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Using Cox's Proportional Hazard Models to Implement Optimal Strategies: An Example from Behavioural Ecology

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Abstract—Simple behavioural rules, or "rules of thumb", which lead to behaviour that closely approximates an optimal strategy, have generated a lot of recent interest in the field of foraging behaviour. In this paper, we derive rules of thumb from a stochastic simulation model in which the foragers behave optimally. We use a particular biological system: the patch leaving behaviour of a parasitoid. We simulate parasitoids whose patch leaving behaviour is determined by a stochastic dynamic programming (SDP) model, while allowing parasitoids to make mistakes in their estimation of host density when arriving in a patch. We use Cox's proportional hazards models to obtain statistical rules of thumb from the simulated behaviour. This represents the first use of a proportional hazard approximation to generate rules of thumb from a complex optimal strategy. © 2001 Elsevier Science Ltd. All rights reserved.

Keywords—Rules of thumb, SDP model, Cox's proportional hazards model, Optimal strategies.

1. INTRODUCTION

Stochastic dynamic programming (SDP) models are widely used to find state-dependent optimal solutions in biology [1], especially in the study of foraging behaviour (optimal foraging theory or OFT). The SDP approach is a very efficient way to find state-dependent optimal strategies in a stochastic system. However, such strategies are often very complex, especially when the state space is large, and it is very unlikely that a simple organism could implement such complex behaviour. Animals can potentially perform close to the optimum by using "rules of thumb" [2]. However, the connection between such rules and optimal solutions is vague. In this paper, we suggest that Cox's proportional hazards model [3,4] can condense the results of an SDP model into

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rules that could be easily implemented by an animal. A reliable method to translate complex optimal strategies from an optimization procedure into simple rules has wide application. In fields outside foraging behaviour, rules of thumb are used in conservation, e.g., management of plant populations [5], reserve design [6], integrated range resources management [7], and fisheries management [8].

For the remainder of this paper, we use a specific ecological example from foraging theory to demonstrate the suggested method of translating optimal strategies into rules of thumb. The optimal length of time a consumer should exploit a patch of depleting resources has been widely studied both theoretically and empirically. Furthermore, the answer to this question has applications in biocontrol [9], wildlife management [10], and fisheries [11]. Attempts to understand the factors influencing the optimal patch exploitation time have fallen into three main categories: theoretical optimization models, simple rules of thumb, and statistical models of the leaving tendency.

The best known theoretical model of optimal patch residence times is Charnov's marginal value theorem [12]. In this model, a forager leaves a patch when the net rate of energy gain drops below the environmental average. This model assumes that patch leaving behaviour is independent of internal states of the forager. This rate-maximization approach, in general, has difficulty in coping with dynamic states. Stochastic dynamic programming (SDP) models find optimal solutions that can take dynamic states of the forager into account [13], but as already discussed, the optimal strategies from these models are often very complex.

An alternative to predicting an optimal strategy with a mathematical model is to summarize what is known about the system in a "rule of thumb". For the patch departure problem, the best known rules of thumb are to remain until a fixed number of prey has been consumed [14,15], remain for a fixed time period [4], or remain until the time between encounters with individual prey exceeds a fixed value [16,17]. However, empirical work suggests that these simple rules do not describe patch leaving behaviour adequately [13].

The final possibility is to estimate a statistical model directly from observations of behaviour. Survival analysis such as Cox's proportional hazards model is widely used to study the relationship between the latency of the occurrence of an event (survival times) and explanatory variables. The method finds important applications in product life testing and a range of disciplines from physics to econometrics [4]. Starting with the pioneering work of [18], Cox's proportional hazards models have been used to analyze the behaviour of insects, in particular parasitoids [13]. The result is a statistical model of the probability of leaving a patch at any given point in time (leaving tendency) as a function of covariates such as the density of resources within the patch. In contrast to simple rules of thumb, this model is more sophisticated because it incorporates the influence of particular states, i.e., covariates. Hence, this statistical model of leaving behaviour can be interpreted as a state-dependent rule of thumb.

The particular consumer in our example is a solitary parasitoid wasp. Empirical results in the literature suggest that the patch residence time of parasitoids is influenced by both the host density and the number of ovipositions in a patch (see [13] for an overview). Generally, the probability of leaving a patch (leaving tendency) is lower the higher the number of hosts in that patch. The effect of oviposition depends on the fitness consequences of laying more than one egg in a host, or superparasitism.

Only one larva ever emerges from a single host in a solitary parasitoid. Even so, superparasitism can increase fitness under very specific circumstances in solitary parasitoids [19,20]. Generally, a wasp would be better off only laying eggs in unparasitised hosts. This is particularly true if the parasitoid cannot discriminate parasitised from unparasitised hosts. In this case, the wasp must estimate the risk of wasting an egg in superparasitism, and this risk increases with each oviposition. Therefore, we expect each oviposition to increase the tendency of such parasitoids to leave the patch. This effect has been shown to occur for other solitary parasitoids, even when error rates in host discrimination are quite low [21].

In this paper, we combine statistical modelling of survival processes with optimization modelling to simplify an optimal patch leaving strategy for a parasitoid wasp into a rule of thumb. First, we construct an SDP model that describes the optimal patch leaving behaviour of the parasitoid wasp *Cotesia rubecula* exploiting patches containing its host, the butterfly *Pieris rapae*. Second, we use a Monte Carlo simulation to generate sequences of behavioural decisions by simulated wasps determined by the optimal strategy from the SDP. Third, we analyze the simulated decision sequences with a proportional hazards model to generate statistically estimated, state-dependent rules of thumb. The end result is a state-dependent rule of thumb that is explicitly connected to an optimal foraging model. This approach is applicable to areas other than animal behaviour, such as economics and industry where rules of thumb are often needed to manage complex state-dependent problems.

2. WASP BEHAVIOUR MODEL

We briefly describe the biological scenario before outlining the structure of the model. An adult female wasp oviposits a single egg in its host. After hatching, a wasp larva feeds internally on the host's tissue and kills the host at the end of larval development. The host larvae live and feed on cabbage plants, and we define a cabbage plant as a patch. During her life, a wasp flies from patch to patch foraging for hosts. Plants change the amount and composition of odour constituents in response to herbivore damage. These infochemicals are attractive to the wasps. It has been demonstrated for some parasitoid species that they can distinguish patches with different host densities based on the concentration of infochemicals [22]. When a wasp arrives in a patch, she starts searching for hosts. She attacks every host she encounters (M. Keller, personal observation), even if the host is already parasitised (superparasitism). *C. rubecula* is a solitary parasitoid, and only one egg can develop within a single host [23]. Therefore, the profitability of a plant decreases with time, because the risk of encountering a previously parasitised host increases with each oviposition, as described in the introduction. Eventually, the wasp leaves the patch to search for hosts elsewhere. The optimal time for her to leave depends on the local host density, how many eggs she has laid in the current patch, and the distribution of hosts among and between patches in the habitat at large (Tenhumberg *et al.* unpublished manuscript).

In the following, the biological details included in the model and the model structure are described. This model has been described in more detail elsewhere (Tenhumberg *et al.*, unpublished manuscript), and a complete sensitivity analysis and description is beyond the scope of this paper. We assume that parasitoid females adjust their behaviour to maximize their expected lifetime reproduction. This is not necessarily the same as rate maximization, which is an instantaneous optimization criterion, rather than a lifetime criterion. We use SDP to calculate the optimal behaviours [1]. In the framework of behavioural ecology, SDP finds the solution that maximizes some fitness currency. This modelling technique takes stochastic events into account and allows the optimal behaviour to vary as a function of different states, such as number of ovipositions or host density in a patch. SDP models start at the end of an individual's life (the time horizon, T), then work backwards in time to calculate for each combination of states the behaviour that results in the highest lifetime reproduction.

The time horizon (T) is determined by the maximum lifespan of forty days [24]. Assuming a wasp forages for twelve hours per day and one time step is 2.5 minutes, then the maximum foraging time T is 11520 time steps. The state space of the wasp behaviour model includes time t ($t = 1, 2, 3, \dots, 11520$), host density d ($d = 0, 1, 2, \dots, 10$), number of ovipositions e ($e = 0, 1, 2, \dots, 17$), and time spent in the current patch t_p ($t_p = 1, 2, \dots, 17$). Therefore, the lifetime fitness function is defined as $F(t, d, t_p, e)$. Here, we provide a brief description of the most important parts of the model.

We assume that wasps have perfect knowledge about the average density and distribution of hosts in the environment. While in a patch, wasps search for hosts. At a given host density, the probability of encountering a host p in each time step is drawn from a Poisson distribution. She successfully oviposits an egg with the probability s. As wasps cannot distinguish parasitised from unparasitised hosts, we also compute the probability that an encountered host has already been parasitised during the current visit (Appendix A). Parasitoids receive the fitness payoff α if they oviposit in an unparasitised host; they receive zero fitness payoff for ovipositing in already parasitised hosts. Parasitoids spend h time steps handling the host. We ignore the possibility that other wasps could have visited the patch previously. Wasps remember the time since arrival and the number of ovipositions in that patch.

When the optimal patch residence time is reached, the wasps leave the patch. Wasps encounter a new patch every time step during flight. In order to keep the state space manageable, we allow wasps to fly for a maximum of ten time steps, corresponding to 25 minutes. Field observations indicate that most between plant flights last less than 25 minutes (Keller, unpublished data). The probability that a patch contains d hosts after flying r time steps (λ_{dr}; see Tenhumberg *et al.*, unpublished manuscript, for the derivation) depends on the distribution of hosts between and among patches. When a wasp encounters a patch, she assesses its host density from the infochemical concentration. The probability of landing (φ_d) is an increasing function of the host density in that particular patch (Keller, unpublished data), and is independent of flight time.

This scenario is described in the following dynamic programming equation:

$$F(t,d,t_p,e) = \max\left(\text{payoff}_{\text{leave}}, \text{payoff}_{\text{stay}}\right), \tag{1}$$

$$\text{payoff}_{\text{leave}} = \sum_{r=1}^{10}\left(\left(1-m_2^r\right)\prod_{i=1}^{r-1}\left(\sum_{d=0}^{10}\lambda_{dr}\left(1-\varphi_d\right)\right)\sum_{d=0}^{10}\left(F(t+r,d,1,0)\lambda_{dr}\varphi_d\right)\right), \tag{2}$$

$$\text{payoff}_{\text{stay}} = \left(1-m_1\right)\left(\text{host}_{\text{good}}\,p_{\text{good}} + \text{host}_{\text{bad}}\,p_{\text{bad}} + \text{host}_0\,p_0\right), \tag{3}$$

where m_1 and m_2 are the mortality rates in the patch and while flying between patches, respectively, with $m_1 < m_2$. The payoff for leaving a plant is summed over all possible encounters with plants up to the maximum flight time of ten steps, conditional on not landing in any previous time step. p_{good}, p_{bad}, or p_0 are the probabilities of encountering an unparasitised, parasitised, or no host; $\text{host}_{\text{good}}$, host_{bad}, or host_0 are the corresponding payoffs, defined as follows:

$$\text{host}_{\text{good}} = p\left(\left(F\left(t+h,d,t_p+h,e+1\right)+\alpha\right)s + F\left(t+1,d,t_p+1,e\right)(1-s)\right), \tag{4}$$

$$\text{host}_{\text{bad}} = p\left(F\left(t+h,d,t_p+h,e+1\right)s + F\left(t+1,d,t_p+1,e\right)(1-s)\right), \tag{5}$$

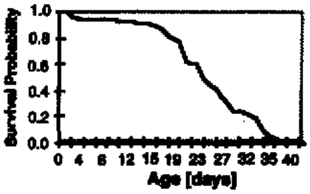
$$\text{host}_0 = F\left(t+1,d,t_p+1,e\right). \tag{6}$$

Numerical values for the parameters used in the example are given in Table 1.

3. SIMULATION EXPERIMENT

We used Monte Carlo simulations to examine how host density and number of ovipositions influence the behaviour of wasps that use the optimal strategy determined by the SDP (see Section 2) and analyze the simulation results with Cox's proportional hazards analysis. We choose to use these state variables based on our expectation that they are the primary determinants of patch leaving behaviour in *C. rubecula*. For the statistical analysis not to degenerate, we need variability in the behaviour of wasps, but all wasps from the SDP model behave in the same way given the same host density and number of ovipositions. In order to add variability, we allowed the wasps in the simulations to make mistakes in estimating the host density of patches. Note, in the SDP model, wasps never make mistakes. The estimate of wasps arriving in a patch is drawn from a normal distribution with mean d (i.e., the actual number of hosts present) and a standard deviation of two. These errors will influence the landing probability of wasps (φ_d) which is dependent on host density. We recorded the "giving up time" (GUT), which is the period of time from the last oviposition until the wasp leaves. If there is no oviposition, the GUT

Table 1. Parameter values and functions included in the SDP model. (d = host density in patch.)

Parameter		Value or Formula
φ_d	prob{landing | d}	$\frac{e^{-1.0613+0.1125d}}{(1+e^{-1.0613+0.1125d})}$
m_1	mortality rate in patch	1 − survival probability 
m_2	mortality rate while flying	1 − (survival probability $*$ 0.99)
p_{good}	prob{encounter an unparasitised host | d}	f (no. ovipositions, d), Table A1
p_{bad}	prob{encounter a parasitised host | d}	$1 - e^{-d/7} - p_{\text{good}}$
p_0	prob{encounter no host | d}	$e^{-d/7}$
s	prob{successful oviposition}	0.84
h	handling time	1
α	relative fitness reward	0.956

is simply the total time spent in the patch. To study the effect of host density d, we released simulated wasps on patches of 0, 2, 4, 6, 8, and 10 hosts, respectively. To examine the effect of previous ovipositions e, we allowed the wasps to oviposit $n = 0, 1, \ldots, 5$ times, and then we set the probability to find another host equal to zero. This way we obtained GUT for each density and after 0–5 ovipositions. This simulation experiment generates results with a similar structure to other empirical work on parasitoid leaving tendency [25].

4. PROPORTIONAL HAZARDS ANALYSIS

We analyzed the distribution of GUT of simulated wasps using the optimal strategy provided by the SDP with Cox's proportional hazards model. The result is a statistical rule of thumb of the optimal strategy. We assume that parasitoids have a basic tendency to perform a certain behaviour (baseline hazard), which is reset after certain renewal points. The observed hazard rate is assumed to be the product of the baseline hazard and a factor that gives the joint effect of a set of covariates $z_1, \ldots, z_p$. The general form of the model is

$$\lambda(t, z) = \lambda_0(t) \exp\left(\sum_{i=1}^{p} \beta_i z_i(t)\right), \tag{7}$$

where $\lambda(t; z)$ denotes the observed hazard rate, $\lambda_0(t)$ the baseline hazard, t is the time since the last renewal point, and $\beta_1, \ldots, \beta_p$ are the relative contributions of the covariates. The form of $\lambda_0(t)$ is left unspecified. The baseline hazard $\lambda_0(t)$ and $\beta_1, \ldots, \beta_p$ are estimated by means of likelihood maximization (see [3,18] for further details).

We formulated the model in terms of the leaving tendency. This is the chance per time unit that a wasp leaves a patch, given that she is currently in a patch. Note, a leaving tendency is different from a GUT; the GUTs are the data used to calculate the leaving tendency. We assume that λ_0 is reset after each oviposition and after each time the patch has been left and re-entered. In the model, we include the covariates host density d and number of ovipositions e in the current patch. To examine whether the effect of oviposition depends on the oviposition number, we included for each oviposition a separate covariate. Therefore, the leaving tendency is

$$\lambda(t;z) = \lambda_0(t)\exp\left(\beta_0 d + \sum_{i=1}^{5}\beta_i e_i\right), \tag{8}$$

where t is the time since the last renewal point, e_i refers to 1–5 ovipositions, d represents the host density in a given patch, and $\beta_{0,\dots,5}$ are the corresponding covariates. Note, when i ovipositions have occured, $\beta_1,\dots,\beta_i$ are all 1. For example, when a wasp arrives in a patch with two hosts, then $e_1,\dots,e_5 = 0$ and $d = 2$; after her first oviposition, e_1 changes to 1, while all other covariates remain the same.

We tested the fit of the model using Martingale residuals [26]. The proportionality assumption was tested via stratification, which is dividing the original sample into subgroups (= strata) according to the value of the variable d, respectively. The stratification results and the Martingale residuals are illustrated in Appendix B.

5. RESULTS

The average GUT for simulated *C. rubecula* increases with host density and decreases with the number of ovipositions in the current patch (Figure 1). The curves representing the increase in GUT with host density for 0–1 ovipositions are virtually parallel. As the number of ovipositions increases, the slope decreases, indicating a decreasing effect of host density on the patch leaving behaviour of the wasps. After five ovipositions, there is no effect of host density (horizontal curve). Wasps may lay an egg in an already parasitised host (superparasitism), which may result in more ovipositions than there are hosts present, e.g., three ovipositions at a host density of two. The risk of superparasitism decreases with host density. Five ovipositions occurred only at host densities of six or more, suggesting that most ovipositions were in unparasitised hosts.

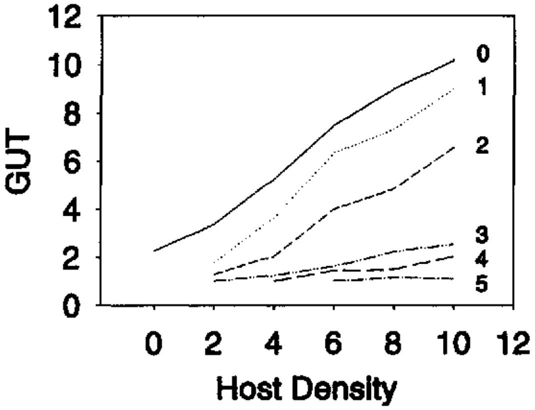


Figure 1. Average GUT as a function of host density. The numbers on the right-hand side of the curves indicate the number of ovipositions before leaving the patch.

We quantified the influence of host density and number of ovipositions of simulated wasps using Cox's proportional hazards model. The baseline leaving tendency $\lambda_0(t)$ is illustrated in Figure 2, and the estimates of the coefficients if the covariates (β_i) are given in Table 2. Now, we use these results to replace the parameters of equation (8) and obtain the rule of thumb. The β-values indicate how the baseline leaving tendency changes with host density and number of ovipositions. A negative value of β_i indicates a reduced leaving tendency or increased GUT. The higher the host density, the lower the probability that a wasp leaves a patch. Here, the β-value refers to the change in the different density classes of the simulation experiment ($d = 0, 2, 4, 6, 8, 10$). For

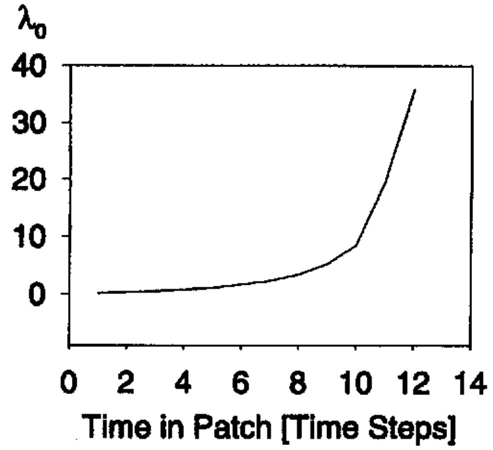


Figure 2. Cumulative baseline leaving tendency λ_0 (see equation (8)).

Table 2. Estimates of the coefficients of the covariates (see text for details).

	β	se(β)	z^*	p
Host Density	−0.324	0.0147	−22.01	< 0.0001
1st Egg	0.258	0.0945	2.73	0.0064
2nd Egg	1.025	0.107	9.58	< 0.0001
3rd Egg	1.513	0.122	12.4	< 0.0001
4th Egg	0.455	0.1473	3.09	0.002
5th Egg	0.943	0.2075	4.55	< 0.0001

The overall fit of the model is significant (likelihood ratio test = 887 on 6 df, $p < 0.0001$, $r^2 = 0.611$, $n = 939$).

example, when the host density was two, the leaving tendency was 72% (i.e., exp[−0.324]) of the baseline leaving tendency when there were no hosts on the plant.

Each subsequent oviposition increases the leaving tendency (positive β-values). However, their influence depends on the total number of ovipositions. The first three ovipositions have progressively greater influence on the leaving tendency. The leaving tendency of a female wasp increases by 30% (exp[0.258]) after she lays her first egg, and 4.5 times (exp[1.513]) higher after she lays her third egg. The influence of subsequent ovipositions is intermediate in strength to that of the first and second ovipositions.

The quality of the statistical rule is indicated overall by the r^2 value for the entire model of 0.61 (Table 2). This seems reasonable given that half of the state variables included in the SDP were not included in the proportional hazard fit. None of the other rules of thumb suggested in the introduction can produce the kinds of patterns observed, because they predict fixed, state-independent outcomes. A direct comparison is not warranted.

6. CONCLUSIONS

This paper has explored a novel method of deriving rules of thumb from optimal state-dependent behaviour. We developed an SDP model of the patch leaving behaviour of a parasitoid wasp. The SDP model provides an optimal strategy for each combination of time, number of ovipositions, and host density in a patch (see state space given in Section 2); consequently, the optimal strategy provides for 2,280,960 different situations a unique optimal patch residence time.

Then, we condensed the complex results of the SDP into rules of thumb by analysing the behaviour of simulated wasps, whose behaviour is determined by the SDP, with Cox's proportional hazards model. The general approach will be useful where optimal decisions are state dependent, and can be expressed as the probability of taking an action at some specified point in time.

Our example biological optimization problem is the optimal time for a parasitoid to leave a patch. The solution depends on the trade-off between the costs and benefits of staying in a particular patch. These trade-offs are quite different for predators. Predators deplete a patch by consuming prey, reducing prey density over time. Decreasing prey density increases search costs and decreases encounter rates, and eventually it is advantageous for the predators to leave the patch and hunt elsewhere [27]. In parasitoids, patch exploitation results in a reduction of host qualities. Parasitised hosts are of low quality, especially for solitary parasitoids, such as *C. rubecula*, where only one larva can develop in a single host [23]. The source of costs for a parasitoid to remain in a patch depends on her ability to recognize parasitised hosts. For parasitoid species that can recognize parasitised hosts, patches become less valuable as more time is spent assessing already parasitised hosts. For parasitoid species that lack the ability to recognize parasitised hosts, wasps are more likely to lay an egg in an already parasitised host (superparasitism). Hence, wasps waste more and more eggs in superparasitism. How costly this egg wastage is depends on how egg limited the species is.

We studied the effect of host density and oviposition on patch leaving behaviour. However, we could easily have included other factors in the foraging environment, such as the distribution of resources within and between patches and travel times between patches, by extending the vector of the covariates ($\beta_i z_i$, see equation (7)) of the Cox's proportional hazards model.

Our derived rule of thumb is admittedly only an approximation of the optimal strategy. Given the underlying noise in behavioural records of real animals, this approach probably describes their behaviour adequately. In fields outside of behaviour, such as decision theory, it might be advantageous to implement the optimal strategy, even if the optimal strategy is very complex. If the decision being approximated carried a high penalty for poor decisions, e.g., burning patches of scrub containing endangered species [28], a thorough analysis of the derived rule would include an estimate of how costly its use is relative to the optimal decision. In such an analysis, the cost of obtaining sufficient accurate information to implement the optimal strategy would also have to be included.

There are several advantages to simplifying complex optimal strategies using our method. First, the interpretation of the covariates is straightforward. Consequently, our derived rules of thumb provide more easily interpreted insights than SDP results, especially if the state space is large. Second, the validity of rules of thumb can easily be tested empirically simply by comparing the β-values against empirical data. Third, the possibility of condensing the results of SDP models makes it feasible to incorporate optimal behaviour of individuals into population models. This increases the chances that the model will tell us something relevant about particular systems. For example, the patch leaving behaviour of animals could be directly implemented in an individual-based population model by using equation (8). Alternatively, rules of thumb could be used to estimate species specific attack rates of parasitoids in patches with different host densities, or the aggregation of parasitoids in patches with higher host densities. Both are common elements of population models. This will close the gap between optimality models of individual behaviour and population models. Even simple representations of optimal behaviour can have profound effects on population dynamics [29]. Including optimal behaviour invites realistic population models tailored to specific systems. Specific and realistic models will also be useful as tools for addressing applied questions, such as the relative performance of predators in biological control [30].

This paper represents the first use of a proportional hazards approximation to generate rules of thumb from a complex optimal strategy. This approach is applicable to areas other than animal behaviour such as economics, industry, and natural resource management, where rules of thumb are often needed to manage complex state-dependent problems.

APPENDIX A

SDP MODEL

The probability of encountering an unparasitised host depends on the number of eggs that have already been laid, and the number of hosts into which they have been laid (Table A1). The key is the probability distribution of the number of parasitised hosts on the plant, A. This can be calculated iteratively for each host density using the observation that a particular number of parasitised hosts can only arise in two ways, if hosts are parasitised one at a time. First, if the encountered host is unparasitised, there will be one more parasitised host. Second, if the encountered host is parasitised, then the number of parasitised hosts will not change. The probability of i parasitised hosts after e eggs have been laid is

$$A_i' = A_i \frac{i}{d} + A_{i-1} \frac{d-i+1}{d}, \tag{A1}$$

where A_i is the probability that there are i parasitised hosts after laying $e-1$ eggs, and d is the number of hosts in the patch. The initial distribution for $e = 0$ is

$$A_i = \begin{cases} 1, & \text{if } i = 0, \\ 0, & \text{if } i \geq 1. \end{cases} \tag{A2}$$

We use this to calculate p_{good} for a patch with d hosts and e eggs already laid as the sum of the probability of encountering an unparasitised host when i hosts have been parasitised times the probability that i hosts have been parasitised,

$$p_{\text{good},d,e} = \sum_{i=1}^{d} \frac{d-i}{d} A_i', \tag{A3}$$

$$p_{\text{good},d,0} = 1, \qquad \forall d \geq 1. \tag{A4}$$

By applying (A1) and (A3) iteratively from $e = 1$ up to the maximum number of eggs laid in a patch, we get all the probabilities required.

Table A1. Probability of encountering an unparasitised host as a function of host density in the patch (# hosts) and the number of eggs already laid.

	# Eggs Laid			
# Hosts	0	1	2	$\cdots$
0	0	0	0	$\cdots$
1	1	0	0	$\cdots$
2	1	0.5	0.25	$\cdots$
$\vdots$	$\vdots$	$\vdots$	$\vdots$	
d	1	$\frac{d-1}{d}$	$\sum_{i=1}^{d} \frac{d-i}{d} A_i'$	$\cdots$

APPENDIX B

COX'S PROPORTIONAL HAZARDS MODEL

The validity of proportionality assumption for our model is demonstrated in Figure A1. The baseline hazards stratified for host density are parallel; i.e., the lines do not cross each other. The functional form of proportional hazard models can be checked with the Martingale residuals. Martingale residuals are different from standard residuals; the largest possible value is one, and

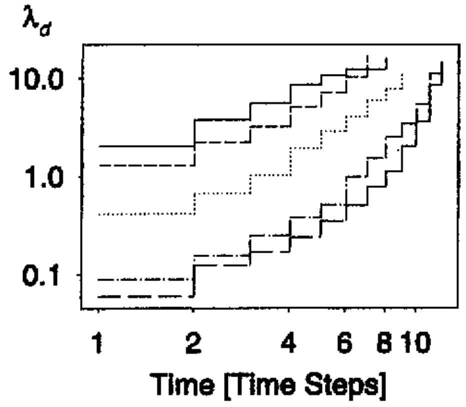


Figure A1. Cumulative leaving tendencies stratified for host densities (λ_d). (From top down: 0, 2, 4, 8, 10 hosts per plant.)

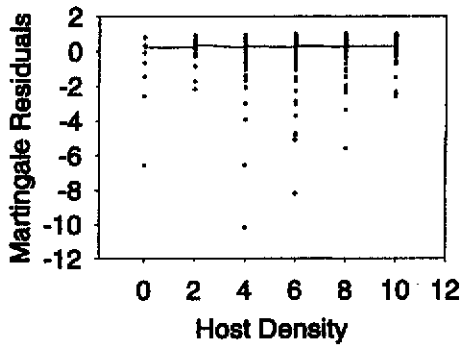


Figure A2. Martingale residuals versus host density for Cox's proportional hazards model.

outliers are represented by large negative values. A smooth fit to the Martingale residuals should be horizontal, as shown in Figure A2.

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