

Dynamic Information in Uncertain and Changing Worlds

MARC MANGEL

*Zoology Department and Center for Population Biology,
University of California, Davis, CA 95616, U.S.A.*

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A general theory for information processing by organisms living in uncertain and changing worlds is developed. The three fundamental properties of the theory are: (i) the use of a memory parameter that allows the organism to forget the more distant past, (ii) a succinct representation of encounters and information and (iii) flexibility in the estimates of parameters by including the uncertainty in these estimates in a consistent manner. The theory is developed using Bayesian methods (but can also be applied to maximum likelihood estimation) and is applied to the encounter models standardly used in ecology (Poisson, binomial, and negative binomial). Two applications are discussed: (i) patch selection and the matching rule and (ii) superparasitism by a parasitoid.

Introduction

Most models in behavioral ecology assume that key environmental parameters are known to the organism. For example, in the theory of diet choice (Stephens & Krebs, 1986; Mangel & Clark, 1988), organisms are assumed to know the encounter rate, energy value and handling time of each prey item. In the theory of patch selection, the patch residence time is determined by solving an equation that involves the energetic return to the organism when it stays in the patch for t units of time and τ is the travel time between patches; both the travel time and reward function are presumed to be known.

Nearly all organisms, however, live in an uncertain environment. The uncertainty might be caused by natural fluctuations of non-biotic elements or by fluctuations of biotic elements. In addition, very often the environment will have its own dynamics. For example, consider a solitary bee visiting a patch containing flowers of different species. Each species of flower may have its own timing for nectar production and each individual of each species may have slight variations in this timing. The precise nature of the timing will depend upon non-biotic factors in the patch (e.g. rainfall, sunlight) and all these together lead to a considerable level of uncertainty in the overall nectar reward rate from the patch. Other pollinators may remove nectar from the patch, causing the already uncertain system to have quite complicated dynamics. It is unlikely that bees will know all timings of the flower species or count the number of other pollinators in the patch. Yet, they must somehow deal with the uncertainty and dynamics of the patch.

The key question is how organisms develop information to deal with the uncertain and changing environment. Here, "symbolic representations" are used in which the organisms summarize physical entities by parameters that are estimated (Lewis,

1986; Kamil & Roitblat, 1985). The organism replaces encounters with real objects (e.g. prey items for a predator or unparasitized and previously parasitized hosts for a parasitoid) by estimates of the occurrences of those items (e.g. encounter rates with prey items or host types). The general features of an information processing theory should include: (i) a decay of memory, so that events which happened a long time ago have less impact on the estimate than more recent events, (ii) succinctness of the estimate, so that the organism can summarize its encounter history in an efficient way, and (iii) flexibility of the estimate, through a consistent treatment of uncertainty. In the body of the paper, Bayesian methods (DeGroot, 1970) are concentrated on and, in the Appendix, the same ideas are applied to Maximum Likelihood Estimate (MLE) computations.

The theoretical work closest to this paper is McNamara & Houston (1985, 1987) and Stephens (1987, 1989); they also develop various aspects of models for memory and information in uncertain, dynamic worlds. This paper represents an extension of those in a number of ways but particularly by including both memory and uncertainty (or variance) and by linking them, via state variables, directly to fitness. McNamara & Houston (1985) model optimal foraging and learning, but choose as their fitness function the long-run reward rate, as in the marginal value theorem. Stephens (1987) also uses a long-run reward rate. Their work is extended here by showing how information can be treated as a *state* variable in the fitness function. McNamara & Houston (1987) also use linear operators and Bayesian analysis. The differences between their paper and this one are the: (i) whereas McNamara & Houston also derive the linear operator from a Bayesian approach, they only consider the case of perfect memory, (ii) McNamara & Houston only treat the case of a normally distributed parameter with a normally distributed prior as the model for Bayesian analysis, (iii) McNamara & Houston specify rules for changing the unknown encounter rate parameter, whereas here the change is not specified, (iv) McNamara & Houston implicitly deal with constant streams of information whereas the methods developed here can be used to treat situations in which information is obtained intermittently, and (v) McNamara & Houston concentrate on the dynamics of the mean, whereas here the uncertainty in the estimate figures prominently. Stephens (1989) shows how variance affects the value of information, but does not provide an explicit way of linking information, variance and fitness. This paper extends his, by showing how to do this.

In the next section, the fundamental ideas are illustrated by considering an organism that encounters resources according to a Poisson process. The encounter rate is estimated using a Bayesian method incorporating a way of forgetting past information; this extends the previous uses of Bayesian methods in behavioral ecology. (In the Appendix, Maximum Likelihood Estimation with the forgetting is analyzed.) In section 3, the same ideas are applied to other common encounter models such as the binomial and the negative binomial is shown. Sections 4 and 5 are concerned with applications in behavior and evolution. First, patch choice by an organism is modeled; and the "matching rule" which is a natural prediction of the methods developed here, is shown. Second, superparasitism by a parasitoid is modeled and dependence of decisions and realized fitness upon the memory para-

meter and upon time is shown. I conclude with a general discussion of the role of sampling and forgetting.

2. Random Encounters with Resources

Suppose that the organism encounters resources (food, mates, refugees) according to a Poisson process with parameter λ , which is both unknown and changing over time. Thus, encounters are random and the encounter rate at each spatial point of the world is identical to the rate every other spatial point. Under the Poisson assumption

$$\text{Prob \{encounter } n \text{ items in } t \text{ units of time\}} = e^{-\lambda t} (\lambda t)^n / n!. \quad (1)$$

Assume that an interval of interest is $[0, s]$ and is divided into s periods of unit length. Encounters (data) occur in each period, so that the organism receives a "constant stream" of data (cf. McNamara & Houston, 1987). Let s denote the current time and represent the data by $\{n_1, n_2, n_3, \dots, n_s\}$, where n_i is the number of encounters in the i th preceding period.

If the world is changing, then the information provided by data gathered a number of periods previously should be less valuable than the information provided by recent data. Thus, in the likelihood function (DeGroot, 1970), the data gathered i periods ago is weighted by raising (1) to $\gamma(i)$, where $0 \leq \gamma(i) \leq 1$. McNamara & Houston (1985) have done a similar weighting—but using an *ad hoc* rate function instead of the likelihood function—and show, in fact, that $\gamma(i) = \gamma^i$, which corresponds to exponential weighting, may be the optimal weighting. Weighting the likelihood function in this manner is analogous to a weighted least squares (Miller, 1986: 210–214). By employing this kind of weighting in a Bayesian framework, one interweaves frequentist and Bayesian approaches and is thus limited in the statistical foundations. However, the weighted likelihood function provides a relatively firm basis from which to derive updating rules for estimates of parameters.

The likelihood function for the entire data set thus becomes

$$\mathcal{L} = \prod \{e^{-\lambda} \lambda^{n_i} / n_i!\}^{\gamma(i)}. \quad (2)$$

This form of the likelihood function is determined by the way that the data are counted: n_i is the datum from the i th preceding period and is thus weighted by $\gamma(i)$, which approaches 0 as i increases (the past becomes more distant). If n_i were the datum from the i th period, then the weighting would be $\gamma(s-i)$. The results that follow would be the same; the convention chosen here is used for simplicity of the likelihood function.

In the Bayesian approach, the appropriate conjugate prior is the gamma density (DeGroot, 1970) for which

$$f_0 = e^{-\alpha\lambda} \alpha^\nu \lambda^{\nu-1} / \Gamma(\nu). \quad (3)$$

Here α and ν are parameters and $\Gamma(\nu)$ is the gamma function.

For the gamma prior, the mean and coefficient of variation (CV) of the unknown parameter λ are $E\{\lambda\} = \nu/\alpha$ and $CV\{\lambda\} = 1/\nu^{0.5}$.

The posterior density f_p is obtained by multiplying the prior (3) by the likelihood (2) and normalizing. It is

$$f_p = k \exp [-\lambda(\alpha + \sum \gamma(i))] \lambda^{(\alpha + \sum n_i \gamma(i) - 1)}. \quad (4)$$

Here k is a constant. Equation (4) shows that the posterior density is another gamma density, with changed parameters. After s periods of data collection, the parameters change from α and ν to

$$\begin{aligned} \alpha &\rightarrow \alpha + \sum \gamma(i) \\ \nu &\rightarrow \nu + \sum n_i \gamma(i). \end{aligned} \quad (5)$$

Equation (5) is an updating rule, so that all of the data do not need to be tracked; instead all of the information is summarized in the updated parameters.

Suppose that before any data are collected, the prior values of the parameters are

$$\begin{aligned} \alpha(0) &= \alpha_0 \\ \nu(0) &= \nu_0. \end{aligned} \quad (6)$$

These have an evolutionary interpretation as the long term environmental parameters.

In order to further simplify the updating rules, assume that $\gamma(i) = \gamma$. Then applying the updating rules (5) and simplifying shows that if $\alpha(s)$ and $\nu(s)$ are the parameter values after s periods of data collection, then

$$\begin{aligned} \alpha(s+1) &= \gamma\alpha(s) + 1 + (1-\gamma)\alpha_0 \\ \nu(s+1) &= \gamma\nu(s) + n_{s+1} + (1-\gamma)\nu_0. \end{aligned} \quad (7)$$

These equations are similar to a linear operator (see Kacelnik *et al.*, 1987: table 4.1) and show the interplay of the memory parameter and the data in determining the parameters of the posterior distribution.

An advantage of using the memory parameter is that it prevents the updated parameter ν from approaching ∞ as more data are collected. Thus, by forgetting the more distant past, the organism never "locks itself" into an estimate of the encounter rate; there will always be uncertainty in this estimate. By using the memory parameter, one thus eliminates a least desirable feature of Bayesian analysis (the constant reduction of uncertainty as information is collected). The parameters α_0 and ν_0 can be viewed as "long-term" or "environmental" averages of the parameters. An advantage of the Bayesian method over the MLE method described in the Appendix is that because of these long term parameters, the Bayesian method consistently treats situations in which an organism receives an intermittent stream of information. For example, suppose that instead of foraging in a period, the organism hides and thus neither samples nor encounters resources. There is no way to build this into the MLE, but it is easily done in the Bayesian approach. A specific example is given below.

3. Other Common Encounter Models

The analysis of the previous section can be extended for other encounter models. Two of the most commonly used models are the situations in which at most one encounter can occur in each period or in which encounters involve an aggregated distribution.

In the first case, the appropriate encounter model is simply

$$\text{Prob \{encounter an item in a period\}} = p, \quad (8)$$

and the parameter p must be estimated. The data in each period are then either $n_i = 1$ (if an item is encountered) or $n_i = 0$ (if an item is not encountered).

In the second case, an appropriate model is the negative binomial distribution for which

$$\begin{aligned} \text{Prob \{n encounters in a period of unit length\}} \\ = [\Gamma(k+n)/\Gamma(k)n!](k/k+m)^k(m/k+m)^n. \end{aligned} \quad (9)$$

Here k and m are parameters. The mean number of encounters in a period of unit length is given by m and the variance is $m + (m^2/k)$, where k is the overdispersion parameter. In this case, presume that m is unknown and to be estimated, but that k is known. The data for each period are the numbers of items encountered in that period.

The results of analysis similar to that in the previous section are summarized in Table 1. For the case of a single encounter per period, further details on the Bayesian analysis can be found in DeGroot (1970). For the Bayesian approach with negative binomial encounters, further details are found in (Mangel, 1987).

TABLE 1

Results for encounters of one item per period (binomial) or aggregated (negative binomial) encounters

Variable	Encounter model	
	One per period	Negative binomial
Estimated parameter	p	m
Likelihood	$\prod \{p^{n_i}(1-p)^{1-n_i}\}^{\gamma(i)}$	$\prod \{[\Gamma(k+n_i)/\Gamma(k)n_i!]$ $\times (k/k+m)^k(m/k+m)^{n_i}\}^{\gamma(i)}$
Curvature at the MLE (see Appendix)	$-\sum \gamma(i)/[\hat{p}(s)(1-\hat{p}(s))]$	$-k \sum \gamma(i)/[\hat{m}(s)(k+\hat{m}(s))]$
Conjugate prior for Bayesian analysis	$\{1(\delta+\omega)/\Gamma(\delta)\Gamma(\omega)\}p^{\delta-1}(1-p)^{\omega-1}$	$cm^{\alpha}(k+m)^{\beta}$
Parameters of prior	δ, ω	α, β (c is a normalization constant)
Updating rule for parameters	$\delta \rightarrow \delta + \sum n_i \gamma(i)$ $\omega \rightarrow \omega + \sum (1-n_i) \gamma(i)$	$\alpha \rightarrow \alpha + \sum n_i \gamma(i)$ $\beta \rightarrow \beta - \sum (n_i + k) \gamma(i)$

4. Role in Behavior and Evolution: Patch Selection and the Matching Rule

A much studied problem in behavioral ecology involves patch choice by an organism such as a bird or fish presented with two patches that have uncertain rewards. Examples, with citation to the literature, are found in Kacelnik & Krebs (1985) and Kacelnik *et al.* (1987). Such choice problems have also been studied by psychologists for many years (see Mackintosh, 1983: 257 for discussion and citation to the literature; Barnard, 1983: 150; Stephens & Krebs, 1986: 179 for the animal behavior context). One commonly observed feature of such choice problems is the "matching rule". Suppose that p_i is the probability that the i th patch presents the animal with a reward on a visit and that f_i is the long term fraction of visits to the i th patch.

The matching rule is the observation that very often even though $p_1 > p_2$, say,

$$f_i = p_i^\kappa / (p_1^\kappa + p_2^\kappa), \quad (10)$$

where κ is a parameter. It is clear that for fixed p_i an allocation rule such as (10) cannot maximize long run rate of reward and this has been used to argue that animals do not optimize. Here, the patch selection problem is reformulated as one involving Bayesian updating with forgetting and where implications for the matching rule are investigated.

Krebs *et al.* (1978) analyze a patch selection problem in which the probability of reward is fixed but unknown. Mangel & Clark (1983, 1986, 1988) analyze a patch selection problem in which the encounter rate is fixed but unknown. These cases correspond to the memory parameter $\gamma = 1$. The results of those analyses show that some initial periods of sampling determine which is the best patch and that the organism settles into that patch for the remainder of the periods. Here, the analyses are extended to the case in which the memory parameter is less than 1, for use with temporally changing encounter rates.

Consider a time horizon from $t = 1$ to $t = T$, at which point fitness is assessed (e.g. reproduction occurs) and assume that fitness is proportional to the total number of prey captures between 0 and T . Let R_i denote the prey capture rate in the i th patch and assume that the prey capture rate is a Poisson process with parameter λ_i . Consider periods of unit length. Since the λ_i are unknown, each patch has an associated prior gamma density with initial values of the parameters given by α_{0i} and ν_{0i} and, for definiteness, consider two patches. For any intermediate time t , define the fitness function

$$F(\nu_1, \alpha_1, \nu_2, \alpha_2, t, T) \\ = \max E \{ \text{total prey captures between } t \text{ and } T | \text{current parameters} \}. \quad (11)$$

In this equation, the maximum is taken over behavioral decisions; meaning the sequence of patches to visit.

Since no prey captures occur after period T , we have the end condition

$$F(\nu_1, \alpha_1, \nu_2, \alpha_2, T, T) = 0, \quad (12)$$

and this shows that when $t = T - 1$ any information collected by the foraging organism is of no value, so that

$$F(\nu_1, \alpha_1, \nu_2, \alpha_2, T - 1, T) = \max_i E\{\lambda_i\} = \max_i \{\nu_i / \alpha_i\}. \quad (13)$$

For a general intermediate period, we need to compute the probability that if patch i is visited $R_i = r$, given the current values of the parameters. This is

$$\text{Prob}\{R_i = r | \text{parameters are } \alpha_i, \nu_i\} = [\Gamma(\nu_i + r) / \Gamma(\nu_i) r!] (\alpha_i / \alpha_i + 1) \nu_i (1 / \alpha_i + 1)^r. \quad (14)$$

Note that eqn (14) is the negative binomial distribution (9)

The equation for $F(\nu_1, \alpha_1, \nu_2, \alpha_2, t, T)$ is

$$F(\nu_1, \alpha_1, \nu_2, \alpha_2, t, T) = \max_i \{(\nu_i / \alpha_i) + \sum_{r=0}^{\infty} \text{Prob}\{R_i = r\} F(\nu'_i, \alpha'_i, \nu'_2, \alpha'_2, t + 1, T)\}. \quad (15)$$

In this equation, ν'_i and α'_i are updated values of the parameters, depending upon the patch that is visited (i), the number of encounters in that patch (r) and the memory parameter. Assuming that the organism forgets past information even if it does not visit the patch gives the following updates for the parameters in the first patch:

$$\nu'_1 = \begin{cases} \gamma \nu_1 + (1 - \gamma) \nu_{10} & \text{if } i = 2 \\ \gamma \nu_1 + (1 - \gamma) \nu_{10} + r & \text{if } i = 1, \end{cases}$$

and

$$\alpha'_1 = \begin{cases} \gamma \alpha_1 + (1 - \gamma) \alpha_{10} & \text{if } i = 2 \\ \gamma \alpha_1 + (1 - \gamma) \alpha_{10} + 1 & \text{if } i = 1. \end{cases} \quad (16)$$

The updates for the parameters in the second patch are defined in a similar way. Note that when the organism does not visit a patch, it is still possible to "update" that patch's parameters using the Bayesian formulation.

Two important qualitative features emerge from eqns (15) and (16). First, for reasonable values of the patch parameters, the organism will never settle permanently into one of the two patches. Instead, it will continually revisit and resample each of the patches, because it forgets the past encounters. In particular, the most interesting case is one in which $\nu_1 / \alpha_1 > \nu_2 / \alpha_2$, so that on average patch 1 is superior to patch 2, and $\nu_1 > \nu_2$, so that patch 1 is also more certain than patch 2. Thus, although patch 2 is inferior on average, there will be realizations in which it is superior to patch 1. The behavioral predictions that emerge from (15) and (16) is that the organism will sample both patches and initially choose one in which to reside and forage. Over time, however, information about the other patch is forgotten, and this may lead to resampling of the other patch, especially if ν_0 is small (so that there is considerable uncertainty). The rate of revisit and resample will depend upon the memory parameter γ . Such behavior, however, is clearly consistent with the matching rule (10). In addition, the use of the memory parameter has an advantage for numerical solutions in that the curse of dimensionality which arises in the numerical solution of eqn (15) when $\gamma = 1$ is somewhat mitigated by the memory parameter, which puts a natural limit on the values of the parameters.

5. Role in Behavior and Evolution: Superparasitism by a Wasp or Tephritid Fruit Fly

Many solitary parasitoids and fruit parasitic insects mark hosts with a pheromone after they have laid an egg in the host. Superparasitism refers to the phenomenon of attacking a previously parasitized and marked host. In recent years, it has been realized that superparasitism may, in fact, be an adaptive strategy and not simply an error in detection of the mark (for review see van Alphen & Visser, 1990). Here, the role of information in the oviposition decision of the parasitoid is investigated.

A foraging parasitoid will encounter two kinds of hosts: those that are unparasitized (subscript u) and those that are previously parasitized and marked with a pheromone (subscript p). Let λ_i denote the probability that a host of type i is encountered in a unit interval of time and assume that $\lambda_u = \lambda\rho$ and $\lambda_p = \lambda(1-\rho)$, so that λ is the probability that a host of either type will be encountered in a single period and ρ is the conditional probability that if a host is encountered, then it is unparasitized. Assume that both λ and ρ are unknown and changing. In this case, the appropriate prior density is the beta density; let λ have a beta density with parameters δ and ω and let ρ have a beta density with parameters ν and α . Thus, for example, the mean and coefficient of variation of λ are $\delta/(\delta+\omega)$ and $[\omega/(\delta(\delta+\omega+1))]^{1/2}$ respectively. Specifying a mean value of λ and associated coefficient of variation provides a unique determination of the two parameters. In each period, the parasitoid either encounters no host, encounters an unparasitized host or encounters a previously parasitized host. If no host is encountered, then the updating rule for the parameters becomes

$$\begin{aligned}\delta(s+1) &= \gamma\delta(s) + (1-\gamma)\delta_0 \\ \omega(s+1) &= \gamma\omega(s) + 1 + (1-\gamma)\omega_0 \\ \nu(s+1) &= \gamma\nu(s) + (1-\gamma)\nu_0 \\ \alpha(s+1) &= \gamma\alpha(s) + (1-\gamma)\alpha_0.\end{aligned}\tag{17}$$

In this equation, γ is the memory parameter (assumed to be the same for updating the overall encounter rate and the specific encounter rate) and δ_0 , ω_0 , ν_0 and α_0 are the long-term, evolutionary values of the encounter parameters. If a host of either type is encountered in a given period, then the first two equations in (17) are replaced by

$$\begin{aligned}\delta(s+1) &= \gamma\delta(s) + 1 + (1-\gamma)\delta_0 \\ \omega(s+1) &= \gamma\omega(s) + (1-\gamma)\omega_0,\end{aligned}\tag{18}$$

and if the encountered host is unparasitized then the last two equations in (17) are replaced by

$$\begin{aligned}\nu(s+1) &= \gamma\nu(s) + 1 + (1-\gamma)\nu_0 \\ \alpha(s+1) &= \gamma\alpha(s) + (1-\gamma)\alpha_0,\end{aligned}\tag{19}$$

whereas if the encountered host is previously parasitized, then the last two equations in (17) are replaced by

$$\begin{aligned} \nu(s+1) &= \gamma\nu(s) + (1-\gamma)\nu_0 \\ \alpha(s+1) &= \gamma\alpha(s) + 1 + (1-\gamma)\alpha_0. \end{aligned} \quad (20)$$

In order to fully model the behavioral problem, consider an interval of length T in which the parasitoid forages for hosts. For example, T might be the fruiting interval of a tree, the length of day for a synovigenic parasitoid unable to hold mature eggs overnight, or the length of existence of a patch of hosts. Oviposition in an unparasitized host increases lifetime accumulated fitness by an amount f_u and oviposition in a previously parasitized host increases lifetime fitness by an amount f_p with $f_u > f_p$. The probability that the parasitoid survives a single period in which oviposition does not occur is $1 - \mu$ and the probability that the parasitoid survives a single period in which oviposition does occur is $(1 - \mu)\psi$ where $0 < \psi < 1$ so that ψ is a measure of the survival or somatic cost of reproduction (e.g. Carey, 1984; Roitberg, 1989). It can easily be shown that with these assumptions, oviposition in an unparasitized host is always optimal. The "decision" is then to oviposit or not in a previously parasitized host.

Let $F(\omega, \delta, \nu, \alpha, t, T)$ denote the maximum expected fitness accumulated through ovipositions between period t and period T , given that the current values of the parameters are ω, δ, ν , and α . The dynamic programming equation that lifetime fitness satisfies is

$$\begin{aligned} F(\omega, \delta, \nu, \alpha, t, T) &= [\omega/(\omega + \delta)](1 - \mu)F(\omega', \delta', \nu', \alpha', t+1, T) \\ &\quad + [\delta/(\delta + \omega)][\nu/(\nu + \alpha)] \\ &\quad \times \{f_u + (1 - \mu)\psi F(\omega'', \delta'', \nu'', \alpha'', t+1, T)\} \\ &\quad + [\delta/(\delta + \omega)][\alpha/(\nu + \alpha)] \\ &\quad \times \max \{f_p + (1 - \mu)\psi F(\omega''', \delta''', \nu''', \alpha''', t+1, T), \\ &\quad \times (1 - \mu)F(\omega''', \delta''', \nu''', \alpha''', t+1, T)\}. \end{aligned} \quad (21)$$

The three terms on the right hand side of (21) correspond to: (i) not encountering a host in period t , in which case the updated parameters ω', δ', ν' , and α' are given by (17), (ii) encountering an unparasitized host in period t , in which case the updated parameters are $\omega'', \delta'', \nu''$, and α'' are given by (18) and (19) or (iii) encountering a parasitized host in period t , in which case the updated parameters are $\omega''', \delta''', \nu'''$, and α''' are given by (18) and (20). The end condition for (21) is that $F(\omega, \delta, \nu, \alpha, T, T) = 0$ for all values of the parameters. Because the updating rules lead to fractional values of the parameters, in order to solve (21) a four-dimensional interpolation is needed.

As (21) is solved, optimal oviposition decisions are determined. These decisions are denoted by $d^*(\omega, \delta, \nu, \alpha, t) = 1$ if it is optimal to oviposit in a parasitized host encountered in period t when the parameters are ω, δ, ν , and α or $d^*(\omega, \delta, \nu, \alpha, t) = 0$

if it is optimal to reject a parasitized host encountered in period t when the parameters are ω , δ , ν , and α . Figure 1 shows, as a function of t for three values of the memory parameter γ , the fraction of $\{\omega, \delta, \nu, \alpha\}$ -space in which the optimal decision is to oviposit in a previously parasitized host. If $\gamma = 0$, then no learning occurs and the decision is to either always (i.e. for all parameter values) oviposit or to always reject. For values of $\gamma > 0$, the step function corresponding to $\gamma = 0$ is smoothed out by the updating of information.

If the world is changing, however, the solution of (21) does not give the actual fitness realized by the organism. That is, suppose that the encounter probabilities are functions of time, $\lambda(t)$ and $\rho(t)$, and let $V(\omega, \delta, \nu, \alpha, t, T)$ denote the actual realized value of expected fitness between t and T , given that the current parameters are ω, δ, ν , and α and that the optimal decisions are followed. Then

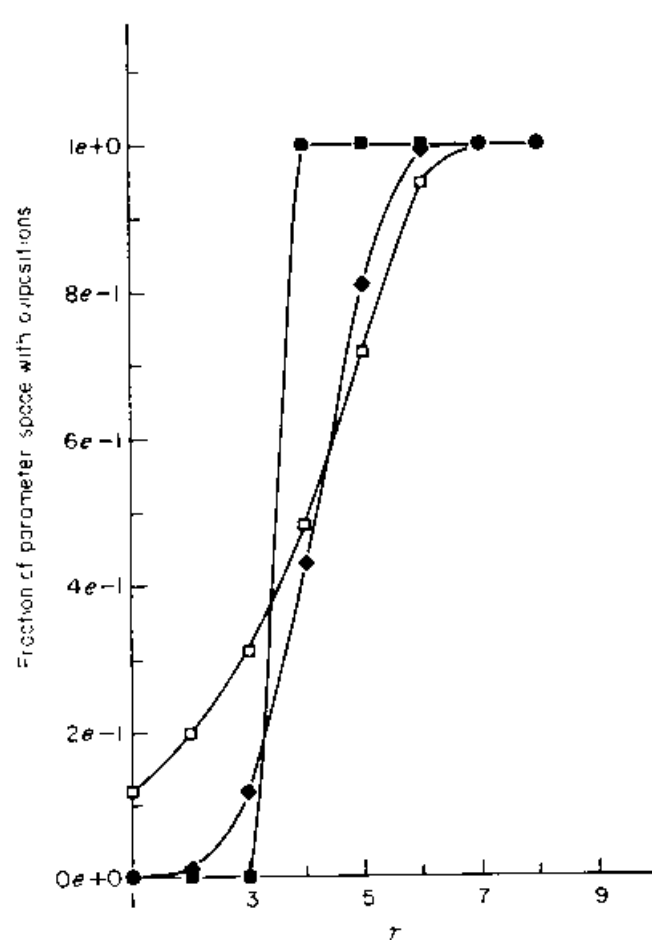


FIG. 1. The fraction of $\{\omega, \delta, \nu, \alpha\}$ -space, as a function of t for three values of the memory parameter γ , in which the optimal decision is to oviposit in a previously parasitized host. If $\gamma = 0$, then no learning occurs and the decision is to either always (i.e. for all parameter values) oviposit or to always reject. For values of $\gamma > 0$, the step function corresponding to $\gamma = 0$ is smoothed out by the updating of information. Parameters are: $T = 9$, $\mu = 0.005$, $\psi = 0.8$, $f_u = 1.0$, $f_p = 0.2$, $\omega_0 = 1$, $\delta_0 = 1$, $\nu_0 = 1$ and $\alpha_0 = 1$. (■), Corresponds to $\gamma = 0$ (no memory); (◆), to $\gamma = 0.5$ and (□), to $\gamma = 1$ (perfect memory).

$V(\omega, \delta, \nu, \alpha, T, T) = 0$ and $V(\omega, \delta, \nu, \alpha, t, T)$ satisfies the following dynamic iteration equation

$$\begin{aligned}
 V(\omega, \delta, \nu, \alpha, t, T) &= [1 - \lambda(t)](1 - \mu)V(\omega', \delta', \nu', \alpha', t+1, T) \\
 &\quad + \lambda(t)\rho(t)\{f_v + (1 - \mu)\psi V(\omega'', \delta'', \nu'', \alpha'', t+1, T)\} \\
 &\quad + \lambda(t)[1 - \rho(t)]\{[f_r + (1 - \mu)\psi V(\omega''', \delta''', \nu''', \alpha''', t+1, T)]d^*(\omega, \delta, \nu, \alpha, t) \\
 &\quad + (1 - \mu)V(\omega''', \delta''', \nu''', \alpha''', t+1, T)(1 - d^*(\omega, \delta, \nu, \alpha, t))\}, \quad (22)
 \end{aligned}$$

where the updated parameters are determined as described following (21). The value $V(\omega, \delta, \nu, \alpha, 1, T)$ gives the realized fitness of a certain set of decisions, and thus memory parameter.

By combining the decisions determined by (21) with the realized fitness value determined by (22), one can consider the evolutionary consequences of various values of the memory parameter γ . For example, $\lambda(t)$ could be fixed at 0.5 and $\rho(t)$ is periodic or $\rho(t)$ could be fixed at 0.5 and $\lambda(t)$ is periodic. Figure 2 shows a typical result. The general pattern exhibited by this figure was common in all of the

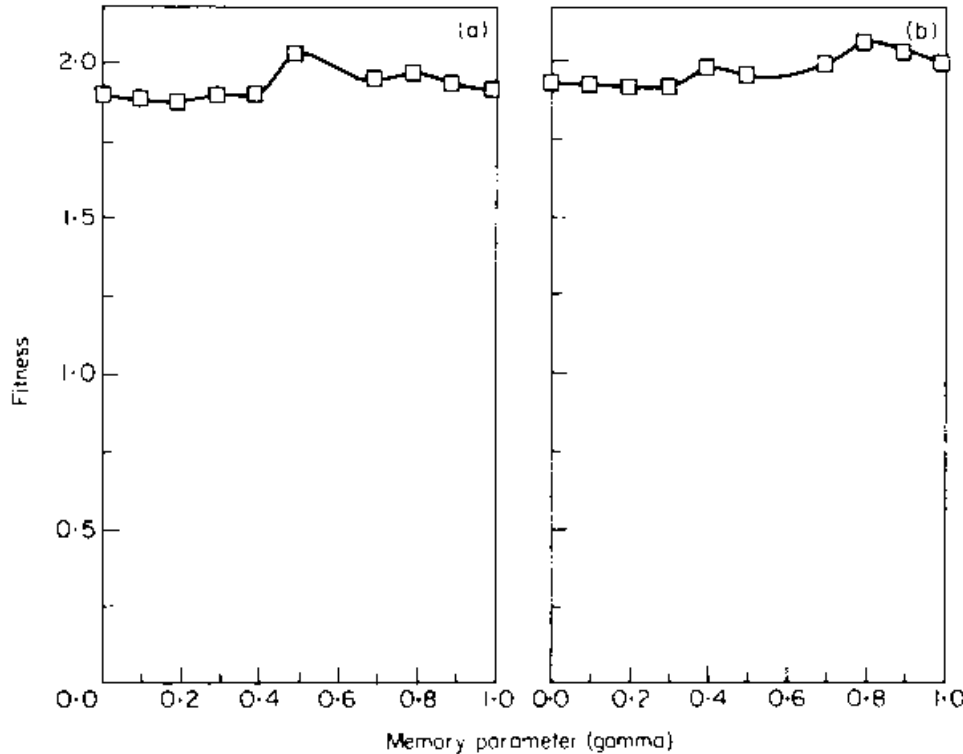


FIG. 2. The realized fitness $V(\omega, \delta, \nu, \alpha, 1, T)$ at $t=1$ as a function of the memory parameter γ for a fluctuating environment. (a) $\omega = \delta = \alpha = \nu = 5$, $\rho(t)$ fixed at 0.5 and $\lambda(t)$ periodic with period 2; (b) $\omega = \delta = \alpha = \nu = 7$, $\lambda(t)$ fixed at 0.5 and $\rho(t)$ periodic with period 2. In both cases, the long term environmental parameters are equal to 1.

computations for a wide variety of initial parameters: as a function of γ , the realized fitness was relatively flat, exhibiting a maximum variation of about 20%.

In addition, the maximum occurred at an internal value of the memory parameter γ , i.e. for a value of γ bounded away from both 0 and 1. These results suggest that evolutionary pressure on the memory parameter will be such that neither perfect memory nor total forgetfulness are selected.

6. Discussion

The ideas developed here suggest two principles of information handling: sample and forget the distant past. The application of such general principles in biology requires us to consider the way that information is used by the organism, and not abstract measures of "informational content". The examples in sections 4 and 5 show how such information can be used. The use of information should take into account not only the mean of the estimated parameter, but the uncertainty in this estimate. If gathering information is costly (in terms of time, energy or both), then the methods illustrated in sections 4 and 5 show how it is possible to determine how much information should be collected. A number of authors have examined the time course of memory of different organisms and have produced results that are consistent with the theory developed in this paper. Getty & Krebs (1985) studied the time course of memory of great tits searching for cryptic prey and modeled their experiments by the theory of signal detection. Plowright (1988) studied the behaviors of pigeons experiencing a two-armed bandit with changing arms and modeled her work by the theory of rate maximizing behavior. Brandes *et al.* (1988) studied the time course of memory of honey-bees and the nature of selection for learning and memory. Good learners and bad learners differ in the rate of accumulation of useful memory and the rate of forgetting. Shettleworth *et al.* (1988) and Tamm (1987) studied environmental tracking by pigeons and hummingbirds respectively. The theory developed by Stephens (1987) and its extensions was compared with experiments. In both cases, although there was qualitative agreement with the theory, the quantitative details deviated considerably from the optimality model. Tamm concluded that "none of four birds avoided the varying feeder when low mean amount and low predictability made it so unprofitable to the constant alternative that a rate maximizer should not have visited it at all" (abstract: 1725).

It is likely that the specific forgetting rule is itself subject to evolution, in the sense that an "optimal forgetting rule" may exist given the measure of fitness and a characteristic fluctuation frequency of the environment. If the environmental fluctuations are very rapid, then there is little use for memory and if they are very slow, then there is little use for forgetting. In cases for which the environment fluctuates on the same time scale as important events occur to the organism, memory and forgetting will be important. Although an "optimal forgetting rule" may exist, the optimum in fitness is likely to be broad (cf. Mangel & Clark, 1983). In such a case, it is not crucial to function at the optimum, but to follow the general procedure of sampling and forgetting. Similar conclusions have been drawn by McNamara & Houston (1985, 1987). An entirely different approach would be to simply assume

that organisms forage with the "wrong" parameter estimates and to then estimate the fitness costs of such errors, which can sometimes be remarkably small (Roitberg, personal communication; Bouskila & Blumstein, personal communication).

Even with an arbitrary weighting function $\gamma(i)$, the updating rules derived here will have the general form of a linear operator. Harley (1981) modeled the learning of the evolutionarily stable strategy (also see Houston, 1983; Harley, 1983) using linear operators. Kacelnik *et al.* (1987) showed how linear operators can be used in changing environments. The contribution of this paper is to show how the information, via the linear operator, can be incorporated directly into a fitness function. Ollason (1980) gives the germ of the idea that McNamara & Houston (1987), Stephens (1987) and I used. The difficulty with Ollason's work is the confounding of physiological and informational states and rules for behavior. It is simply too hard to use his formulation to understand the selection for behavior in uncertain and changing worlds. Finally, it should be noted that many authors write on "information in biological systems" meaning entropy or Shannon-Weaver information (e.g. Wagensberg *et al.*, 1988 provide a recent example). This approach tries to adapt physical science ideas directly to the biological framework, but it is not clear that Shannon-Weaver information is the correct representation of information for organisms. It is not the bit content of information, but what the organism does with the information, that is important.

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APPENDIX

The Likelihood Approach

In this Appendix, I show how the method of Maximum Likelihood Estimation (MLE) can be extended to include the memory parameter. Details and theory of the MLE can be found in Edwards (1972). The general mathematical theory underlying the methods developed here can be found in Barndorff-Nielsen (1980, 1983). To begin, reconsider the case of random encounters described in section 2. The support function is the logarithm of the likelihood (2). For the case of general $\gamma(i)$, the support function and its first two derivatives are

$$\begin{aligned}\mathcal{S} &= \sum [-\lambda \gamma(i) + n_i \gamma(i) \log(\lambda)] + o.1 \\ \mathcal{S}_\lambda &= \sum [-\gamma(i) + n_i \gamma(i) / \lambda] \\ \mathcal{S}_{\lambda\lambda} &= -\sum [n_i \gamma(i) / \lambda^2].\end{aligned}\tag{A.1}$$

The curvature of the support function plays a crucial role in determining the uncertainty associated with the value of the parameter λ that maximizes the likelihood (or log-likelihood); see Edwards (1972) for further details.

From eqn (A.1), the Maximum Likelihood Estimate (MLE) for λ , denoted by $\hat{\lambda}(s)$, is

$$\hat{\lambda}(s) = \sum n_i \gamma(i) / \sum \gamma(i). \quad (\text{A.2})$$

For the particular case of exponential weighting, the MLE is

$$\hat{\lambda}(s) = \sum n_i \gamma^i / \sum \gamma^i = \{ \sum n_i \gamma^i \} (1 - \gamma / 1 - \gamma^{s+1}), \quad (\text{A.3})$$

and the curvature of the support function evaluated at the MLE is given by

$$\mathcal{F}_{\lambda\lambda} \hat{\lambda} = (1 - \gamma^{s+1} / 1 - \gamma) [1 / \hat{\lambda}(s)]. \quad (\text{A.4})$$

Equations (A.3) and (A.4) summarize the current information (the MLE) and the uncertainty about the current information (the curvature of the support function evaluated at the MLE). Additional information is incorporated by an updating rule. That is, suppose that the number of encounters in period $s+1$, $n_{s+1} = n$. Using eqn (A.3) shows that

$$\hat{\lambda}(s+1) = (1 - \gamma)n / (1 - \gamma^{s+2}) + \gamma \hat{\lambda}(s) (1 - \gamma^{s+1}) / (1 - \gamma^{s+2}). \quad (\text{A.5})$$

When s is large, eqn (A.5) is approximately $\hat{\lambda}(s+1) = (1 - \gamma)n + \gamma \hat{\lambda}(s)$. Similar procedures were applied to derive the results shown in Table 1.

These results show how to obtain parameter estimates and measures of uncertainty of those estimates (the curvature of the support function). The Bayesian methods give, as part of the computation, an entire probability distribution that can be used in the equations for fitness. The maximum likelihood methods provide an estimate of the parameter and a curvature that can be used to assess the likelihood of other parameter values other than the MLE. For the Poisson case, the curvature goes as $1/\hat{\lambda}$. For the binomial case the curvature goes as $1/\hat{p}(1 - \hat{p})$. For the negative binomial case, the curvature goes as $1/\hat{m}(k + \hat{m})$. For all three, as the MLE approaches 0, the uncertainty in the MLE—measured by the curvature—increases. In addition, the same increase in uncertainty occurs for the binomial case when the MLE approaches 1. From the curvature, one can obtain approximate distributions for the MLE. For example, based on the theory for the normal distribution (Edwards, 1972) we could assume that the true parameter θ is normally distributed with mean given by the MLE $\hat{\theta}$ and variance $1/|\mathcal{F}_{\theta\theta}|$, where the curvature is evaluated at the MLE. The two main limitations of this approach are (i) for high levels of uncertainty infeasible values of the parameter may have considerable probability and (ii) the normal distribution is symmetrical about the mean, whereas the underlying probability model (Poisson, binomial or negative binomial) need not be. These deficiencies can be corrected, to some extent, by truncating the distribution for feasible parameter values.

An alternative is to use the likelihood as if it were an unnormalized probability density (this is essentially a Bayesian approach in which the uniform prior density $f_0 = 1$ is chosen). In this approach, the posterior density is proportional to the likelihood, so that in terms of the support function we have

$$f_p(\theta) = \exp \{ \mathcal{F}(\theta | \hat{\theta}) \} / \int \exp \{ \mathcal{F}(\theta | \hat{\theta}) \} d\theta. \quad (\text{A.6})$$

Here $\mathcal{S}(\theta|\hat{\theta})$ is the support function for the true parameter θ given the MLE (which summarizes the data). It is constructed by substituting the MLE for the data in the original support functions. We can rewrite eqn (A.6) as $f_p(\theta) = k \exp \{\mathcal{S}(\theta|\hat{\theta})\}$ where k is a normalization constant. A fourth order Taylor expansion of the term $\exp \{\mathcal{S}(\theta|\hat{\theta})\}$ about the MLE value gives

$$f_p(\theta) = k \exp \{\mathcal{S}(\hat{\theta}|\hat{\theta})\} [1 + (1/2)(\theta - \hat{\theta})^2 \mathcal{S}_{\theta\theta} + (1/6)(\theta - \hat{\theta})^3 \mathcal{S}_{\theta\theta\theta} + (1/24)(\theta - \hat{\theta})^4 \mathcal{S}_{\theta\theta\theta\theta}]. \quad (\text{A.7})$$

Here all of the derivatives of the support function are evaluated at the MLE value and the normalization constant k is chosen so that $f_p(\theta)$ in (A.7) integrates to 1.