Searching and Learning in a Random Environment

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Area concentrated search provides a means by which foragers may exploit heterogeneities in a resource following a simple rule of thumb which reacts to encounters with that resource by changing search speeds. A model with few parameters is presented. It permits an analysis of optimal searching rules in a random environment. We show that optimal search involves a set of conditional rules that reflect the "patchiness" of resource distribution. The optimal area concentrated search strategy is not only a matter of slowing down when encountering a resource, but may involve speeding up when encounering the resource in more uniform environments. The manner in which foragers accumulate information about a resource during searching is analysed as a trade-off between "identification" and "control", or exploration and exploitation. The value of a period of identification, i.e. a period of learning, is analysed in a fluctuating environment in which the state of the environment is sampled from a given distribution following each new foraging bout. The value of learning during searching relates to stochasticity within a bout and variation between bouts. The value of information about the environment within a given foraging bout, and hence the likely value of learning, is analysed by comparing optimal strategies with optimal generalist strategies. Information becomes increasingly valuable as resource distributions becomes more patchy. Foragers adopting conditional searching rules may manifest type three functional responses (sigmoidal functional response) through an apostatic (positive density dependent) effect. The significance of this response, and learning behaviour on population stability, is briefly discussed.

Introduction

The development of optimal foraging theory was prompted by observations showing that resources are often not uniformly distributed in the environment (MacArthur & Pianka, 1966). The theory stressed, on the one hand, the particulate nature of the prey and, on the other, the more or less diffuse assemblages of prey that could constitute, or occur on, patches. The tradition in optimal foraging theory (OFT) has consequently been bicameral, with models of prey handling (Schoener, 1971; Charnov & Orians, 1973) being developed independently of models of patch use (Charnov, 1976). Several authors have pointed out that the prey and patch are rarely distinct (Bond, 1980), and that the presence of prey is often the exclusive indicator of the start of a patch (Kruuk & Sands, 1972; Ayal, 1987). The common indivisibility of prey and patch has prompted the analysis of so-called area concentrated search (ACS) behaviour in which a predator is able to respond to variations in prey distributions by varying its searching efforts: following an encounter with resource, a forager searches intensively in a more circumscribed region, while a failure to encounter a resource leads to a more extensive, less circumspect mode of search (Schoener, 1971; Smith, 1973; Pyke, 1978; Carter & Dixon, 1982). ACS in a continuous patchy environment thereby ensures that foraging behaviour will, to some extent, match the distribution of resource, and may be viewed as a simple form of habitat selection (Wiens, 1976).

ACS behaviour has not, however, become a central component of foraging theory, a fact given away by its scant treatment in Stephens & Krebs's definitive text in this area (Stephens & Krebs, 1986). There are a number of factors that might have contributed to this neglect. Spatial behaviour is

difficult to quantify, hence area concentrated search models are predominantly qualitative (Stillman & Sutherland, 1990; Benhamou, 1992) and consequently hard to test. Learning and memory often guide an animal's subsequent foraging behaviour (Hoffman, 1983; Fourcassie & Tranielle, 1993; Noda *et al.*, 1994), while most ACS models assume that the state of the environment is already known (but see Benhamou, 1994). Foragers are often able to perceive the presence of distant prey items by means of visual scanning and therefore need not rely exclusively on current encounters to dictate foraging efforts (Evans & O'Brien, 1986; Getty & Pulliam, 1993). ACS models are often simulations involving many parameters and consequently provide few simple insights and predictions into foraging or searching behaviour.

In this paper we present a model that involves a small number of parameters and which is investigated using a combination of analytical and computational techniques. We use the model to elucidate the decision rules employed by foragers attempting to maximize their expected energetic intake rate in a simple random environment. We examine:

(1) How a continuous range of resource distributions maps onto a discrete set of foraging strategies, or foraging "rules of thumb", and whether stochasticity in the resource will be matched by stochasticity in the foraging rule.

(2) How tracking errors experienced during searching can provide insights into foraging strategies by highlighting the costs of particular searching rules in different resource distributions.

(3) The resource-dependent choice of a searching rule in "patchy" vs. "uniform" environments, i.e. the degree of sensitivity of searching rules to resource variability.

(4) The impact of fluctuating environments on searching behaviour. How a learning rule that accumulates information about the resource during searching can improve future searching efforts, and how learning can compromise current foraging efficiency: this is explored as a trade-off between identification and control.

(5) The value of information when foraging using an ACS mechanism, i.e. the increase in gains caused by adopting the optimal strategy over a fixed generalist strategy.

The value of information is examined in environments differing in heterogeneity.

(6) How the functional response of an area concentrated searcher reflects underlying searching rules. The question of whether learning could cause populations to become more stable is also examined.

An Area Concentrated Search Model

In this model the distribution of prey is represented as items of resource distributed at discrete points along the length of a straight line (for a similar treatment see Knoppien & Reddingius, 1985). Area concentrated searching thus becomes a function of switching between fast and slow search speeds with low and high encounter probabilities. ACS assumes that regions dense with resource should be explored slowly, to maximize the chances of encounter, and less dense regions explored rapidly, to minimize the time spent searching in unprofitable areas (Gendron & Staddon, 1983; see Fig. 1).

THE DISTRIBUTION OF RESOURCE

The environment is modelled as a chain in which links are specified by an index n. The state of the nth link is described by the variable ϵ_n, which can take two possible values. The presence of a single prey in the link is denoted by $\epsilon_n = 1$, and the absence of prey by $\epsilon_n = 0$. There is never more than one prey in the same link. The distribution of the prey is determined by a Markov chain with the state transition matrix $\mathbf{P}$, in which each row element p_{ij} is the conditional probability that $\epsilon_{n+1} = 1 - j$ given that $\epsilon_n = 1 - i$ $(i, j = 0, 1)$. When the value of elements in the leading diagonal of $\mathbf{P}$ is high, "patches" of resource abundance will be interrupted by stretches of resource scarcity. By modifying the elements of $\mathbf{P}$ we are able to construct regions dense with prey "patches" that
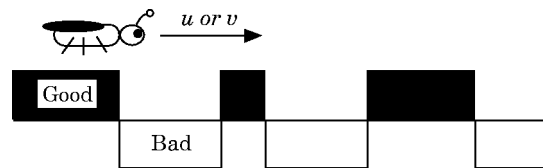

FIG. 1. The forager searches the environment for prey items that occur in links. The prey are distributed according to a Markov process. The forager is able to explore at two speeds: u which is slow and has a high encounter probability, and v which is fast, covers a larger area and has a low encounter probability. Searching strategies are rules for switching between search speeds conditional upon success and failure at encountering prey. An optimal searching policy is a set of optimal search strategies for a range of resource distributions (states of the environment).

alternate with regions poor in resource, of different average lengths.

THE BEHAVIOUR OF THE FORAGER

The forager can be in one of two searching states (or speeds), u or v, corresponding to intensive and extensive search (slow and fast speed), respectively. The encounter probabilities associated with these states are $p_u = prob$(encounter at $u|\epsilon_n = 1$) and $p_v = prob$(encounter at $v|\epsilon_n = 1$). These are state-dependent encounter probabilities and follow Gendron & Staddon's model (1983) in which a reduction in searching speed increases the probability of encounter and reduces the time available to search. The encounter probabilities at each speed are given by

$$p_u = 1 - \frac{u}{MaxSpeed}, \quad (1)$$

$$p_v = 1 - \frac{v}{MaxSpeed}, \quad (2)$$

and the times taken to search each link in each state are given by t_u and t_v respectively. Throughout we assume that $p_u > p_v$, $t_u > t_v$, and $p_u/t_u = p_v/t_v$ which equates the expected intake rate at each search speed on a perfectly homogeneous resource (i.e., all links of the chain are good).

The behaviour of the forager is modelled as a continuous time, discrete state Markov chain with two state transition matrices **S** and **F**. These matrices govern the transitions between the two states (u and v) following either a successful encounter or a failure to encounter prey. We can write down the elements of these matrices as

$s_{ij} = \{$probability of switching to state j|

successful encounter in state i$\}$ (3)

$f_{ij} = \{$probability of switching to state j|

failure to encounter in state i$\}$ (4)

For convenience we abbreviate the elements of the three transition matrices, with one matrix for the environment and two for the forager,

$$\mathbf{P} = \begin{bmatrix} p_1 & 1-p_2 \\ 1-p_1 & p_2 \end{bmatrix}, \quad \mathbf{S} = \begin{bmatrix} s_1 & 1-s_2 \\ 1-s_1 & s_2 \end{bmatrix},$$

$$\mathbf{F} = \begin{bmatrix} f_1 & 1-f_2 \\ 1-f_1 & f_2 \end{bmatrix},$$

and we denote a forager's optimal searching strategy as $\pi(s_1, s_2, f_1, f_2)$.

THE OPTIMALITY CRITERION

We assume that the forager inhabits an environment in which the resource distribution **P** is invariant through time (homogeneous Markov chain). We seek to find the elements of the **S** and **F** matrices that will maximize the expected long term intake rate of the forager γ, searching in this environment with a conditional rule,

$$\gamma = \lim_{t \to \infty} \frac{\text{total number of successful encounters}}{(\text{proportion of time in } u)t_u + (\text{proportion of time in } v)t_v}. \quad (5)$$

We leave the derivation of this equation to Appendix A. Note that eqn (5) describes a rate in which the total number of prey successfully encountered (in units of energy) is divided by the total time spent searching in each of the two searching speeds.

The Optimal Searching Policy

THE DISTRIBUTION OF RESOURCE

Figure 2 illustrates the optimal searching rules corresponding to a range of values for the distribution matrix **P**. The parameters p_1 and p_2 vary continuously between 0 and 1. There is a switching boundary along the line $p_1 = 1 - p_2$. This boundary defines a threshold above and below which an optimal forager switches between two different search strategies.
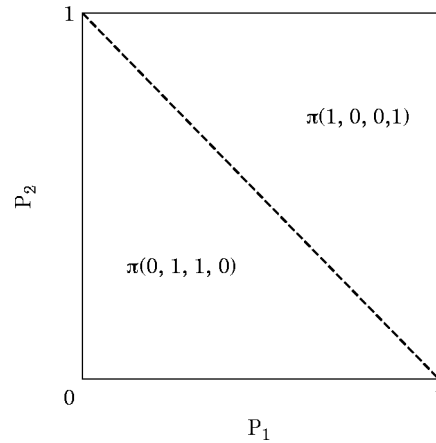

FIG. 2. Optimal foraging strategies in a random environment. The parameters p_1 and p_2 determine the patchiness of the resource distribution. There is a switching threshold at $p_1 = 1 - p_2$. The search strategies are deterministic. Below the threshold, extensive search is favoured when successful and intensive search when unsuccessful: "win–fast, fail–slow". Above the threshold, intensive search is favoured when successful and extensive search when unsuccessful: "win–slow, fail–fast". The optimal foraging policy is the set of two optimal strategies.

Below the boundary the environment is prone to switch between good and bad after each link of the chain ("uniform"), when above the boundary one link is a good predictor of the occupancy of the following link of the chain ("patchy").

THE BEHAVIOUR OF THE FORAGER

A deterministic strategy implies that a switch between states occurs with a probability of one or zero. The stochastic nature of the resource distribution is not reflected in a stochastic decision rule. When $p_1 > 1 - p_2$ the optimal strategy is given by $\pi(1,0,0,1)$, which implies that following a success the forager will search in intensive mode, and following a failure will search in extensive mode ("win–fast:fail–slow"). When $p_1 < 1 - p_2$, the optimal strategy is given by $\pi(0,1,1,0)$ hence following a success the forager searches in extensive mode and following a failure searches in intensive mode ("win–slow:fail–fast"). When adopting the optimal strategy, the behaviour of the forager is only conditional upon having been successful or unsuccessful at capturing a prey in the previous site, it is not dependent upon the state in which the site was searched.

Tracking Errors in Area Concentrated Search

Stephens (1982) has argued that foragers must balance the costs of sampling too often (sampling errors) against the opportunity costs of sampling too seldomly (overrun errors). These errors are collectively referred to as tracking errors. An optimal forager adopting an ACS strategy commits overrun errors by searching extensively when the environment is good, and commits sampling errors when searching intensively when the environment is bad. In order to examine these errors we must construct four new "composite states" that represent each searching speed in a good or bad link. In mathematical terms we need to find the stationary probabilities associated with intensive and extensive search when a link is occupied or vacant (see Appendix B). These new states are denoted as u^+, u^-, v^+, v^- (not to be confused with u_+, u_-, v_+, v_- in Appendix A). Sampling errors encountered when adopting a strategy $\pi(s_1, s_2, f_1, f_2)$ are given by the mean of u^-, and overrun errors are given by the mean of $v^+(1-p_v)$. Figures 3(a–d) are plots of sampling and overrun errors over a range of values of p_1 and p_2. Increasing p_1 when adopting the strategy $\pi(0,1,1,0)$ leads to an increase in overrun errors [Fig. 3(a)], and a slight reduction in sampling errors [Fig. 3(b)]. Increasing p_2, increases the magnitude of sampling errors at all values of p_1 but does not influence the overrun errors. Increasing p_1
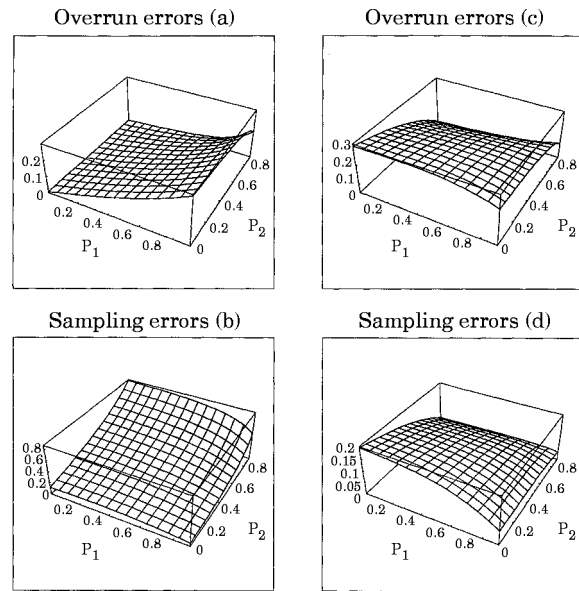

FIG. 3. Tracking errors in area concentrated search with different values of the resource distribution **P**. (a) Overrun errors when adopting the win–fast:fail–slow strategy. (b) Sampling errors when adopting the win–fast:fail–slow strategy. (c) Overrun errors when adopting the win–slow:fail–fast strategy. (d) Sampling errors when adopting the win–slow:fail–fast strategy.

when adopting the strategy $\pi(1,0,0,1)$ leads to a slight decrease in overrun errors [Fig. 3(c)], and a large reduction in sampling errors [Fig. 3(b)]. In the latter case, increasing p_2 decreases the magnitude of errors at all p_1.

Errors are experienced even when the optimal strategy has been adopted. The win–fast:fail–slow strategy consistently experiences greater overrun errors than the win–slow:fail–fast strategy because, following a failure, win–fast:fail–slow will search extensively, and is consequently likely to miss an occupied link, while win–slow:fail–fast is likely to detect the next link because it searches intensively in bad areas and is prepared for an encounter. Win–slow:fail–fast experiences greater sampling errors than win–fast:fail–slow from sampling too often in bad links. The threshold for switching between intensive and extensive search when following a conditional search policy—in which a policy is made up of both win–slow:fail–fast and win–fast:fail–slow strategies—can be thought of as a trade-off between these two types of tracking errors.

Learning During Area Concentrated Search

Thus far it has been assumed that the forager "knew" the parameters that determined the distribution of a resource in its environment. In other words, we sought to find the optimal switching rule

for fixed values of the resource process **P**, assuming the forager had perfect information about the environment. In this section we drop the assumption of perfect information. Foragers are now required to learn about the environment. We assume that foragers are not required to learn a strategy during search, but are required to learn about the prey distribution, and utilize this information in deciding which strategy to employ. This is equivalent to assuming that evolution has established the strategy set, and learning is required to activate an appropriate strategy. We explore a learning rule whereby information is acquired during the process of area concentrated searching. By adopting a Bayesian learning rule (McNamara & Houston, 1980) the forager is able to update incrementally its current assessment of the environment after each link of the resource is sampled.

BAYESIAN PROBABILITIES

The forager's current estimate of the llikelihood of some given values for **P** is summarized by a prior probability distribution. Following an encounter with a resource, or a failure to encounter a resource, Bayes's theorem provides one way in which a forager's prior assessment of the resource distribution can be updated to form a posterior distribution which provides a more accurate representation of the state of the environment (see Appendix C for the rules for updating this distribution). The fundamental problem faced by a learning forager lies in choosing between identification and control. The forager must decide between sampling the environment in order to improve its current estimate of the resource distribution (identification) or adopt a strategy conforming to its current best estimate of the resource distribution (control). During ACS, the cost of identification is related principally to sampling errors experienced during intensive searching, because intensive search provides the most reliable information about the distribution of resource when failing. The dilemma is, therefore, whether a forager should perform a period of intensive search prior to adopting a full conditional strategy based on its current estimate of **P**, or accumulate information during the course of searching based on its current estimate of **P**.

Figure 4 shows the results of a simulation in which the resource distribution was fixed at a point where $p_1 + p_2 < 1$, and in which the forager was required to estimate the value of this sum while exploring the environment starting with a prior estimate $p_1 + p_2 = 1$. The forager pursues an identification strategy (unconditional intensive search) for 100 iterations,
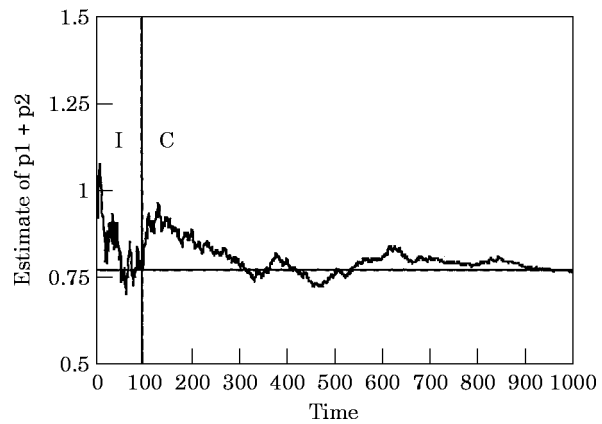

FIG. 4. Bayesian learner's estimated parameter values of resource distribution p. Points on the curve are estimates of the parameters p_1 and p_2 at time t when following either an identification or control strategy. The switching threshold between optimal strategies lies at 1. The true value of p_1 and p_2 is shown with a horizontal line ($= 0.76$). To the left of the vertical line the forager pursues an identification (I) policy and to the right a control (C) policy (see section 5 for full details).

followed by a switch to the control strategy consistent with its current estimate of **P**. Figure 4 illustrates how an early identification phase can allow
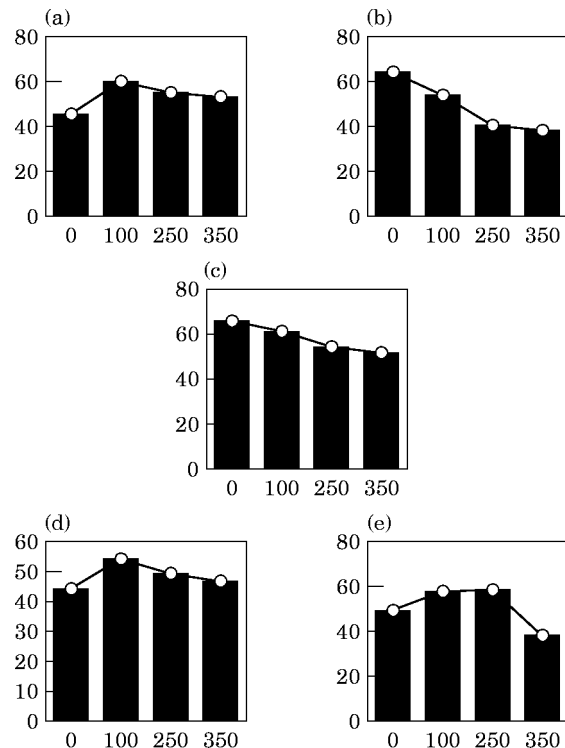

FIG. 5. Identification profiles. Mean, net intake of forager employing periods of identification varying from 0–350 time steps (a) Uniform distribution of resource, mean $= 1$, skew $= 0$. (b) Gaussian distribution of resource, mean $= 1$, skew $= 0$. (c) Gaussian distribution of resource, mean $= 1.2$, skew $= 0.4$. (d) Gaussian distribution of resource, mean $= 1.4$, skew $= 0.8$. Total bout length 1000.

a forager to converge rapidly on the true values of **P**, and also shows that a control strategy can cause the estimate to depart from its true value. By 1000 iterations the forager has converged on the true state of the environment.

WHEN IS A PERIOD OF IDENTIFICATION OPTIMAL?

In order for an identification phase to be adaptive, the total gain during a foraging bout—starting at time $t = 0$ and terminating at a final time T ($T = 1000$ in the simulation)—must be greater when it involves a pure identification phase followed by a control phase, than when employing control exclusively. We assume that a forager enters the environment with a prior estimate of **P** that is equal to the mean of the distribution from which the elements of **P** are drawn. We then investigate how the character of this distribution will influence the choice of identification strategies by running a number of simulations.

We examine four cases in which p_1 and p_2 are sampled from one of four Gaussian type distributions with different amounts of skew, and from one uniform distribution. In each case the elements of **P** are randomly sampled from a joint density function $\zeta(p_1, p_2)$ with mean μ and standard deviation σ. We assume that the prior is also given by $\zeta(p_1, p_2)$. For each of the five distributions, 50 random samples of p_1 and p_2 are taken. The environment is thus made to fluctuate between searching bouts. For each sample (one bout) the forager is made to search the environment employing an unconditional intensive search (identification) for a fixed duration, followed by the optimal conditional search strategies (control) for the remaining time. The conditional search strategy deployed depends on the foragers current estimate of p_1 and p_2 at time t. Setting a total foraging bout to T ($T = 1000$) iterations, we vary the length of the identification duration and calculate the net intake over T. In this way for each distribution, we obtain 50 different foraging bouts randomly sampled from the same distribution from which to calculate the mean intake for different identification times.

Figure 5 illustrates the results of the simulations with the five different distributions. We shall refer to these plots as identification profiles. The identification profiles summarize the net intake of a forager that allots 0, 100, 250, or 350 time steps to an identification phase in a bout of 1000 time steps. When the distribution of resource is uniform [Fig. 5(a)], the prior estimates of p_1 and p_2 lie on the switching threshold. An identification phase that lasts 100 iterations, followed by 900 iterations of control, produces the maximum net intake over the foraging bout. The identification profile therefore suggests that

a short period of identification is optimal and that no period of identification is worst of all. When the distribution is Gaussian [Fig. 5(b–e)], the optimal time spent in identification is an increasing function of the skewedness of the distribution. Hence low skewedness favours a pure control policy [Fig. 5(b)], while a high skewedness [Fig. 5(e)] favours an identification phase lasting 250 iterations (one quarter of the total time).

The Value of Information in Area Concentrated Search

Learning provides foragers with a mechanism for tracking changes in environmental parameters, but may involve costs (Williams, 1966) that offset this advantage. Hence evolution may, in some cases, favour fixed generalist strategies. In section five we demonstrated the advantage of a "learning" period when used in conjunction with a control policy. We did not however demonstrate the absolute value of the optimal strategy in comparison with a fixed generalist strategy. The value of possessing information about the true state of the environment, and hence the value of learning, should be compared with the value of a fixed behaviour that yields the best mean intake rate in a number of different environments (Gould, 1974; Stephens, 1989). This is because unless information has a high value, the costs of learning (not treated in this paper) might offset any advantages. Information leading to the optimal choice of strategy, may vary in its value according to the distribution of resource. Gould's and Stephens's approach can be applied to ACS.

The environment can be in one of two states, S_1 (corresponding to $p_1 + p_2 < 1$) And S_2 (corresponding to $p_1 + p_2 > 1$). The forager's prior knowledge of the state of the environment is given by q_1 and q_2, with $q_i = \text{Prob}(S_i)$. The forager forms an estimate of the environment which is denoted e (note that e is a discrete estimate, for example S_1 or S_2), such that the payoff to the forager in environment S_i is given by $G(e|S_i)$. This latter function is the instantaneous rate of gain g when adopting a strategy π based on the current estimate of e. The optimal strategy in environment S_i is given by,

$$G(e_i^*|S_i) = \max_e G(e|S_i), \qquad (6)$$

and the best strategy "on average" is given by,

$$\sum_{i=1,2} q_i G(e'|S_i) = \max_e \sum_{i=1,2} q_i G(e|S_i). \qquad (7)$$
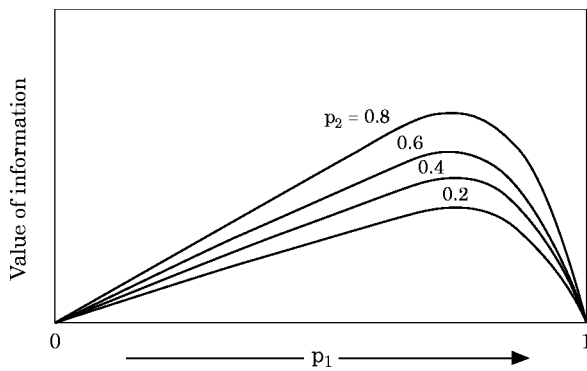
FIG. 6. The value of information in area concentrated search. Each curve represents the difference in expected long term intake rate between a forager adopting the optimal searching policy and a forager adopting the best fixed generalist strategy. As the resource distribution becomes more patchy, the value of information about the true state of the environment increases.

The formula Gould derived to demonstrate the value of information can be used to demonstrate the value of learning for ACS. The value of learning is given by,

$$v = \sum_{i=1,2} q_i G(e_i^*|S_i) - \sum_{i=1,2} q_i G(e'|S_i). \qquad (8)$$

We may interpret this expression as the value of information about the true state of the environment for a forager, with prior knowledge e' and searching in an environment S_i, adopting a generalist strategy. The best generalist strategy may be found using eqn (7). Here we seek to maximize the sum of eqn (7) over p_1 and p_2. Hence we find,

$$\max_{s_1, s_2, f_1, f_2} \sum_{p_1, p_2} \gamma(q_1, q_2, q_3, q_4, t_u, t_v) \qquad (9)$$

in terms of a single strategy $\pi(s_1, s_2, f_1, f_2)$. This strategy is found by numerically maximizing eqn (9) at 50 values of p_1 and p_2. Using this approximate method the best generalist strategy is given by $\pi(0, 1, 1, 0)$. In other words this strategy is a win–fast:fail–slow strategy, which is an optimum strategy when $p_1 < 1 - p_2$. The best generalist strategy is therefore also a conditional strategy, and one taken from the existing strategy set.

Figure 6 illustrates a family of curves showing the value of information about the true state of the environment at different values of **P**. There is a maximum value for information when contiguous links are likely to have the same state, i.e. as the resource becomes more patchy ($p_1, p_2 \gg 0$). Infor-

mation is least valuable in cases in which the environment possesses a low density of resource ($p_1, p_2 \approx 0$), or in cases in which resource is available continuously ($p_1 \approx 1$; uniform distribution).

The Functional Response in Area Concentrated Search

The functional response (Holling, 1959) relates the intake rate of a predator to the density of the resource/prey. Perhaps the most common functional response curve is Holling's type two in which intake rate increases with prey density, but at a decelerating rate. This form is commonly accounted for by assuming that intake rate increases in concert with prey density, and that the time spent handling prey becomes increasingly limiting at higher densities. We can plot a functional response curve for the optimal area concentrated searcher by calculating the density of resource for a given **P**, and calculating the forager's intake rate using eqn (5). The functional response for a searching forager is plotted in Fig. 7. This curve is a type three (sigmoidal) functional response. This form is a consequence of an increase in the forager's searching success as resource density increases, followed by an asymptotic phase as handling time becomes limiting. The accelerating phase is a result of an apostatic effect (Endler, 1991)—similar to that found under the optimal search rate hypothesis of Gendron & Staddon (1983)—in which a predator chooses to spend more time searching in high density
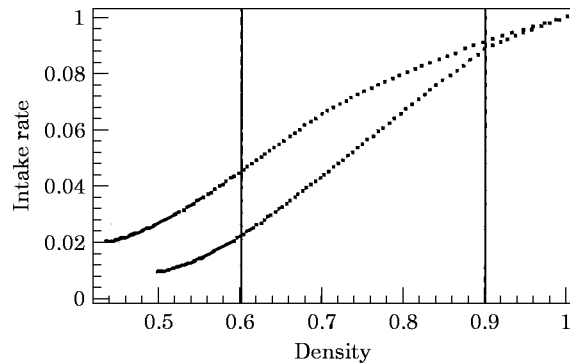

FIG. 7. Functional responses of an area concentrated searcher (type three). Each point on the curve represents the mean long interkerate for a given density of a resource. The two curves differ in the values of p_2 employed in the simulation. The upper curve was calculated with $p_2 = 0.4$ and the lower curve with $p_2 = 0.1$. The vertical lines denote switching thresholds for optimal searching policies in which $p_2 = 0.4$ (left) and $p_2 = 0.1$ (right). In this graph, the value of p_1 ranges from 0–1. Density is equal to

$$\frac{1 - p_2}{2 - p_1 - p_2}, p_u = 0.8, \ p_v = 0.4, \ t_u = 8, t_v = 4.$$

areas than in alternative areas with lower rates of encounter.

Discussion

ACS strategies provide simple rules of thumb for exploiting heterogeneous distributions of resource. Many foragers are likely to adopt ACS strategies rather than random search or complex patch leaving strategies (Charnov, 1976; Iwasa *et al*., 1981), because a resource may remain distributed in clusters, while patches *per se*, will not always exist (Bond, 1980). When discrete patches do exist, foragers may still be unable to perceive them (Wiens, 1976). We have sought to examine searching rules using ACS models. ACS models apply to cases in which a resource is randomly distributed but not restricted to discrete patches. A simple stochastic model with few parameters allows us to identify a number of important principles operating in searching behaviour, and to analyse the role of learning during search in fluctuating environments. The results of the model are summarized below:

(1) A random distribution of resource results in a simple, deterministic rule of thumb for exploring the environment. This rule is a conditional one that responds to the presence or absence of resource by changing searching speeds.

(2) The optimal searching rule is resource dependent, a feature which allows a simple representation of the resource distribution to be formed. ACS is often thought of as a uniquely win–slow:fail–fast strategy. Optimal ACS takes account of the patchiness of resource and consequently can include a win–fast: fail–slow strategy.

(3) Optimal searchers are not immune from making errors, and optimal searching strategies can be viewed as attempts to minimize searching errors. The type of errors experienced will depend on the patchiness of the resource.

(4) Foragers are likely to require information about the distribution of the resource, and hence must learn during searching. The need to learn will conflict with a forager's need to exploit the resource (identification vs. control), and consequently observed behaviours should reflect this trade-off, with a period of time dedicated to searching strategies that enhance learning.

(5) The time spent acquiring information, and hence foregoing immediate exploitation, reflects the extent to which the resource distribution fluctuates between foraging bouts. The greater the discrepancy between prior expectations, and the

possible states of the environment, the more valuable information becomes.

(6) The absolute value of information about the true state of the environment (employing the optimal strategy), depends on the nature of the resource distribution. As the resource distribution becomes more patchy, information becomes more profitable. Identification is therefore profitable in patchy environments.

(7) Individual searching strategies will be reflected in the functional response. A resource dependent searching strategy is able to produce a type three (sigmoidal) functional response. Proportionately more time is spent searching in high density areas than in low density areas (an apostatic effect), causing an acceleration in intake rate as resource density increases, followed by a deceleration in intake rate as search time becomes limiting.

Deterministic searching rules provide a parsimonious solution to environmental stochasticity. In highly irregular environments, from which information can not be consistently extracted, simple, deterministic policies can be as effective as behaviourally complex responses requiring memory coupled with imperfect information. In the economics literature, Heiner (1988) has argued that stereotyped behaviour is a natural response of an agent with limited information:

> "agents with bounded rationality ... must be limited by processes that systematically restrict behaviour away from selecting action that optimising agents would choose. Behaviour restricted in this fashion is said to be ... rule-governed behaviour".

During ACS, heterogeneities in resource distributions are exploited by conditionally intensifying search when occupying good areas of resource. Thus a simple searching strategy produces adaptive responses without the need for a memory of many previous encounters, or for a perception of patch boundaries. Simple as ACS rules might be, they are not simply a matter of searching intensively when encountering a resource, and extensively when failing to encounter the resource (win–slow:fail–fast). Searching rules can demonstrate a simple resource dependence, which in environments that regularly alternate between good and bad links, favour a win–fast:fail–slow strategy. ACS only involves, therefore, a switch to intensive search in cases where the chance of neighbouring links being occupied is high.

Searching rules can be assessed in terms of the tracking errors that are made by sampling too often

in poor areas (sampling errors) or too seldomly in good areas (overrun errors) (Stephens, 1982). When adopting a win–fast:fail–slow strategy, overrun errors are not influenced by stretches of bad links, but only by stretches of good links [Fig. 3(a)], while the reverse is true for sampling errors [Fig. 3(b)]. This is because as the number of contiguous good links increase, the probability of missing a good link while searching fast increases. Sampling errors are unaffected when searching fast over good links and increase when searching slowly over bad links. When adopting a win–slow:fail–fast strategy, stretches of bad links influence both the overrun errors and sampling errors [Figs 3(c–d)]: both types of error are reduced as the resource becomes more patchy ($p_1 \rightarrow 1$, $p_2 \rightarrow 1$). The optimal choice of searching strategy reflects the incidence of errors, and search strategies can be interpreted as mechanisms which minimize searching errors. If one restricts the analysis of foraging exclusively to rates of gain, one may fail to recognize that the immediate cause of a behaviour is the avoidance of error.

There are many examples of rule-based concentrated searching in the foraging literature. Waterbugs increase the frequency and duration of active foraging bouts when failing to encounter prey (Cloarec, 1990), thus demonstrating a preference for extensive search upon failure to encounter resource. The solitary centipede, *Scolopendra polymorpha*, employs active search at low densities of resource, and ambush predation at higher densities (Formanowicz & Bradley, 1987). Coccinelid larvae predate patchy distributions of aphid populations. Thus, following an encounter with an aphid, a ladybird larva employs intensive search, increasing the probability of future encounters (Ferran & Dixon, 1993). In each of these cases, the forager adopts the canonical win–slow:fail–fast strategy. As suggested above, this strategy constitutes an optimal response in highly patchy resource distributions, but not in all patchy distributions. We would encourage experimentalists to analyse cases in which the alternative strategy, win–fast:fail–slow is optimal. These are cases in which the patchy distribution is not sufficient to overcome the high incidence of errors associated with a win–slow:fail–fast strategy. This error arises because when good links have a limited extent, successful encounters are likely to be followed by bad links. Hence a consideration of errors allows us to predict an alternative area concentrated search rule.

Johnston's neural economy hypothesis (1982) contends that the world is too complex for every behavioural contingency to come pre-programmed as a reflex response. Learning can provide a means of enhancing relevant existing responses, for application to new situations. Foragers must learn about their environment by expanding prior estimates about the environment through experience, and applying this information when making foraging decisions (Oaten, 1977; Ollason, 1980). Ollason (1980) has suggested that the need to learn about an environment prevents an animal from foraging optimally. McNamara & Houston (1985) have argued that this need not be true when foraging rules take account of learning components. The analysis of foraging is thus transformed from one in which the forager performs the current best behaviour to one in which the forager "perform(s) as well as possible, given that it starts without complete knowledge of the environment" (our italics, McNamara & Houston, 1985, p. 246).

Area concentrated search, coupled to a Bayesian learning rule can be viewed as an example of optimal foraging *sensu* McNamara & Houston, in which the need to learn about the environment causes observed behaviours to differ from behaviours under an assumption of omniscience. Foragers can either accumulate information during the course of searching, using current estimates of the resource distribution (control strategy) or employ a dedicated information acquisition strategy (identification strategy) for a short while, followed by a control phase. In temporally fluctuating environments the relationship between the median value of a resource distribution **P** and its mean determines whether an identification phase is likely to be favoured. When each encounter or failure, can occur with a probability far from the prior estimate of these events, identification is favoured. When the prior distribution is uniform [Fig. 5(a)] the mean of the distribution is not a good predictor of a sample drawn from the environment. An encounter or failure is therefore moderately informative. When the resource parameters (p_1, p_2) are sampled from a Gaussian [Fig. 5(b)], each successive environment is much like the last and the resource is always distributed closely around the mean of the prior. Hence identification is of limited value because the informational gains following a period of enforced intensive search, are of less value than the loss in encounters. As the Gaussian distribution becomes more skewed [Fig. 5(c–e)], successive environments fluctuate, with a resource that is frequently distributed far from the previous mean, causing identification to become more profitable. Identification is therefore useful in cases in which the previous mean is least informative about the permissable states of the environment.

There is a correspondence between these results and those of Stephens (1991) who draws a distinction between "within-generation predictability" and "between-generation predictability". Learning is favoured given some within-generation structure in the stimulus and a degree of unpredictability either within- or between-generations. In our searching model, the resource distribution is specified by two parameters, fixed in each bout, which specify the patchiness of the resource. Encounters with resource vary probabilistically (within-generation predictability). Between bout parameters are sampled from a range of distributions (between-generation predictability), and it is the structure of these distributions which controls the extent to which learning is favoured. Stephens emphasizes the evolution of learning by employing phylogenetic nomenclature (generations), our results can be interpreted as readily as ontological effects, in which environments fluctuate over a short time scale, and change significantly only in the longer term.

These results were pre-empted in the experiments of Shetleworth et al. (1988) who demonstrated that pigeons will increase their rate of sampling at fluctuating feeders as resource quality drops. A perceived change in the environment precipitates sampling (identification) behaviours. This was also shown by Kramer & Weary's observation (1991) that foraging chipmunks dedicate more time to exploration (identification) when food sources change unpredictably in time. Similarly, Formanowicz & Bradley (1987) found that centipedes would engage in a period of assessment prior to adopting a preferred search tactic predicated on this assessment.

Environments that fluctuate in time may favour identification, but the extent to which this is favoured will also depend on the value of having accurate information about the resource. In some environments, pursuing a sub-optimal strategy is less costly than in others. We have found that the cost of sub-optimal decisions increases as the resource becomes more patchy (Fig. 6). A patchy distribution describes a resource which becomes aggregated in clumps and is separated by large, resource-free stretches. The value of information is not equivalent to the period of time spent in conditional search, and does not depend on within- or between-generation variability in the resource. The value of information only gives us some idea about the likelihood of learning in a natural environment. In conclusion, identification is therefore most likely to be seen in cases in which environments fluctuate, the resource distribution is skewed, and the environment is patchy (mean resource parameters p_1 and p_2 are high).

Several authors have stressed the need to include behavioural and physiological processes in the description of predator-prey interactions (Metz & Diekman, 1986; Casas et al., 1993). The functional response relates the number of prey attacked per unit of time to the resource density, and provides a convenient summary of the predator prey relationship. An ACS model provides explicit treatment of foraging rules within an optimality framework, and can serve as an individual based model of predator–prey interactions. The functional response of an ACS foraging in a patchy resource distribution takes the form of a type three functional response (Holling, 1953). This arises through an apostatic effect: as the number of contiguous good links increases, the amount of time searching in high density areas increases with a switch to intensive search. At the highest resource densities, resource is continuously encountered and the minimum search time limits any further increase in intake rate. Hence the functional response flattens out. The point of inflexion in the response curve is given by the switching threshold between win–slow:fail–fast and win–fast:fail–slow strategies. Apostatic predation during ACS is different to the apostatic effect explained by the optimal search rate hypothesis of Gendron & Staddon (1983), because in ACS the forager is not required to learn to spend more time in high reward rate areas, but does so as a consequence of a conditional strategy that restricts searching effort to smaller areas upon encounter with prey.

The sigmoidal functional response (type three) has been reviewed by Hassell et al. (1977) in invertebrate predators such as the Hemiptera, Coleoptera and Hymenoptera. Hassell et al. maintain that this functional form is likely to be found in all cases in which there is a threshold prey density below which the efficiency of searching by a predator drops, leading to prey switching. The ACS model demonstrates that a switching threshold can produce the sigmoidal functional response, but that this threshold need not imply reduced efficiency. The threshold represents a shift in emphasis, from predominantly extensive searching when encountering resource, to predominantly intensive searching as the prey density increases.

Ecologists are familiar with the concept that an accelerating functional response curve can lead to stability in populations through positive density dependence. It is also true that a decelerating curve can lead to instability through negative density dependence (Murdoch & Oaten, 1975). Perhaps less familiar to ecologists are the behavioural mechanisms giving rise to these functional forms. It is well known

that the degree of aggregation or patchiness of a resource has consequences on the searching strategies of a predator (Hassell, 1978). Less familiar again is how individual responses to resource heterogeneity, in particular apostatic predation and a resource dependent switch between searching rules, could cause the functional response to become a type three: a stability promoting form. Aggregation may promote population stability through a partial refuge effect (Hassell & May, 1974), through tardy learning of individual prey properties at low densities (Holling, 1965) or, as suggested by our results, by promoting an identification strategy that reduces the pressure on the resource population thereby mitigating exploitation. Models of area concentrated search, coupled with information acquisition strategies, may therefore provide a means of explaining population phenomena in terms of individual foraging mechanisms.

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APPENDIX A

To find the values of the elements of the **S** and **F** matrices that maximize γ, we construct four composite states that combine search speed with foraging success. The states are as follows:

$$u_+: \text{intensive search with reward} \quad (A.1)$$

$$u_-: \text{intensive search with no reward} \quad (A.2)$$

$$v_+: \text{extensive search with reward} \quad (A.3)$$

$$v_-: \text{extensive search with no reward} \quad (A.4)$$

We develop terms for the transition probabilities between these four states.

The probability of switching from u_+ to any other state:

$$u_+ \to u_+ = s_1 p_1 p_u$$

$$u_+ \to u_- = s_1(1 - p_1 p_u)$$

$$u_+ \to v_+ = (1 - s_1)p_1 p_v$$

$$u_+ \to v_- = (1 - s_1)(1 - p_1 p_v)$$

The probability of switching from v_+ to any other state:

$$v_+ \to u_+ = (1 - s_2)p_1 p_u$$

$$v_+ \to u_- = (1 - s_2)(1 - p_1 p_u)$$

$$v_+ \to v_+ = s_2 p_1 p_v$$

$$v_+ \to v_- = s_2(1 - p_1 p_v)$$

The probability of switching from u_- to any other state:

Switching from a negative state represents a more complex problem for a forager than switching from a positive state. A positive state implies that food was present, while a negative state could result either from an absence of the resource or from failure to acquire the resource present. Because in our model the forager has no memory for anything previous to the last result, we must calculate the probability of the environment being in state $\epsilon_{n+1} = 1$ given that the forager did not encounter a prey in the nth link searching at speed u. We denote this probability m_u. From **P** we can calculate the stationary distribution of the resource. We know that a randomly chosen site contains food with probability

$$\frac{1 - p_2}{2 - p_1 - p_2}, \quad (A.5)$$

and thus from Bayes's theorem of conditional probability,

$$m_u = \frac{(1 - p_2)(1 - p_u)}{(1 - p_2)(1 - p_u) + (1 - p_1)}. \quad (A.6)$$

The probability that the forager does not find resource in state u because there was no food is given by $1 - m_u$, and hence the full state transitions are,

$$u_- \to u_+ = f_1\{m_u p_1 + (1 - m_u)(1 - p_2)\}p_u$$

$$u_- \to u_- = f_1\{1 - p_u[m_u p_1 + (1 - m_u)(1 - p_2)]\}$$

$$u_- \to v_+ = (1 - f_1)\{m_u p_1 + (1 - m_u)(1 - p_2)\}p_v$$

$$u_- \to v_- = (1 - f_1)\{1 - p_v[m_u p_1 + (1 - m_u)(1 - p_2)]\})$$

The probability of switching from v_- to any other state:

Similarly, the probability that the forager does not find resource in state v because there was no food is given by $1 - m_v$, where

$$m_v = \frac{(1 - p_2)(1 - p_v)}{(1 - p_2)(1 - p_v) + (1 - p_1)}, \quad (A.7)$$

and hence the full state transitions are,

$$v_- \to u_+ = (1 - f_2)\{m_v p_1 + (1 - m_v)(1 - p_2)\}p_u$$

$$v_- \to u_- = (1 - f_2)\{1 - p_u[m_v p_1 + (1 - m_v)(1 - p_2)]\}$$

$$v_- \to v_+ = f_2\{m_v p_1 + (1 - m_v)(1 - p_2)\}p_v$$

$$v_- \to v_- = f_2\{1 - p_v[m_v p_1 + (1 - m_v)(1 - p_2)]\}$$

These composite states form the stochastic four by four matrix **M**. We then solve the equation

$$\check{q}(t+1) = \mathbf{M}\check{q}(t), \quad (A.8)$$

where $\check{q}(t)$ is the probability distribution of composite states at time t. Hence we have,

$$q_1 = \text{prob(forager is in state } u_+), \quad (A.10)$$

$$q_2 = \text{prob(Forager is in state } u_-), \quad (A.11)$$

$$q_3 = \text{prob(forager is in state } v_+), \quad (A.12)$$

$$q_4 = \text{prob(forager is in state } v_-). \quad (A.13)$$

The expected intake rate is then simply given by,

$$\gamma = \frac{q_1 + q_3}{(q_1 + q_2)t_u + (q_3 + q_4)t_v}. \quad (A.14)$$

The optimal foraging strategy, which we denote by $\pi(s_1, s_2, f_1, f_2)$, is obtained by numerically maximizing A.14.

APPENDIX B

We seek to find the errors associated with searching intensively when resource is present or absent in a link of the Markov chain. We construct four composite states that combine search speed with environmental state (good/bad). These states are written as,

u^+: intensive search when link occupied, (B.1)

u^-: intensive search when link vacant, (B.2)

v^+: extensive search when link occupied, (B.3)

v^-: extensive search when link vacant. (B.3)

We can write down the expressions for transitions between these states:

$$u^+ \rightarrow u^+ = (p_u s_1 + (1-p_u)f_1)p_1$$

$$u^+ \rightarrow u^- = (p_u s_1 + (1-p_u)f_1)(1-p_1)$$

$$u^+ \rightarrow v^+ = (p_u(1-s_1) + (1-p_u)(1-f_1))p_1$$

$$u^+ \rightarrow v^+ = (p_u(1-s_1) + (1-p_u)(1-f_1))(1-p_1)$$

$$u^- \rightarrow u^+ = f_1(1-p_2)$$

$$u^- \rightarrow u^- = f_1 p_2$$

$$u^- \rightarrow v^+ = (1-f_1)(1-p_2)$$

$$u^- \rightarrow v^- = (1-f_1)p_2$$

$$v^+ \rightarrow u^+ = (p_v(1-s_2) + (1-p_v)(1-f_2))p_1$$

$$v^+ \rightarrow u^- = (p_v(1-s_2) + (1-p_v)(1-f_2))(1-p_1)$$

$$v^+ \rightarrow v^+ = (p_v s_2 + (1-p_v)f_2)(1-p_1)$$

$$v^+ \rightarrow v^+ = (p_v s_2 + (1-p_v)f_2)p_1$$

$$v^- \rightarrow u^+ = (1-f_2)(1-p_2)$$

$$v^- \rightarrow u^- = (1-f_2)p_2$$

$$v^- \rightarrow v^+ = f_2(1-p_2)$$

$$v^- \rightarrow v^- = f_2 p_2$$

These composite states form the stochastic square matrix $\mathbf{N}$, we then solve the equation

$$\check{r}(t+1) = \mathbf{N}\check{r}(t) \qquad \text{(B.4)}$$

and the stationary distribution of errors is given by the eigenvector r for the unit eigenvalue. Hence the probabilities $r_i (i = 1, 4)$ correspond to the probabilities of searching intensively in an occupied link, searching intensively in a vacant link (sampling error), searching extensively in an occupied link (overrun error), and searching extensively in a vacant link.

APPENDIX C

We consider four cases corresponding in turn to the four possible outcomes of two consecutive searches. We will denote by $\overset{*}{_{(n)}} \rightarrow \overset{*}{_{(n+1)}}$ the transition between sites n and $n+1$. In this notation, $\overset{*}{_{(m)}} = $ "+" if a prey was encountered in the mth site and $\overset{*}{_{(m)}} = $ "$-$" if the forager failed to encounter food in the mth site. Let $\zeta(p_1, p_2)dp_1 dp_2$ be the prior probabilities that $P \in [p_i, p_i + dp_i]$, $i = 1, 2$. For short, we will write p_1, p_2 instead of $P \in [p_i, p_i + dp_i]$. Bayes's rule then gives us,

$$prob(p_1, p_2 | + \rightarrow +) = \frac{prob(+ \rightarrow +|p)prob(p)}{prob(+ \rightarrow +)} = \frac{p_f p_1 p_u p_v \zeta(p_1, p_2)}{\iint q_f q_1 q_u q_v \zeta(q_1, q_2)dq_1 dq_2} dp_1 dp_2 \qquad \text{(C.1)}$$

$$prob(p_1, p_2 | + \rightarrow -) = \frac{prob(+ \rightarrow -|p)prob(p)}{prob(+ \rightarrow -)} = \frac{p_f p_u(1-p_1 p_v)\zeta(p_1, p_2)}{\iint q_f q_u(1-q_1 q_v)\zeta(q_1, q_2)dq_1 dq_2} dp_1 dp_2 \qquad \text{(C.2)}$$

$$prob(p_1, p_2 | - \rightarrow +) = \frac{prob(- \rightarrow +|p)prob(p)}{prob(- \rightarrow +)} = \frac{[(1-p_f)(1-p_2) + p_f p_1(1-p_u)]p_v \zeta(p_1, p_2)}{\iint [(1-q_f)(1-q_2) + q_f q_1(1-q_u)]q_v \zeta(q_1, q_2)dq_1 dq_2} \times dp_1 dp_2 \qquad \text{(C.3)}$$

$$prob(p_1, p_2 | - \rightarrow -) = \frac{prob(- \rightarrow -|p_1, p_2)prob(p_1, p_2)}{prob(- \rightarrow -)}$$

$$= \frac{p_f(1-p_u)(1-p_1 p_v) + (1-p_f)(1-p_v + p_2 p_v)\zeta(p_1, p_2)}{\iint q_f(1-q_u)(1-q_1 q_v) + (1-q_f)(1-q_v + q_2 q_v)\zeta(q_1, q_2)dq_1 dq_2} dp_1 dp_2 \qquad \text{(C.4)}$$

where u and v represents the search speeds during the nth and $(n+1)$th steps respectively and

$$p_f = \frac{1-p_2}{2-p_1-p_2}.$$