{b} \tag{8}$$

Then, using the transformation (7),

$$h_1(t)=\frac{\exp[(1/2)(t-(I/b))^2]}{\int_{t-(I/b)}^{+\infty}\exp[(1/2)(s-(I/b))^2]ds} \tag{9}$$

Expression (9) is obviously the translation of expression (5) by a quantity I/b. $h_1(t)$ cannot be a proportional transformation of expression (5) (Fig. 4a). This results from the fact that a Cox regression analysis and the Waage (1979) model are not based on the same theoretical framework. In the former, the effect of an encounter with a host is additive on a mechanistic and hypothetical state variable, while the latter is multiplicative on a stochastic variable, the giving up rate. This point was already pointed out

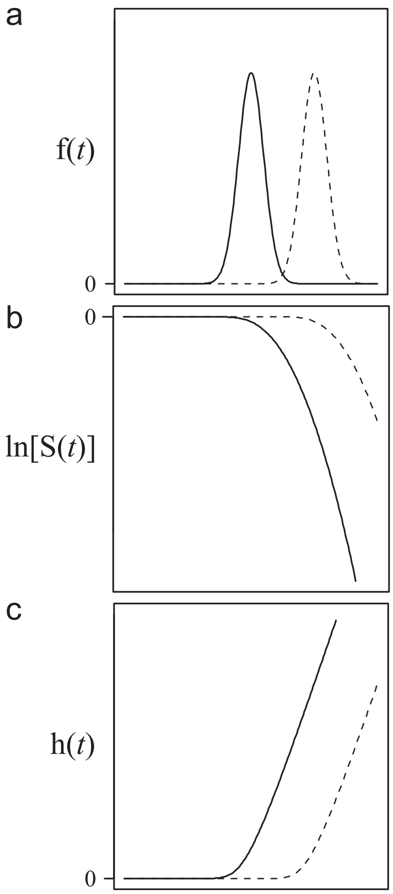

Fig. 4. Probability density functions (a), log-survivor functions (b) and hazard rate functions (c) of patch residence times theoretically obtained by introducing a random normal variation in *aP*/*b* in the Waage (1979) model. In each graph, the curve on the left represents the function obtained without host encounter, the curve on the right represents the function obtained with one host encounter. Axis scales are arbitrary.

by Driessen and Bernstein (1999), Wajnberg et al. (2000), Tenhumberg et al. (2001b) and Wajnberg (2012) who built simulation models of patch-leaving decision rules directly on the Cox hypotheses and not on the basis of Waage (1979)-like motivational processes. However, Cox regression analysis has proved to be efficient in estimating incremental or decremental effects on the patch residence time and, by way of consequence, has been considered as a support to motivational models like the one proposed by Waage (1979).

2.5. The relationship between Waage's increments and Cox proportional hazard regression coefficients cannot be linear

2.5.1. General relationship

Providing that the proportional hazard framework holds, what should be the relationship between the regression parameters β_is of the Cox model and the increment I in the Waage (1979) model? Suppose that a set of data containing distinct observations with 0, 1,…,n host attacks is analyzed by means of a Cox's regression model, and let β be the effect of every single host attack in such a model. Reasoning by identification, we obtain the relationship:

$$I = b\,\exp(\beta)\int_0^{\infty} t h_0(t)[S_0(t)]^{\exp(\beta)}dt - aP \tag{10}$$

(See Appendix A for a proof).

In this equation, both the baseline survivor function $S_0(t)$ and the baseline hazard function $h_0(t)$ remain unspecified.

2.5.2. Particular case: exponential distribution

In the particular case where these two functions correspond to an exponential distribution of the patch residence time, $S_0(t)=\exp(-\mu t)$ and $h_0(t)=\mu$ for all t. Thus, Eq. (10) reduces to:

$$\frac{I}{b} = \frac{1}{\mu\,\exp(\beta)} - \frac{aP}{b} \tag{11}$$

The link between the β estimates of the Cox's regression model and the parameters of the Waage (1979) model should thus be:

$$\beta = \ln\frac{b}{\mu} - \ln(I + aP) \tag{12}$$

Even in this simple case, the relationship between β and I, although monotonous, is not linearly decreasing but has a logarithmic shape. Such considerations as well as the examination of a substantial number of datasets led us to propose an alternative model replacing the Waage (1979) model, taking care of keeping its best feature, i.e., the idea of an incremental or decremental process during foraging bouts.

3. A stochastic model

3.1. Description of the model

Let us again consider the motivation of the Waage (1979) model as a hidden random variable, decreasing over time, but with a random intercept *aP* and a random slope *b*. Stochasticity occurs both between and within individuals for each new foraging sequence. The result is that the time when the decision to leave the patch is reached becomes also a random variable with some density distribution $f(t)$. Each motivation change at the time when hosts are encountered translates the mean of the distribution to the right or to the left in the incremental or decremental case, respectively. However, there is at least one distribution for which the translation of the mean results in a constant modification of the hazard rate, i.e., the exponential distribution. Indeed, its expected value is the inverse of the hazard rate, so the effect of an encounter with a host is thus to increase or decrease the hazard rate, and thus to decrease or increase the mean residence time on the patch. What we observe is the tendency to leave the patch, measured by a hazard rate at a population level. When no hosts are discovered, the hazard rate remains constant, meaning that the forager can leave the patch at any time, although its hidden motivation to forage in the current patch decreases. As a consequence, the accurate time of patch departure is no longer a constant but a random variable, exponentially distributed (this is a well known property: a constant hazard rate results in an exponential distribution). If we again suppose that each resource item discovered changes suddenly the hazard rate, the global survivor function will be a piecewise exponential with different coefficients. The probability density function of the residence time at time t, conditionally to the events of encounters, corresponds to an exponential distribution with upward or downward jumps in the incremental or the decremental case, respectively. Then, such a conditional density function has dynamics that appear to be very similar to Waage (1979) and Iwasa et al. (1981) functions.

The patch-leaving model we propose, that can overcome the difficulties inherent to the deterministic approach initially proposed by Waage (1979), used the following approach: Once a foraging animal enters a patch, its foraging time X_0 is exponentially distributed with a constant hazard rate $\alpha_0(\alpha_0>0)$. Each time a host is encountered, its current hazard rate is increased or decreased. Let us denote α_i the hazard rate obtained after i previous host attacks and X_i the random variable that results from an exponential distribution with hazard rate α_i. In the next steps, we will consider the series α_0, $\alpha_1,\ldots,\alpha_i$, … as the hazard rates obtained after 0, 1,…,i,… host attacks. Attacking hosts constitutes a Poisson process of rate λ (thus the attack times are exponentially distributed with hazard rate λ). For a mathematical tractability, this rate is supposed to be constant in time and independent of i and t (i.e., very large patches or no depletion). Let us denote $\{T_i\}$ the sequence of time lags between successive resource encounters. The T_i are therefore the intervals between two successive attack times.

We now compute the probability for a forager to be still on the patch at time t, whatever the number of resource items found. The fact that the forager is still on the patch at time t and knowing that it already attacked 0, 1, i, hosts, i varying from 0 to $+\infty$, is expressed in the following equation:

$$(X>t)=[(X_0>t)\cap(X_0<T_1)]\cup_{i=1}^{\infty}\Big\{(T_1+\cdots+T_i +X_i>t)\cap_{j=0}^{i-1}(X_j\geq T_{j+1})\cap(X_i<T_{i+1})\Big\} \tag{13}$$

where X denotes the random total time spent in the patch.

Hence, the probability of the forager to be still on the patch at time t is:

$$P(X>t)=P(X_0>t,X_0<T_1) +\sum_{i=1}^{\infty}P\Big\{(T_1+\cdots+T_i+X_i>t)\cap_{j=0}^{i-1}(X_j\geq T_{j+1})\cap(X_i<T_{i+1})\Big\} \tag{14}$$

where commas stand for the intersection (logical "and"). Evaluation of this expression leads to a repeated integral which is fully developed in Appendix B. The final result for the survival function is an infinite weighted sum of exponentials. This sum is the survivor function of the process and converges in i for any t:

$$P(X>t)=S(t)=\sum_{i=0}^{\infty}\sum_{j=0}^{i}a_i^j e^{-(\lambda+\alpha_j)t} \tag{15}$$

where the a_j^i are coefficients which can be estimated by recurrence as

$$a_i^j=\frac{(-1)^j}{\mu_i}\Pi^j{}_{\substack{k=1\\k\neq i}}\frac{1}{\mu_i-\mu_k} \tag{16}$$

with $\mu_\eta=\lambda+\alpha_\eta$, η standing for any index, i, k, etc. Appendix B gives the proofs of (15) and (16). Let us note that this survivor function is unconditional, providing that the series of α_i is known. It is the survivor function expected if only the patch leaving time is recorded (the times of successive encounters are not). The practical estimation of the α_i requires the recording of the rank i of each α_i and the times of attacks, as will be shown below.

3.2. Estimation

Data needed to estimate the model consists of a set of patch residence times associated with the record of the successive host attacks. Two approaches can be proposed to estimate the parameter of the stochastic model we are proposing, either a parametric one based on a likelihood function obtained from (15) and (16), or a semi-parametric one by fitting a classical Cox proportional hazards model. The first approach allows estimating directly the α_i but is based on the strong assumption that the hazard function remains constant (i.e., exponential distribution of patch residence times). The second one leads to estimating the α_is through the Cox regression coefficients β_i. Both results should be similar if the distribution of the patch residence time is exponential.

3.2.1. Parametric estimation

We need experimental data in which residence times as well as the successive times of encounters with hosts are recorded for a set of individuals. For the sake of simplicity, we shall not consider the case in which some total residence times are censored (see Bressers et al., 1991; Haccou and Meelis, 1992 for a discussion on censoring). For each individual, the patch is considered to be entered at time 0, then a first host is encountered at time t_1, a second at time t_2, and so on until time t_m when the animal encounters the last host before leaving the patch at time $T\geq t_m$. These events correspond to a series of renewal intervals. Each interval is a survival data beginning at t_i and censored by the next encounter event at t_{i+1}. Only the last interval $[t_m, T]$ is uncensored. At each renewal time, the survival probabilities between t_i and t_{i+1} are conditioned by the survival of the process at time t_i. Under the assumption that the ith interval is a survival process of hazard rate α_i the likelihood of a series of events is therefore:

$$V(t_1,\ldots,t_i,\ldots,t_m,\ldots,T|\alpha_0,\alpha_1,\ldots)=\alpha_{m+1}e^{-\alpha_{m+1}(T-t_m)}\prod_{j=0}^{m}e^{-\alpha_j\delta_j} \tag{17}$$

and the log-likelihood is thus:

$$\ln V=\ln\alpha_{m+1}-\alpha_{m+1}(T-t_m)-\sum_{j=0}^{m}\alpha_j\delta_j \tag{18}$$

where $\delta_j=t_j-t_{j-1}$

Then, for n individuals observed:

$$\ln V=\sum_{i=1}^{n}[\ln\alpha_{m_i+1}-\alpha_{m_i+1}(T_i-t_{m_i})]-\sum_{i=1}^{n}\sum_{j=0}^{m_i}\alpha_j\delta_{ij} \tag{19}$$

Expression (19) is easier to handle if the number of host encounters m is considered as being an index varying from 0 to M (maximum number of encounters observed), collecting the sum of individuals having experienced no encounter with hosts, those who encountered only one host, two hosts, etc. Expression (19) can then be changed by denoting by i ($i=1,\ldots,m_i$), the rank of the ith encounters in the sequence and by j ($j=1,\ldots,r_i$), the jth individual that met exactly m_i hosts. Doing this, the likelihood function becomes:

$$V(t_{1j},\ldots,t_{ij},\ldots,t_{mj},\ldots,T_j|\alpha_0,\alpha_1,\ldots)=\prod_{m=0}^{M}\prod_{j=1}^{r_m}\alpha_{m+1} e^{-\alpha_{m+1}(T_{mj}-t_{mj})}\prod_{i=1}^{m}e^{-\alpha_i\delta_{mij}} \tag{20}$$

The log-likelihood follows straightforwardly, and through derivation with respect to the coefficients α and equating to zero, the maximum likelihood estimators lead to:

$$\hat{\alpha}_i=\frac{r_i}{\sum_{j=1}^{r_i}(T_{ij}-t_{ij})+\sum_{m=i+1}^{M}\sum_{j=1}^{r_m}\delta_{mij}} \tag{21}$$

for any $i<M$ and

$$\hat{\alpha}_M=\frac{r_M}{\sum_{j=1}^{r_M}(T_{iMj}-t_{iMj})}=\frac{1}{\overline{\delta}_{iM}} \tag{22}$$

for the last term corresponding to exactly M encounters. Obviously, one recognizes the classical estimator of a constant hazard rate in the case of an exponential model while in (21) one recognizes the hazard rate between two successive events given in the parametric exponential model with time-dependent events (Collett, 1994; Kalbfleisch and Prentice, 2002).

An asymptotic estimation of the variance of these coefficients is also easily obtained by computing the inverse of the Hessian of the log-likelihood function (Fisher's information matrix) leading to:

$$Var(\hat{\alpha}_i) = \frac{\alpha_i^2}{r_i} \tag{23}$$

An *R* (R development core team, 2011) function was written to calculate the results and can be obtained from the authors.

3.2.2. Semi-parametric estimation

Alternatively, standard statistical packages fitting a Cox proportional hazards model can be used to compute a semi-parametric estimation on the same data. For this, the number of encounters observed for each individual is treated as a time-dependent covariate (see Collett, 1994; Therneau and Grambsch, 2000; Kalbfleisch and Prentice, 2002). In this case, the baseline hazard rate does not need to be modeled and, if the basic process is exponential, the coefficients β are linked to the coefficients α defined in (22) by the relation:

$$\exp(\beta_i) = \frac{\alpha_i}{\alpha_0} \Leftrightarrow \beta_i = \ln\alpha_i - \ln\alpha_0 \tag{24}$$

This relationship implies that the coefficients $\alpha_i s$ can be estimated directly from the estimations of the $\beta_i s$ of a Cox's model:

$$\alpha_i = \alpha_0 \exp \beta_i \tag{25}$$

Then, a separate estimation of α_0 is needed through a standard estimation of the baseline hazard function by fitting a Cox regression model to the data.

4. Examples of estimations of the stochastic model

The proposed stochastic model for patch residence time of a foraging animal was estimated on two different data sets. The first one consists of observations realized on the egg parasitoid *Trichogramma brassicae* (Hymenoptera; Trichogrammatidae) placed on artificial patches of nine host eggs (i.e., eggs of the factitious host *Ephestia kuehniella*, Lepidoptera, Pyralidae). The experimental observations are those of Wajnberg et al. (2000). The second was provided by J. van Baaren and M.-H. Guislain (unpublished data) and comes from experiments done on the aphid parasitoid *Aphidius picipes* exploiting patches of the aphid *Sitobion avenae* F. on wheat leaves.

In both cases, we first fitted an exponential distribution to the survivor functions on individuals that did not meet any host. According to the Waage (1979) model, all these individuals should leave the patch almost at the same time and their corresponding survivor function should vary suddenly from 1 to zero if the model incorporates no random variation (see Fig. 3c). If some slight variation exists, such a function should look like an inverse sigmoid, and the log-survivor function should tend to $-\infty$ (see Fig. 4b). However, as can been seen in Fig. 5a and b, in both cases the survivor function looks like an exponential distribution especially in *A. picipes* ($r^2=0.991$, $df=61$, Fig. 5b) leading to a better fit than in the case of *T. brassicae* ($r^2=0.797$, $df=64$, Fig. 5a). This supports the idea of a stochastic survival process with a constant hazard rate rather than a deterministic process with a fixed departure time.

Fig. 5c and d shows the parametric and semi-parametric estimations of the stochastic model presented above in the case of *T. brassicae* and *A. picipes*, respectively. In these graphs, the α_is reveal an incremental or a decremental effect when they are lower or greater than the previous one, respectively. In the case of *T. brassicae*, the α_is decrease strongly from the first host encountered (incremental effect of the first host encounter). Another, less important decrease is observed with the second host encounter and then the α_is tend to increase from the third to the 9th encounter, revealing a switch from an incremental to a decremental effect, as was observed by the authors (Wajnberg et al., 2000). Both the parametric and semi-parametric estimations look similar until the 5th host encounter, and then diverge progressively despite all estimates remaining within the confidence limits of the parametric estimates of the model presented here.

The same feature is obtained with the *A. picipes* data (Fig. 5c) where the pattern looks more complicated. A slightly incremental effect (i.e., decreasing $\alpha_i s$) is obtained for the first and the second host encounter, followed by a strong decremental effect for the third encounter, and a slightly decreasing mechanism thereafter until the 10th encounter. The agreement between the parametric and semi-parametric estimations of the model is even better than in the *T. brassicae* case, except after 14 encounters, but in this case this estimation relies on a very small number of individuals, those who were still in the patch after 14 encounters ($n=5$).

5. Conclusion

The present work can be viewed as a reappraisal of the Waage (1979) model since it incorporates a fundamental stochasticity in the patch-leaving decision process of foragers. We conserved what has proved to fit well to a large number of datasets found in literature, i.e., the hypothesis of incremental or decremental processes acting on a latent variable, the so-called motivation or tendency to stay in the patch. Contrasting with the original Waage (1979) model, no particular change of this tendency in time is assumed. This results in residence times being exponentially distributed. The two sets of experimental data presented here support this view since the survivor functions when no hosts are found fit well to exponential distributions and not to distributions characterized by a sudden peak of departures from the patch, as expected from a simple Waage (1979) process. The advantage of the stochastic model presented here is its coherence with the Cox's proportional hazards model commonly used for estimating incremental or decremental mechanisms in patch-leaving decision rules (Wajnberg, 2006).

However, our approach pays cost for its simplicity. The Waage (1979) model is easier to understand and to manage than its stochastic counterpart. Furthermore, it incorporates a feature commonly adopted by those working on animal behavior, i.e., a decline in motivation through habituation. Such a feature explicitly disappears in the stochastic version presented here. The motivation to forage is completely hidden, and only the tendency to leave the patch is estimable as a hazard rate. As a consequence, our model becomes fully relevant within the framework of survival analysis through the fit of a Cox regression model.

The mathematical analysis of the stochastic process presented in this paper leads to a quasi closed form in the case where the distribution of patch residence times is exponential. However, the same ideas could be applied with different survival processes (e.g., a Weibull distribution) but would probably become mathematically intractable, the hazard rates between two encounters with hosts being strongly time-dependent when any other distribution than the exponential is used. However, such models would remain fully accessible to the survival data analysis. In this case, it should be noted that the semi-parametric and parametric estimations will in general not coincide.

The main feature of our approach is that the set of parameters used reduces to successive hazard rates in a fully estimable way, leading to an accurate estimation of the effects every encounter with resource items might have on the patch-leaving decision of a forager. More work is now needed to find how such a stochastic, and thus imperfect decision process can lead animals to reach an optimum. The key of the answer is

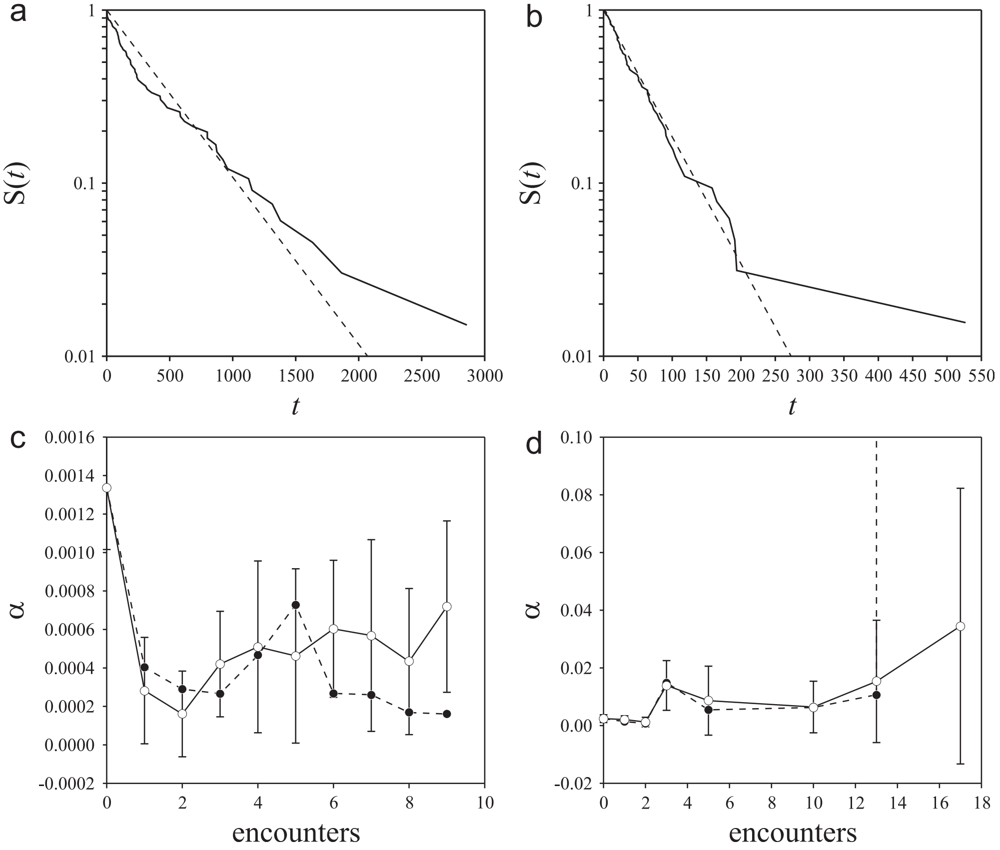

Fig. 5. Upper part: Observed (solid line) and fitted exponential distribution (dashed line) of the log-survivor functions for females of *Trichogramma brassicae* (a) and *Aphidius picipes* (b) that did not meet any host during the observation. Lower part: results of the stochastic model fitted on *T. brassicae* (c) and *A. picipes* (d) datasets compared to a Cox's regression fitting. Solid line + open circles: parametric estimation of the coefficients α_i (± confidence interval) (hazard rate after *i* encounters); dashed line + closed circles: semi-parametric estimations of the α from the β coefficients of the Cox's proportional hazards model. In the case of *A. picipes* some encounters were never observed (4, 6, 7, 8, 9 and 11) and therefore, their effect was not estimable.

probably the tuning of risk sensitivity in a partly unpredictable environment.

Acknowledgments

We thank Joan van Baaren and Marie-Hélène Ghislain for allowing us to use a part of their unpublished data. We also thank Odile Pons for her useful comments and corrections of the mathematics of a former version of this manuscript, and Terence Neil Ledger and Ann Cloarec for the English revision of the manuscript. Two anonymous referees are thanked for their comments on the original version of the manuscript. We thank also Christine Curty for her help in drawing the figures.

Appendix A. General relationship between the regression coefficient β of a Cox's proportional hazards model and the increments *I* of the Waage (1979) model

We consider that the assumption of proportional hazard rates holds. In the case of a Cox's regression analysis, we consider that each host encounter has the same effect on the hazard rate. Therefore, the effect of *n* host discoveries on the hazard rate function is:

$$h_n(t) = h_0(t)\exp(n\beta) \tag{A.1}$$

or, for the survivor function:

$$S_n(t) = [S_0(t)]^{\exp(n\beta)} \tag{A.2}$$

From this classical result (Collett, 1994; Kalbfleisch and Prentice, 2002) it follows that the probability density function of the patch residence times is:

$$f_n(t) = h_n(t)S_n(t) = h_0(t)\exp(n\beta)[S_0(t)]^{\exp(n\beta)} \tag{A.3}$$

Assuming now that the Waage (1979) process holds, at the price of adding some random noise to the effects. It is reasonable to assume that the expected time spent on the patch after *n* hosts are attacked is equal to the mean of the density function defined in (A.3). Therefore, when only one host is encountered:

$$E\{t_1\} = \int_0^\infty t f_1(t)dt \tag{A.4}$$

And, after *n* encounters:

$$E\{t_n\} = \int_0^\infty t f_n(t)dt \tag{A.5}$$

In the case of a single encounter with a host and taking the Waage (1979) result for the left side of this equation, replacing expression (A.3) in the right side leads to:

$$\frac{1}{b}(aP+I) = \exp(\beta)\int_0^\infty t h_0(t)[S_0(t)]^{\exp(\beta)}dt \tag{A.6}$$

or

$$I = b\,\exp(\beta)\int_0^{\infty} th_0(t)[S_0(t)]^{\exp(\beta)}dt - aP \tag{A.7}$$

as stated in Eq. (10) in the main text.

Appendix B. Derivation of the survivor function of the stochastic model

We searched the survivor function for the times passed in a patch, when resources were discovered according to a Poisson process of rate λ, and proved Eq. (15). Here and in what follows, lower case letters indicate possible values of random variables that are noted in upper case letters. The survivor function at time t is the infinite sum of the probabilities of being still in the patch at time t after having found i hosts, i varying from 0 to $+\infty$. To achieve this goal, let us set up the first terms of the series and try to find a recurrence equation giving the ith term.

Consider first the probability to remain on the patch at time t when no host is found:

$$P_0(t) = P(X_0 > t, X_0 < T_1) \tag{B.1}$$

and second the probability to remain in the patch at time t after having found exactly i hosts:

$$P_i(t) = P(T_1 + T_2 + \cdots + T_i + X_i > t, X_0 \geq T_1, \cdots, X_{i-1} \geq T_i, X_i < T_{i+1}) \quad for\ i \geq 1 \tag{B.2}$$

X_0 and T_1 are stochastically independent and their joint density is $\lambda\exp(-\lambda t_1)\alpha_0\exp(-\alpha_0 x_0)$. Let us define the new random variables $Y_1 = T_1 - X_0$ and $Y_2 = X_0$. Their joint density is $\lambda\alpha_0\exp(-\lambda y_1)\exp[-(\alpha_0+\lambda)y_2]$ and thus:

$$P_0 = \lambda\alpha_0\int_{y_1>0}\left[\int_{y_2>t}\exp(-\lambda y_1)\exp[-(\alpha_0+\lambda)y_2]dy_2\right]dy_1 \tag{B.3}$$

which solves into:

$$P_0(t) = \alpha_0\frac{\exp[-(\alpha_0+\lambda)t]}{\alpha_0+\lambda} \tag{B.4}$$

Let us proceed identically for $i \geq 1$. The random variables $X_0,\ldots,X_i$; $T_1,\ldots,T_{i+1}$ are independent and their joint density $\varphi(x_0,\ldots,x_i;\ t_1,\ldots,t_{i+1})$ is the product of their marginal densities:

$$\varphi(x_0,\ldots,x_i;t_1,\ldots,t_{i+1}) = \alpha_0\exp(-\alpha_0 x_0)\lambda^{i+1}\left(\prod_{j=1}^{i}\alpha_j\exp(-\alpha_j x_j)\exp(-\lambda t_j)\right)\exp(-\lambda t_{i+1}) \tag{B.5}$$

for $x_j \geq 0$, $j=0, \ldots, i$ and $t_k \geq 0$, $k=1,\ldots,i+1$, $\varphi(x_0,\ldots,x_i;\ t_1,\ldots,t_{i+1}) = 0$ otherwise.

Hence

$$P_i(t) = \int_{D_t^i}\varphi(x_0,\ldots,x_i;\ t_1,\ldots,t_{i+1})dx_0\cdots dx_i dt_1\cdots dt_{i+1} \tag{B.6}$$

where $\mathcal{D}_t^i$ is the domain defined as

$$\mathcal{D}_t^i = \{t_1+t_2+\cdots+t_i+x_i \geq t;\ x_0 \geq t_1;\cdots;x_{i-1} \geq t_i;\ x_i < t_{i+1}\} \tag{B.7}$$

To handle this integral we define, as previously, the new variables:

$$Y_1 = X_0 - T_1,\ldots,Y_i = X_{i-1} - T_i \tag{B.8}$$

Eq. (B.6) then becomes:

$$P_i(t) = \int_{D_t^i}\alpha_i\exp(-\alpha_i x_i)\lambda^{i+1}\prod_{j=1}^{i}\exp[-(\lambda+\alpha_j)t_j]\exp(-\lambda t_{j+1})dx_0\cdots dx_i dt_1\cdots dt_{i+1}. \tag{B.9}$$

As we integrate any x_i between 0 and $t-(t_1+\cdots+t_i)$, the evaluation of $P_i(t)$ reduces to:

$$P_i(t) = \lambda^i\alpha_i\int_{t_1+\cdots+t_i+x_i\geq t}\prod_{j=0}^{i-1}\exp(-\mu_j t_{j+1})\exp(-\mu_j x_i)dt_1\cdots dt_i dx_i \tag{B.10}$$

with $\mu_\eta = \lambda + \alpha_\eta$, η standing for i, j or any necessary index, or:

$$P_i(t) = P(A_i) - \lambda^i\alpha_i\int_{t_1+\cdots+t_i+x_i<t}\prod_{j=0}^{i-1}\exp(-\mu_j t_{j+1})\exp(-\mu_j x_i)dt_1\cdots dt_i dx_i \tag{B.11}$$

where $P(A_i)$ is the probability of the event “the animal leaves the patch after exactly encountering i resource items”. Such a probability is equal to:

$$P(A_i) = \lambda^i\alpha_i\int_0^{+\infty}\cdots\int_0^{+\infty}\prod_{j=0}^{i-1}\exp(-\mu_j t_{j+1})\exp(-\mu_j x_i)dt_1\cdots dt_i dx_i \tag{B.12}$$

which leads, by successive integration, to the simple expression:

$$P(A_i) = \frac{\lambda^i\alpha_i}{\prod_{j=0}^{i}\mu_j} \tag{B.13}$$

The repeated integral in (B.12) is easily evaluated recursively as suggested in Feller (1966). The result is an appropriate linear combination of $\exp(-\mu_j t)$, $(j=0,\ldots,i)$.whose coefficients must be determined. Let us note:

$$S_j(\mu_1,\cdots,\mu_j;x) = \int_{t_1+\cdots+t_j<=x}\prod_{i=1}^{j}\exp(-\mu_i t_i)dt_1\cdots dt_j \tag{B.14}$$

the integral to be evaluated. Finally, we find the recurrence equation:

$$S_j(\mu_1,\cdots,\mu_j;x) = \frac{1}{\mu_j}S_{j-1}(\mu_1,\cdots,\mu_{j-1};x) - \exp(-\mu_j x)S_{j-1}(\mu_1-\mu_j,\cdots,\mu_{j-1}-\mu_j;x) \tag{B.15}$$

The survivor function $P(X \geq t)$ is obtained by summing the $P_i(t)$: $P(X \geq t) = \Sigma_{i=0}^{+\infty}P_i(t)$, the appropriate infinite linear combination of $\exp(-\mu_j t)$, $(j=0,\ldots,+\infty)$.

All the terms in this series are positive (i.e., probabilities) and the entire series is bound by 1. We can thus obtain an approximation as good as needed of $P(X \geq t)$ by summing a finite number of the first terms of the series.

A simplification

Eqs. (B.13) and (B.15) provide a recursive method for computing the desired survivor function but something simpler and numerically safer can be achieved. Resuming from (B.15), let us note:

$$S_{j-1}^{*}(\mu_1,\mu_2,\ldots,\mu_{j-1},\mu_j;x) = S_{j-1}(\mu_1-\mu_j,\mu_2-\mu_j,\ldots,\mu_{j-1}-\mu_j;x) \tag{B.16}$$

Similarly, we will note a_i^{*j} the coefficients obtained by replacing any μ_η by $\mu_\eta - \mu_{j+1}$ in the corresponding a_i^j, η representing, as previously, any necessary index i or j.

From what precedes, $S_j(\mu_1,\ldots,\mu_j;x)$ has the form:

$$S_j = a_0^j + \sum_{i=1}^{j}a_i^j\exp(-\mu_i x). \tag{B.17}$$

It is quite straightforward that $a_0^0 = 1$ and $a_0^{*0} = 1$. Then,

$$\begin{cases} S_{j-1} = a_0^{j-1} + \sum_{i=1}^{j-1}a_i^{j-1}\exp(-\mu_i x) \\ S_{j-1}^{*} = a_0^{*j-1} + \sum_{i=1}^{j-1}a_i^{*j-1}\exp[-(\mu_i-\mu_j)x] \end{cases} \tag{B.18}$$

Hence, from (B.17):

$$S_j = \frac{1}{\mu_j}\left\{a_0^{j-1} + \left(\sum_{i=1}^{j-1} a_i^{j-1}\exp(-\mu_j x)\right)\right.$$
$$\left. -\exp(-\mu_j x)\left(a_0^{*j-1} + \sum_{i=1}^{j-1} a_i^{*j-1}\exp[-(\mu_i-\mu_j)x]\right)\right\} \tag{B.19}$$

$$S_j = \frac{1}{\mu_j}\left\{a_0^{j-1} + \sum_{i=1}^{j-1}(a_i^{j-1} - a_i^{*j-1})\exp(-\mu_i x) - a_0^{*j-1}\exp(-\mu_j x)\right\} \tag{B.20}$$

And by identification:

$$\begin{cases} a_0^j = \frac{1}{\mu_j}a_0^{j-1} \Rightarrow a_0^j = \Pi_{k=1}^j \frac{1}{\mu_k} \\ a_i^j = \frac{1}{\mu_j}(a_i^{j-1} - a_i^{*j-1}) \\ a_j^j = -\frac{1}{\mu_j}a_0^{*j-1} \end{cases} \tag{B.21}$$

Conjecture. the successive development of (B.21) on S_1, S_2, and S_3 suggests that the general term a_i^j of the coefficients, for $i \neq 0$ is given by:

$$a_i^j = \frac{(-1)^j}{\mu_i}\prod_{\substack{k=1\\k\neq i}}^{j}\frac{1}{\mu_i - \mu_k} \tag{B.22}$$

Proof. let us develop the second line of (B.21), replacing the coefficients by their expression given in (B.22). We obtain:

$$a_i^j = \frac{1}{\mu_j}\left(\frac{(-1)^{j-1}}{\mu_i}\prod_{\substack{k=1\\k\neq i}}^{j-1}\frac{1}{\mu_i-\mu_k} - \frac{(-1)^{j-1}}{\mu_i-\mu_j}\prod_{\substack{k=1\\k\neq i}}^{j-1}\frac{1}{(\mu_i-\mu_j)-(\mu_k-\mu_j)}\right) \tag{B.23}$$

an expression that simplifies in (B.22) which completes the proof. All coefficients are then known and easily explicitly calculable. The algorithm of evaluation of the integral is then straightforward: define a precision level ε, evaluate the successive terms $P_i(t)$ at time t, beginning by 0, and sum each new term until $P_i(t) \leq \varepsilon$. The algorithm was used successfully to obtain Fig. B.1 representing the survivor function with a decreasing (incremental model) or an increasing (decremental model) set of hazard rates α_i.

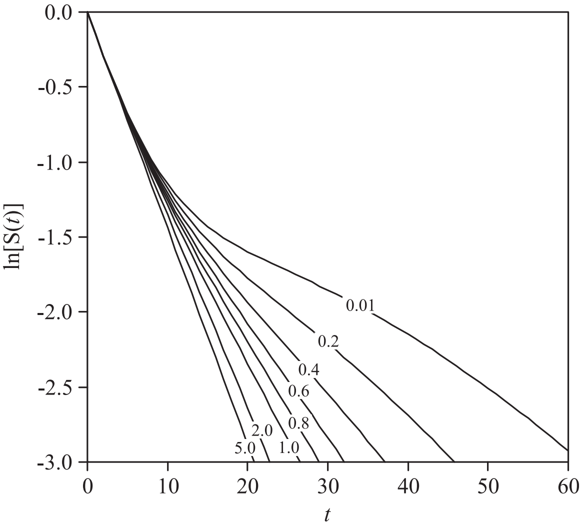

Fig. B.1. Log-survivor function of the stochastic process analogous to the Waage (1979) model for different values of a parameter a governing the modification of the hazard rate α with each host encountered. The baseline rate is α_0, and at the ith host encounter becomes $\alpha_0 a^i$. The values of a are indicated on the graph. Values of a lower than 1 correspond to the incremental model, values of a greater than 1 to the decremental model. Other parameters: λ=0.05, a_0=0.1.

Finally, the complete survivor function of Eq. (15) is

$$S(t) = P(X > t) = \sum_{i=0}^{\infty}\sum_{j=0}^{i}\frac{(-1)^j}{\mu_i}\prod_{\substack{k=1\\k\neq i}}^{j}\frac{\exp(-\mu_j t)}{\mu_i - \mu_k} \tag{B.24}$$

References

Bressers, M., Meelis, E., Haccou, P., Kruk, M., 1991. When did it really start or stop: the impact of censored observations on the analysis of duration. Behav. Processes 23, 1–20.

Charnov, E.L., 1976. Optimal foraging: the marginal value theorem. Theor. Popul. Biol. 9, 129–136.

Collett, D., 1994. Modelling Survival Data in Medical Research. Chapman & Hall.

Cox, D.R., 1972. Regression models and life tables. Biometrics 38, 67–77.

Driessen, G., Bernstein, C., 1999. Patch departure mechanisms and optimal host exploitation in an insect parasitoid. J. Anim. Ecol. 68, 445–459.

Driessen, G., Bernstein, C., van Alphen, J.J.M., Kacelnik, A., 1995. A count-down mechanism for host search in the parasitoid *Venturia canescens*. J. Anim. Ecol. 64, 117–125.

Driessen, G., Hemerik, L., 1992. The time and egg budget of *Leptopilina clavipes*, a parasitoid of larval *Drosophila*. Ecol. Entomol. 17, 17–27.

Feller, W., 1966. An Introduction to Probability Theory, 2. Wiley, New York.

Gibb, J.A., 1962. Tinbergen's hypothesis of the role of specific search images. Ibis 104, 106–111.

Godfray, H.C.J., 1994. Parasitoids. Behavioral and Evolutionary Ecology. Princeton University Press.

Haccou, P., Meelis, E., 1992. Statistical Analysis of Behavioural Data. Oxford University Press.

Haccou, P., de Vlas, S.J., van Alphen, J.J.M., Visser, M.E., 1991. Information processing by foragers: effects on intra-patch experience on the leaving tendency of *Leptopilina heterotoma*. J. Anim. Ecol. 60, 93–106.

Hassell, M.P., 1978. The Dynamics of Arthropod Predator–Prey Systems. Princeton University Press, Princeton.

Hassell, M.P., May, R.M., 1974. Aggregation in predators and insect parasites and its effect on stability. J. Anim. Ecol. 43, 567–594.

Hemerik, L., Driessen, G., Haccou, P., 1993. Effects of intra-patch experiences on patch time, search time and searching efficiency of the parasitoid *Leptopilina clavipes*. J. Anim. Ecol. 62, 33–44.

Hubbard, S.F., Cook, R.M., 1978. Optimal foraging by parasitoid wasps. J. Anim. Ecol. 47, 593–604.

Iwasa, Y., Higashi, M., Yamamura, N., 1981. Prey distribution as a factor determining the choice of optimal foraging strategy. Am. Nat. 117, 710–723.

Kalbfleisch, J.D., Prentice, R.L., 2002. The Statistical Analysis of Failure Time Data, second ed. Wiley, New York.

Krebs, J.R., 1973. Behavioral aspects of predation. In: Bateson, P.P.G., Klopfer, P.H.G. (Eds.), Perspectives in Ethology. Plenum, pp. 73–111.

McNair, J.M., 1982. Optimal giving-up time and the marginal value theorem. Am. Nat. 119, 511–529.

Murdoch, W.W., Oaten, A., 1975. Predation and population stability. Adv. Ecol. Res. 9, 2–132.

Pierre, J.S., van Baaren, J., Boivin, G., 2003. Departure rules from the patch in parasitoids: do they achieve a sequential decisional sampling? Behav. Ecol. Sociobiol. 54, 147–155.

R Development Core Team, 2011. R: A language and environment for statistical computing. 〈http://www.R-project.org〉, R Foundation for Statistical Computing, Vienna, Austria.

Rosenheim, J.A., 1999. The relative contributions of time and eggs to the cost of reproduction. Evolution 53, 376–385.

Sevenster, J.G., Ellers, J., Driessen, G., 1998. An evolutionary argument for time limitation. Evolution 52, 1241–1244.

Stephens, D.W., Krebs, J.R., 1986. Foraging Theory. Princeton University Press.

Tenhumberg, B., Keller, M.A., Possingham, H.P., Tyre, A.J., 2001a. Optimal patch-leaving behaviour: a case study using the parasitoid *Cotesia rubecula*. J. Anim. Ecol. 70, 683–691.

Tenhumberg, B., Keller, M.A., Possingham, H.P., 2001b. Using Cox's proportional hazards model to implement optimal strategies: an example from behavioural ecology. Math. Comput. Model. 33, 597–607.

Therneau, T.M., Grambsch, P.M., 2000. Modeling Survival Data, Extending the Cox Model. Springer.

van Alphen, J.J.M., 1993. Patch residence time and encounters with parasitised hosts: a reaction. Neth. J. Zool. 43, 340–349.

van Alphen, J.J.M., Bernstein, C., Driessen, G., 2003. Information acquisition and time allocation in insect parasitoids. Trends Ecol. Evol. 18, 81–87.

Vos, M., Hemerik, L., Vet, L.E.M., 1998. Patch exploitation by the parasitoids *Cotesia rubecula* and *Cotesia glomerata* in multi-patch environments with different host distributions. J. Anim. Ecol. 67, 774–783.

Waage, J.K., 1979. Foraging for patchily distributed hosts by the parasitoid *Nemeritis canescens*. J. Anim. Ecol. 48, 353–371.

Wajnberg, E., 2006. Time-allocation strategies in insect parasitoids: from ultimate predictions to proximate behavioural mechanisms. Behav. Ecol. Sociobiol. 60, 589–611.

Wajnberg, E., 2012. Multi-objective behavioural mechanisms are adopted by foraging animals to achieve several optimality goals simultaneously. J. Anim. Ecol. 81, 503–511.

Wajnberg, E., Curty, C., Colazza, S., 2004. Genetic variation in the mechanisms of direct mutual interference in a parasitic wasp: consequences in terms of patch-time allocation. J. Anim. Ecol. 73, 1179–1189.

Wajnberg, E., Fauvergue, X., Pons, O., 2000. Patch leaving decision rules and the Marginal Value Theorem: an experimental analysis and a simulation model. Behav. Ecol. 11, 577–586.

Wajnberg, E., Gonsard, P.A., Tabone, E., Curty, C., Lezcano, N., Colazza, S., 2003. A comparative analysis of patch-leaving decision rules in a parasitoid family. J. Anim. Ecol. 72, 618–626.

Wajnberg, E., Rosi, M.C., Colazza, S., 1999. Genetic variation in patch-time allocation in a parasitic wasp. J. Anim. Ecol. 68, 121–133.

Zens, M.S., Peart, D.R., 2003. Dealing with death data: individual hazards, mortality and bias. Trends Ecol. Evol. 18, 366–373.