An application of SDP to generate simple behavioural rules: are parasitoids all thumbs?

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Abstract In all areas of applied optimisation the question of how to implement optimal strategies arises. This is particularly true for the study of animal behaviour where evolution is unlikely to generate the complex behaviour demanded by the optimal strategy. For animal behaviour the question of optimal exploitation of resources in patchy environments has attracted considerable attention from biologists, especially the question of how long an individual should forage in a given patch. In ecological foraging theory there has been considerable interest in simple behavioural rules, or "rules of thumb", which lead to behaviour that closely approximates the evolutionary optimum. The relative performance of these rules will depend on the details of the foraging environment, such as prey resource density. In this paper we derive rules of thumb for patch leaving behaviour in different foraging environments from a stochastic dynamic programming model (SDP). We use a particular biological system: a parasitoid which is an insect that lays eggs in insect host larvae. Empirical work suggests that simple rules of thumb such as leaving a patch after a fixed time period or number of eggs laid do not adequately describe patch leaving behaviour. Therefore, attempts have been made to derive more sophisticated rules of thumb by statistical analysis of real behaviour. However, this statistical approach does not explain the underlying functional mechanism of patch leaving behaviour. An SDP model permits the optimal patch leaving behaviour to depend on both internal and external states of the parasitoid. We simulate parasitoids whose patch leaving behaviour is determined by an SDP model, while allowing parasitoids to make mistakes in their estimation of host density when arriving in a patches. We use proportional hazard models to obtain statistical rules of thumb from the simulated behaviour.

1.1 Introduction

Stochastic dynamic programming (SDP, Mangel and Clark 1988) models are widely used to find state dependent optimal solutions in biology, such as the foraging behaviour of animals (optimal foraging theory or OFT). However, the results of SDP models are often very complex, especially when the state space is large, and it is unlikely that evolution has implemented such complex behaviour. Some speculate that the only way animals could perform close to optimally is to use "rules of thumb" [e.g. Weis 1983]. However, the connection between such rules and optimal solutions is vague. A reliable method to translate complex optimal strategies from an optimisation procedure into simple rules would have wide application. In this paper we use Cox's proportional hazards model [Cox and Oakes 1984, Kalbfleisch and Prentice 1990] as a tool to condense the results of an SDP model into rules that could be easily implemented in animal behaviour.

The optimal length of time to exploit a patch of resources is an important issue in biocontrol, wildlife management and fisheries [e. g. Marschall et al 1989, Newman et al. 1988, Morrison and Lewis 1981]. There have been 3 different general approaches in OFT to predict when a consumer should leave a patch of prey resources: simple rules of thumb, optimisation models, and statistical analysis of empirical data. Here we provide a brief review of these approaches.

The best known rules of thumb are: remain until a fixed number of prey have been consumed [Gibb 1958, Krebs 1973], remain for a fixed time period [Gibb 1962], remain until the time between encounters with individual prey exceeds a fixed value [Hassel and May 1974, Murdoch and Oaten 1975]. However, empirical work suggests that these simple rules do not describe patch leaving behaviour adequately.

The best known theoretical model of optimisation of patch residence times is Charnov's [1976] marginal value theorem. In this model a forager leaves a patch when the intake rate drops below the environmental average. This model ignores that the optimal patch residence time may depend on internal states of the forager. Stochastic dynamic programming (SDP) models find optimal solutions that can take the state of the forager into account [Mangel and Clark 1988].

Survival analysis such as Cox's proportional hazards model is used to study the relationship between survival times and explanatory variables. The method finds important applications in product life testing and a range of disciplines from physics to econometrics [Cox and Oakes 1984]. Starting with Haccou and Hemerik [1985] Cox's proportional hazards models have been used to analyse the behaviour of insects, in particular parasitoids [see review in Godfray 1994]. The result is a model of the probability to leave a patch at any given point in time (leaving tendency) as a function of covariates such as the density of resources within the patch. This statistical model of leaving behaviour could be interpreted as a state dependent rule of thumb.

In this paper we combine these three approaches. 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 model to generate sequences of behavioural decisions by simulated wasps determined by the optimal strategy from the SDP. Third, we analyse the simulated decision sequences with a proportional hazards model to generate statistical rules of thumb. The end result is a state dependent rule of thumb that is explicitly connected to an optimal foraging model.

1.2 Model

We assume that parasitoid females adjust their behaviour to maximise their expected lifetime reproduction (R_0). In order to calculate the optimal behaviours we use SDP. The model starts at the end of an individuals life, then goes backwards in time and calculates, for each combination of states, the behaviour that results in the highest lifetime reproduction.

The state space of the SDP model includes time t, host density d, number of ovipositions e, and time period in a given patch t_p. Time spent between patches (r) is incorporated by using negative values for t_p. Here we provide a brief description of the most important parts of the model.

An adult female wasp oviposits a single egg in its host, the caterpillar larvae of *P. rapae*. After hatching a wasp larva feeds internally on the host's tissue and kills the host at the end of larval development. The caterpillar 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. We assume that wasps have perfect knowledge about the average density and distribution of hosts in the environment.

While in a patch wasps are searching for hosts. At a given host density the probability to encounter a host is drawn from a Poisson distribution. A wasp may encounter hosts at 2 different sizes s with the probability of p_s in which she successfully oviposits an egg with the probability s_s. They cannot distinguish parasitised from unparasitised hosts, so we also compute the probability that an encountered host has already been parasitised during the current visit. Depending on the host size she spends the time h_s to handle the host and receives the fitness payoff α_s. According to her oviposition success (O_1= oviposition; O_0=no oviposition) the state space changes as follows:

$$O_1 = F[t+h_s][d][t_p+h_s][e+1] \qquad (1)$$

$$O_0 = F[t+1][d][t_p+1][e]. \qquad (2)$$

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. The probability to encounter another host occupied patch (λ_{dr}) depends on the density and distribution of hosts. When a wasp encounters a patch the probability to land (β_d) is an increasing function of the host density in that particular patch and equals 1 after 25 minutes.

This scenario is described in the following dynamic programming equation:

$$F(t,d,t_p,e) = \max(\text{payoff}_{\text{leave}}, \text{payoff}_{\text{stay}}) \qquad (3)$$

$$\text{payoff}_{\text{leave}} = \qquad (4)$$

$$\sum_{r=1}^{10}\sum_{d=0}^{10}\left(F(t+r,d,1,0)\cdot\lambda_{dr}\cdot\beta_d\cdot(1-m_2^{\,r})\right)$$

$$\text{payoff}_{\text{stay}} = \qquad (5)$$

$$(1-m_1)\left(host_{good}\,p_{good} + host_{bad}\,p_{bad} + host_0\,p_0\right),$$

where m_1 and m_2 are the mortality rates in the patch and while flying, with $m_1<m_2$. p_{good}, p_{bad} or p_0 are the probabilities to encounter an unparasitised, parasitised or no host; $host_{good}$, $host_{bad}$ or $host_0$ are the corresponding payoffs.

$$\text{host}_{\text{good}} = \qquad (6)$$

$$\sum_{s=1}^{2} p_s(O_1+\alpha_s)s_s + O_0(1-s_s)$$

$$\text{host}_{\text{bad}} = \qquad (7)$$

$$\sum_{s=1}^{2} p_s\left(O_1 s_s + O_o(1-s_s)\right)$$

$$\text{host}_0 = F[t+1][d][t_p+1][e] \qquad (8)$$

1.3. Simulation experiment

Empirical results in the literature suggest that the patch residence time of parasitoids is influenced by the host density of a patch and the number of ovipositions (see Godfray [1994] for an overview). The simulation experiments study the effects of host density d and number of ovipositions e in a given patch on the tendency to leave this patch. For this we recorded the "giving up times" (GUT), which is the period of time from the last oviposition until the wasp leaves. If there is no oviposition the GUT is simply the total time spent in the patch. To study the effect of host density we released wasps on patches of 2, 4, 6, 8, and 10 hosts, respectively. When a wasp arrives in a patch she estimates the host density of that patch based on the semiochemical concentration. Her estimate is drawn from a normal distribution with mean d and a standard deviation of 2, simulating error in the estimation of host density.. Without this added variability the statistical analysis would be degenerate, because all wasps would behave in the same way given the same density and number of ovipositions.

To examine the effect of previous ovipositions we allowed the wasps to oviposit n = 0, 1, ..5 times and then we set the probability to find another host equal to 0. This way we obtained GUT for each density and following 0-5 ovipositions. This experimental protocol mimics the empirical work by Hemerik and al. [1993] on parasitoid leaving tendency.

1.3 Proportional hazard analysis

We analysed the patch residence time with a proportional hazard model. It is assumed 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 $z_1,\ldots\ldots, z_p$. The general form of the model is:

$$\lambda(t,z) = \lambda_0(t)\exp\left(\sum_{i=1}^{p}\beta_i z_i(t)\right), \qquad (9)$$

where h(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. $\lambda_0(t)$ and $\beta_1,\ldots., \beta_p$ are estimated by means of likelihood maximisation (see Haccou and Hemerik [1985], and Kalbfleisch and Prentice [1990] 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. We assume that λ_0 is reset after each oviposition and after each time the patch has been left and reentered. In the model we include the covariates host density d and number of ovipositions e in the current patch. Therefore, the leaving tendency is:

$$\lambda(t;z) = \lambda_0(t)\exp\left(\delta\ d + \sum_{i=0}^{5} \varepsilon_i e_i\right) \qquad (10)$$

where t is the time since the last renewal point, e_i refers to 0-5 ovipositions, d represents the host density in a given patch and ε_i, δ are the corresponding covariates.

We tested the fit of the model using martingale residuals. The proportionality assumption was tested via stratification, which is dividing the original sample into subgroups (=strata) according to the value of the variable d or e, respectively. The stratification results and the martingale residuals are illustrated in the appendix.

1.4 Results

The optimal GUT for simulated *C. rubecula* increases with host density and decreases with the number of ovipositions in the current patch (Figure1). While the curves representing the increase in GUT with host density for 0-3 ovipositions are reasonably parallel, host density has no effect when more than 4 eggs are laid. Wasps may lay an egg in an already parasitised host (superparasitism), which may result in more ovipositions than hosts present such as 3 oviposition at a host density of 3. The risk of superparasitism decreases with host density. 5 oviposition occur only at a minimum host density of 6.

We quantified the influence of host density and number of ovipositions using Cox's proportional hazards model. The baseline hazard is illustrated in Figure 2, and the estimates of the coefficients of the covariates in Table 1. Note that 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. When the host density was 5 the leaving tendency was 74% (i.e. exp[-0.296]) of the leaving tendency when the host density was only 4.

Each oviposition increases the leaving tendency. However, with each additional oviposition the effect on the leaving tendency increases. While the leaving tendency of a female wasp increases 2 times (exp[0.169]) after she lays her the 2nd egg her leaving tendency increase 20 times (exp[2.983]) after she lays her 5th egg. Note that even small increases in β_i have a big effect in the leaving tendency.

The fit of the model has been verified by plots of stratified baseline hazards and martingale residuals (see appendix).

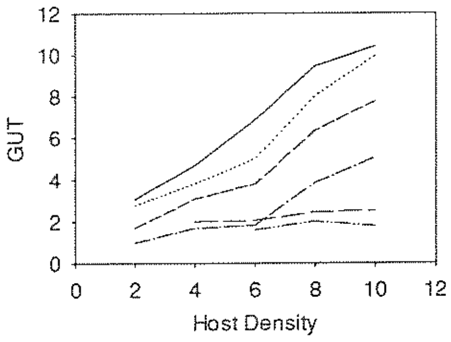

Figure1: Average GUT as a function of host density. The numbers on the right hand side of the curves indicate the number of ovipositions before leaving the patch.

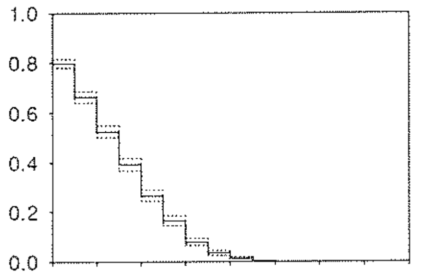

Figure 2: Baseline hazard (solid line) and the corresponding 95% confidence interval (dotted lines). This is the probability to stay in a patch, given the patch has not yet been left.

Table 1: Estimates of the coefficients of the covariates. (see text for details)

	β	se(β)	z	p
Host Density	-0.296	0.0109	-27.08	< 0.0001
1^{st} Egg	0.169	0.0632	2.67	0.0075
2^{nd} Egg	0.694	0.0739	9.39	< 0.0001
3^{rd} Egg	1.659	0.0876	18.93	< 0.0001
4^{th} Egg	2.228	0.1042	21.39	< 0.0001
5^{th} Egg	2.983	0.1785	16.71	< 0.0001

The overall fit of the model is significant (likelihood ratio test, df = 6, $p< 0.0001$, $r^2 = 0.424$)

1.5 Conclusions

This paper has developed 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. 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.

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 4) of the Cox's proportional hazards model.

The possibility of condensing the results of SDP models makes it feasible to incorporate optimal behaviour of individuals into population models. This will close the gap between models of individual behaviour and population models. Even simple representations of optimal behaviour can have profound effects on population dynamics [Roitberg and Mangel 1992]. Including optimal behaviour invites realistic population models tailored to specific systems. This increases the chances that the model will tell us something relevant about that system. Specific and realistic models will also be useful as tools for addressing applied questions, such as in biological control [Murdoch and Briggs 1996].

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1.7 References

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1.8 Appendix

The validity of proportionality assumption for our model including the covariates oviposition and host density is demonstrated in Figures A1: the baseline hazards stratified for each covariate are parallel, ie. 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 1, and outliers are represented by large negative values. A smooth fit to the Martingale residuals should be horizontal, as shown in Figure A2.

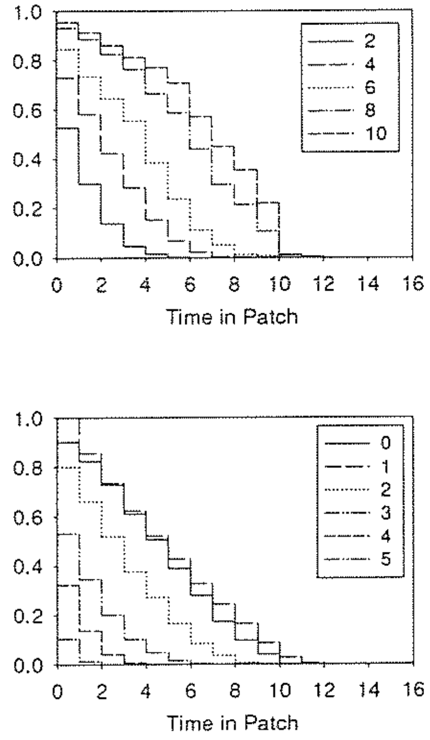

Figure A1: Baseline hazards for the different oviposition and density strata. The numbers in the legend indicate the respective number of ovipositions (upper graph) or host densities (lower graph)

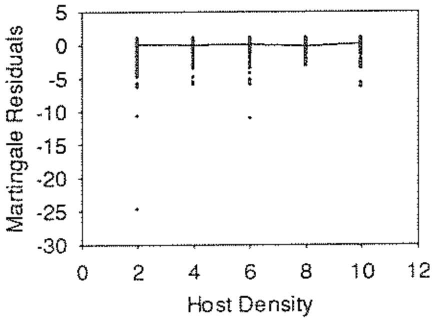

Figure A3: Martingale residuals.