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Density-Dependent Patch Exploitation and Acquisition of Environmental Information

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We study density-dependent resource harvest patterns due to Bayesian foraging for different distributions of resources. We first consider a forager with information about the stochastic properties of its environment. In this case we show that when the number of food items per patch follows a distribution from the exponential family, the density dependence is given by the ratio σ^2/μ of the distribution of number of food items per patch. Bayesian foraging can therefore lead to positive (negative binomial distribution) or negative (binomial distribution) density dependent resource harvest and even to density independent (Poisson distribution) resource harvest, depending on the distribution of resources in the environment. In a second stage we incorporate learning about the distribution of resources in the whole environment. The mean of the distribution of number of food items per patch of a given environment is learnt faster than the variance of the distribution. Learning occurs faster in poorer than richer environments.

Different foraging theory models focus on different aspects of the predator-prey interaction. A large body of the literature concentrates in looking for "optimal" foraging strategies, behaviors that will maximise expected net energy intake during the foraging period in a number of circumstances (see Stephens and Krebs, 1986; Lima and Dill, 1990; Ylönen and Magnhagen, 1992 for different reviews). Other models study the changes in feeding efficiency in response to changes in resource density across patches (Holling, 1965; Charnov, 1976; Green, 1988; Bernstein *et al.*, 1991). This second aspect has obvious links with predator–prey theory and population dynamics and stability (see Murdoch and Oaten, 1975; Hassell, 1978; Comins and Hassell, 1979; Taylor, 1984), a connection that has been partially explored (e.g., Abrams, 1982, 1987; Sih, 1984; Green, 1990; Mitchell and Brown, 1990). However, no attempt has been made to relate foraging under incomplete information with predator-prey dynamics, despite early suggestions of its importance (see Taylor, 1974; Murdoch and Oaten, 1975 for early accounts of the implications of learning in predator–prey theory).

Much of current predator–prey (or parasitoid-host) theory is concerned with spatial heterogeneity (Hassell and May, 1974; Murdoch and Oaten, 1975; Murdoch and Stewart-Oaten, 1989; Pacala *et al.*, 1990; Rohani *et al.*, 1994). Consider for example a host population distributed in n discrete patches, patch i containing h_i hosts ($i = 1, ..., n$). In order to understand the dynamics of this system we must first know the relationship between the number of hosts initially available in the patch and the expected proportion of parasitised hosts at the end of a given period (e.g., season). Most current models (see Hassell, 1978; Taylor, 1984) use some simple function, mainly chosen for mathematical tractability, to link number of hosts with parasitism levels. Would the predictions of these models change if the behaviour of individual predators was taken into consideration?

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Hassell and May (1985) have made some progress in this direction showing how the spatial distribution of a predator could affect population stability. More recent studies include individual-based approaches (see DeAngelis and Gross, 1992; Wilson *et al.*, 1993).

In this paper we study the relationship between the environmental distribution of food items per patch and the density-dependent patterns of resource harvesting by a Bayesian forager. We first study a foraging strategy which uses information gathered during patch exploitation to decide when to leave the patch. In a second stage we add the possibility of using the same information to track environmental changes.

BAYESIAN FORAGING IN PATCHY ENVIRONMENTS

The idea of using Bayesian statistics in the framework of optimal foraging theory is originally due to Oaten (1977). We will develop a particular case modelled by Iwasa *et al.* (1981). The environment will consist of a set of discrete patches, one patch containing k food items with probability p_k and separated from the others by extensions of barren land. When in a patch, foragers search for food items at random and the time required to find one item is assumed to follow the distribution

$$\text{Prob}(T \in [t, t+dt]) = Ake^{-Akt}\,dt, \tag{1}$$

where k is the number of food items in the patch at the time of searching and A the searching efficiency of the forager. Foragers can use Bayes' theorem to calculate $r(n, t)$, the expected number of food items remaining in the patch given that the patch has been exploited for a time t and n food items have been consumed during this time. They are equipped with a foraging rule such that they leave the patch when

$$r(n, t) \leqslant Q, \tag{2}$$

where the fixed quitting threshold Q will depend on the richness of the environment, the distance between patches, predation risk on the forager, and possibly other factors. The method for calculating $r(n, t)$ is given by Iwasa *et al.* (1981). To apply the foraging rule described by Eq. (2), the forager needs to know the probability that a randomly selected patch contains k food items (for $k = 0, 1, \ldots$), since these probabilities enter the calculation of $r(n, t)$. It will also need to know the average distance between patches to estimate the most suitable value of Q.

Let $\rho(N)$ be the probability that a given food item is removed from a patch containing N items when the forager encounters the patch. Let $\Delta\rho(N) = \rho(N+1) - \rho(N)$. When $\Delta\rho(N) > 0$ the proportion of items consumed is an increasing function of initial number of food items and the foraging strategy results in positive density-dependent resource harvesting. When $\Delta\rho(N) < 0$ consumption risk per item decreases with initial number of food items and the foraging strategy leads to negative density-dependent resource harvesting. When $\Delta\rho(N) = 0$ resource harvest is independent of initial density. Finally, resource harvest can be an increasing function of resource density at low levels of concentration of food items and decrease for higher densities. As we will show, a Bayesian foraging strategy can lead to any of these four scenarios depending on the environment in which the forager lives. Equation (3) shows how to calculate $\rho(N)$

$$\rho(N) = E\left(\frac{N - N_l}{N}\right), \tag{3}$$

where N_l is the number of food items left in the patch by the forager and $E(X)$ denotes the expectation of the random variable X.

EXPONENTIAL FAMILY DISTRIBUTION OF RESOURCES

Most unimodal discrete probability distributions can be approximated by either a negative binomial, a Poisson or a binomial distribution, all of them members of the exponential family. Here we study the density dependence of our Bayesian foraging strategy when the distribution of resources in the environment belongs to one of these families. The density dependence of a foraging strategy is determined by the function relating patch residence time to initial number of food items. Patch residence time is in turn given by the solution of Eq. (2). As shown by Iwasa *et al.* (1981), $r(n, t)$ is a decreasing function of t for all values of n. The estimated number of food items, however, can present discontinuities when food is encountered. Let $\Delta r(n, t) \equiv r(n+1, t) - r(n, t)$. If $\Delta r(n, t) > 0$ for all n and t, each item found in a patch will result in an increase in patch residence time. Since richer patches are characterized by a greater feeding rates (Eq. (1)), the condition $\Delta r(n, t) > 0$ will result in positive density-dependent resource harvesting. Conversely, $\Delta r(n, t) < 0$ will lead to negative density dependence and $\Delta r(n, t) = 0$ to a fixed exploitation time, density independent foraging rule.

TABLE I

Effect of Distribution of Food Items on the Density Dependence of a Bayesian Foraging Rule

Distribution of food items[a]	$r(n, t)$[b]	$\Delta r(n, t)$	Resource harvesting
Negative binomial			
$p_n = \binom{\lambda+n-1}{n}\left(\frac{1}{1+\alpha}\right)^{\lambda}\left(\frac{\alpha}{1+\alpha}\right)^{n}$	$\frac{\lambda+n}{e^{At}\frac{\alpha+1}{\alpha}-1}$	$\frac{1}{e^{At}\frac{\alpha+1}{\alpha}-1}>0$	Positive density dependence
Poisson			
$p_n = \frac{e^{-\mu}\mu^{-n}}{n!}$	μe^{-At}	0	Density independence
Binomial			
$p_n = \binom{M}{n} q^n(1-q)^{M-n}$	$\frac{M-n}{e^{At}\frac{1-q}{q}+1}$	$\frac{-1}{e^{At}\frac{1-q}{q}+1}<0$	Negative density dependence

Note. Symbols: negative binomial distribution: mean $= \lambda\alpha$; variance $= \lambda\alpha(1+\alpha)$; Poisson distribution: mean = variance $= \mu$; binomial distribution: mean $= Mq$; variance $= Mq(1-q)$; A = searching efficiency; t = time interval.

[a] $n \geqslant 0$.

[b] From (Iwasa *et al.* 1981).

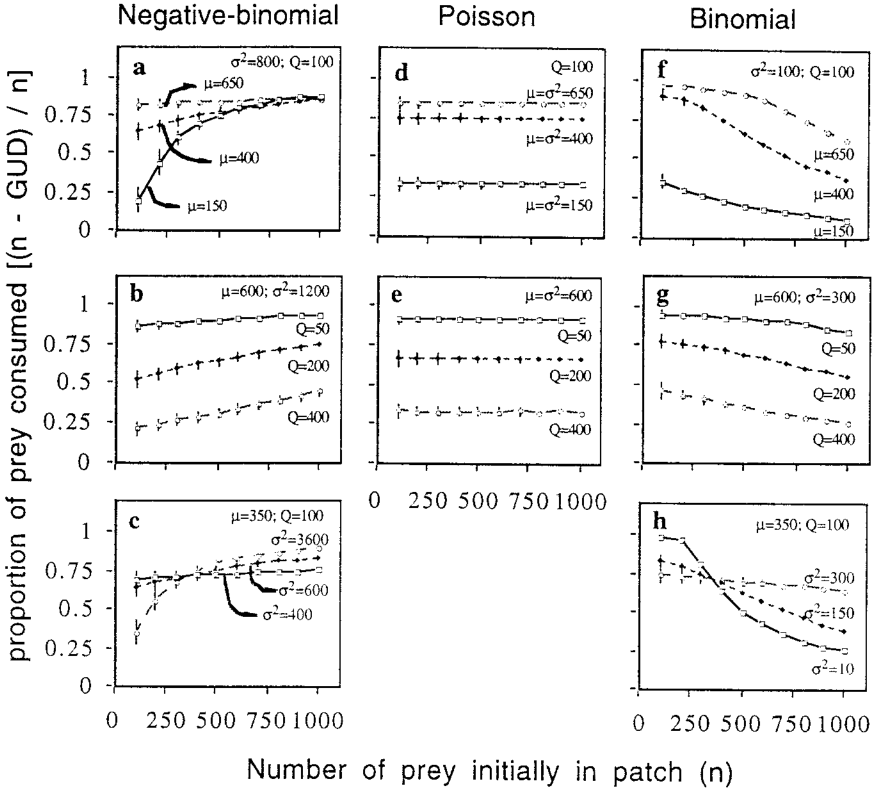

FIG. 1. Proportion of food items consumed (mean ± SD) by a Bayesian forager as a function of the number of items initially in the patch in an environment where the number of food items per patch was negative binomially distributed (a–c), Poisson distributed (d, e), or binomially distributed (f–h). Q is the quitting threshold.

From the expressions of $r(n, t)$ obtained by Iwasa *et al.* (1981) we can easily calculate $\Delta r(n, t)$ for the different types of exponential distribution. These values are summarised in Table I, which suggests that a Bayesian foraging rule will lead to positive density-dependent resource harvesting when the number of food items per patch follows a negative binomial distribution, density independent resource harvesting when the distribution of patches is Poisson and negative density dependence for a binomial distribution of food items per patch.

These predictions are confirmed by computer simulations shown in Fig. 1. Each data point shows the mean of 1000 runs of a simulation in which the proportion of food items consumed by a Bayesian forager with random search were calculated for different environmental parameters. The reason for the difference between binomial and negative binomial distribution may be explained as follows. Upon consumption of one item, one obtains two pieces of information: (i) the patch was richer than it was previously thought, but (ii) the patch has become worse by the one item being eaten. When the number of food items per patch are binomially distributed, the second term is greater than the first one (in absolute value) and the net gain of information is that there are probably less food items left than there were thought to be before capture. With a negative binomial distribution, the first term is greater and the net effect is an expected increase in the number of food items left, while for a Poisson distribution both terms are equal and exactly cancel each other.

The foraging policy summarised by Eq. (2) was proposed without optimality claims (Iwasa *et al.*, 1981). The general optimal strategy (McNamara, 1982) is not easily amenable to further manipulations. Although it is possible to use dynamic programming to derive optimal foraging strategies (Green, 1987), for the sake of mathematical tractability we will adhere to the solution proposed by Iwasa *et al.* (1981). Nevertheless, we will show the following proposition.

Proposition 1. *If $\Delta r(n, t) \leqslant 0$ for all n and t the optimal (long-term energy intake rate maximising) strategy is to stay in the patch as long as the instantaneous reward rate, $R(n, t)$, is greater than the maximum long-term intake rate attainable in the environment, γ (i.e., $Q = \gamma/A$ in Eq. (2)).*

Proof. We will follow the formalism developed by McNamara (1982), who derived similar results. McNamara suggested a possible definition for the instantaneous reward rate in stochastic environments. Under the random search assumption, it is shown in Appendix A that the reward rate for a forager that has obtained n food items in a patch after a time t, $R(n, t)$, is

$$R(n, t) = A \cdot r(n, t). \tag{4}$$

Consider a foraging strategy leading to a patch residence time T, which in general will be a random variable. Consider also a forager that has spent a time t in a patch and has consumed n food items and let $a_T(n, t)$ be the number of items that the forager may be expected to find between t and patch departure, and $b_T(n, t)$ the expected time from t to patch departure. Defining

$$g_T(n, t) = a_T(n, t) - \gamma \cdot b_T(n, t), \tag{5}$$

the optimal policy is the one maximising g (McNamara, 1982). In particular, for a forager exploiting optimally a patch, g is positive during patch exploitation and the forager leaves the patch as soon as $g = 0$.

From the definition of $a_T(n, t)$, we have

$$a_T(n, t) = E\left[\int_t^T R(N(s), s) \cdot ds \mid N(t) = n\right], \tag{6}$$

where the random variable $N(t)$ is the number of items taken in the patch at time t.

(A) Proof that $R(n, t) > \gamma \Rightarrow g^*(n, t) > 0$

Consider the strategy "stay on the patch while $R(n, t) > \gamma$, leave when $R(n, t) \leqslant \gamma$." Let T be the leaving time under this strategy. If $R(n, t) > \gamma$, then by continuity of $R(n, t)$ in t, $P(T > t \mid N(t) = n) > 0$. Since $R(N(s), s) > \gamma$ for $t \leqslant s < T$, we have

$$\begin{aligned} a_T(n, t) &= E\left[\int_t^T R(N(s), s) \cdot ds \mid N(t) = n\right] \\ &> \gamma \cdot E\left[\int_t^T ds \mid N(t) = n\right] = \gamma \cdot b_T(n, t). \end{aligned} \tag{7}$$

Thus $g_T(n, t) > 0$ and $g^*(n, t) = \max_\tau g_\tau(n, t) > 0$.

(B) Proof that $R(n, t) \leqslant \gamma \Rightarrow g^*(n, t) \leqslant 0$

Because $r(n, t)$ is decreasing in t for all n (Iwasa *et al.*, 1981), if $\Delta r(n, t) \leqslant 0$ we have that $R(N(s), s) < R(n, t)$ for all $s > t$. Let τ be any stopping time. Hence, if $R(n, t) \leqslant \gamma$,

$$\begin{aligned} a_T(n, t) &= E\left[\int_t^T R(N(s), s) \cdot ds \mid N(t) = n\right] \\ &\leqslant \gamma \cdot E\left[\int_t^T ds \mid N(t) = n\right] = \gamma \cdot b_T(n, t). \end{aligned} \tag{8}$$

Thus $g_\tau(n, t) \leqslant 0$. Since this is true for all τ, $g^*(n, t) = \max_\tau g_\tau(n, t) \leqslant 0$. This concludes our proof.

COROLLARY. *Equation (2) provides the optimal foraging strategy for a Poisson (Stewart-Oaten, 1992) or binomial distribution of number of food items per patch.*

The simplicity of the foraging rule given by Eq. (2) has allowed us to make predictions about the relationship between environmental resource distributions and resource harvest patterns that were difficult to derive from McNamara's (1987) and Green's (1987) optimal foraging policies. Moreover, Proposition 1 shows that this foraging rule is actually optimal for a variety of food distributions. As it was noted by Green (1987), however, this is not the case for a negative binomial distribution of food items (in this case, $\Delta r(n, t) > 0$ and the statement that $R(N(s), s) < R(n, t)$ for all $s > t$ does not necessarily hold). Nevertheless, for the parameter values used by Green (1987) in the numerical calculation of the optimal strategies with negative binomial distribution of food items, it was still the case that optimal patch residence time was an increasing function of the number of items encountered in the patch. When following the optimal strategy, hence, foragers would on average stay longer in richer patches, leading once more to positive density-dependent harvesting. We can therefore tentatively conclude that the qualitative predictions obtained in this paper would not be modified when the optimal strategy is used instead of Eq. (2) (when the two policies differ).

GENERAL CASE

From the above discussion and given that most unimodal discrete distributions are well approximated by some exponential distribution, it is tempting to conclude that the relationship between the proportion of food items taken from a patch by a Bayesian forager and the number of items initially present in the patch will in general be determined by the σ^2/μ ratio of the distribution of resources in the environment. This temptation is strengthen by the following result (proven in Appendix B).

PROPOSITION 2. *Let $p_k(n, t)$ be the conditional probability that there are k food items left in the patch given that n items have already been removed after searching for a time t. Likewise, let $\mu(n, t)$ and $\sigma^2(n, t)$ be the mean and variance of the $p_k(n, t)$ probability distribution. Then,*

$$\mathrm{Sign}[\Delta r(n, t)] = \mathrm{Sign}[\sigma^2(n, t) - \mu(n, t)]. \tag{9}$$

As explained above, the sign of $\Delta r(n, t)$ controls the density dependence of the foraging strategy. It might therefore look as if Proposition 2 proved the claim that the σ^2/μ ratio of the food distribution controlled the density dependence of a Bayesian forager resource harvesting. This is not so, however, since the sign of $\sigma^2(n, t) - \mu(n, t)$ needs not be constant for all n and t. In particular, this can originate the "domed" relationships between proportion of consumed items and initial density (Fig. 2) sometimes encountered in host–parasitoid systems (see Hassell, 1982; Lessells, 1985). In Fig. 2, the number of food items per patch followed a uniform distribution: the environment was composed of patches having from 0 to 20 food items, each patch type being equally frequent. It can be seen that the proportion of items consumed has a maximum peak at intermediate resource densities. This peak occurs at higher densities as the quitting threshold increases. Furthermore, the overall proportion of items consumed is lower for higher quitting threshold.

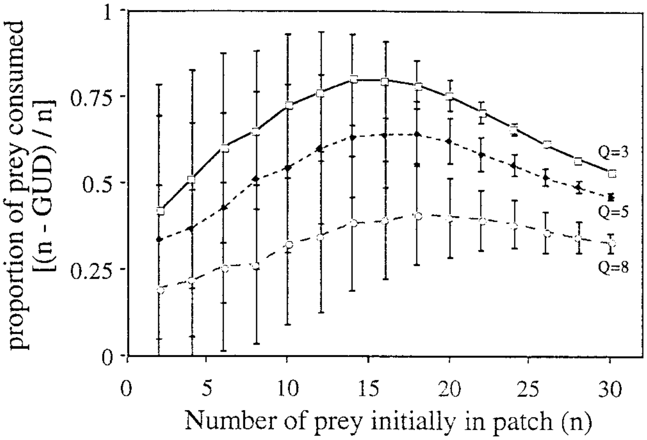

FIG. 2. Proportion of food items captured (mean ±SD over 1000 runs) as a function of the number of items initially in the patch for three different quitting thresholds (Q). In all cases the habitat was composed of patches having from 0 to 20 food items, each number being equally likely to be found.

It is therefore clear that, given an appropriate distribution of resources, a Bayesian foraging strategy may lead to virtually any pattern of resource harvesting. For distributions that are not well approximated by members of the exponential family, a detail calculation of the mean and variance of the $p_k(n, t)$ probability distribution, for all n and t, must be conducted to predict the pattern of resource harvesting.

LEARNING ABOUT THE ENVIRONMENT

We have so far assumed that foragers have precise information concerning the probability that a randomly chosen patch from their environment contains k food items (for all values of k). We now study how Bayes' rule can be used to obtain this information. For this discussion it will be useful to introduce another probability density function, the discrete gamma distribution, given by

$$P_{\alpha,\beta}(n) = \begin{cases} \dfrac{1}{C_{\alpha,\beta}} n^{\alpha-1} e^{-\beta \cdot n}, & n > 0 \\ 0, & n \leqslant 0, \end{cases} \tag{10}$$

where $C_{\alpha,\beta}$ is a normalisation constant,

$$C_{\alpha,\beta} = \sum_{n=1}^{\infty} n^{\alpha-1} e^{-\beta \cdot n}. \tag{11}$$

The gamma distribution depends on two parameters, α and β, and is extremely flexible, since its mean and variance can be independently chosen. In the continuous gamma distribution, they are

$$\mu = \frac{\alpha}{\beta}, \quad \sigma^2 = \frac{\alpha}{\beta^2}. \tag{12}$$

Equation (12) provides an excellent approximation for the discrete distribution when $\alpha > 1$, and we will use it throughout. The great advantage of the gamma distribution is that it can approximate most plausible environmental resource distributions by a judicious choice of α and β. This allows us to use Bayes' rule for learning the properties of the environment: the forager starts with a prior distribution for the parameters α and β, $\rho(\alpha, \beta)$ (in essence, the forager "knows" the likelihood that the mean and variance of the number of food items per patch are μ and σ^2—Eq. 12). After exploiting a patch it can use the information collected (n items taken in a time t) to update its probability distribution. For examples collecting 40 food items makes it extremely unlikely that the mean number of food items per patch in the environment is 10 if the variance is very small. The updated probability, $\rho(\alpha, \beta \mid n, t)$ is (Appendix C)

$$\rho(\alpha, \beta \mid n, t) = \frac{\displaystyle\sum_{k \geqslant 0} \frac{(n+k)!}{k!} e^{-A \cdot k \cdot t} P_{\alpha,\beta}(n+k)\, \rho(\alpha, \beta)}{\left[\begin{array}{c} \displaystyle\iint_{\alpha',\beta'} \sum_{k \geqslant 0} \frac{(n+k)!}{k!} e^{-A \cdot k \cdot t} P_{\alpha',\beta'}(n+k) \\ \times \rho(\alpha', \beta')\, d\alpha'\, d\beta'. \end{array} \right]}. \tag{13}$$

The last piece of information relevant for our forager is the optimal quitting threshold. As we have seen, when $\Delta r(n, t) \geqslant 0$, this is given by

$$Q = \gamma / A. \tag{14}$$

Figure 3 shows the dynamics of Bayesian learning in some simulations. Foragers were placed in an environment where the number of food items per patch followed a gamma distribution with parameters α^0 and β^0. The travel time between patches was random and exponentially distributed. Foragers started the simulation with a prior probability density function for α and β, $\rho(\alpha, \beta)$ and some estimate of the long term average intake rate, γ_e. Upon arrival to a patch they computed the expected values of α and β according to their prior distribution,

$$\begin{aligned} \alpha^* &= \iint_{\alpha,\beta} \alpha \cdot \rho(\alpha, \beta) \cdot d\alpha \cdot d\beta \\ \beta^* &= \iint_{\alpha,\beta} \beta \cdot \rho(\alpha, \beta) \cdot d\alpha \cdot d\beta \end{aligned} \tag{15}$$

and while they exploited the patch they calculated $r(n, t)$ as if the number of food items per patch in their environment was gamma distributed with parameters α^* and β^*. When $r(n, t)$ fell below the quitting threshold calculated as $Q_e = \gamma_e / A$, the forager left the patch and, while searching for a new one, updated its probability density function for α and β (Eq. (13)) and γ_e (merely calculated as total intake over total time spent foraging). As it is always the case in Bayesian processes, the newly updated probability density function becomes the prior probability when a new patch is encountered and the entire process is iterated.

As a general rule, information about the mean number of food items per patch was acquired faster than information about the variance of the distribution. This is quite remarkable if we consider that the foragers were not estimating mean and variance directly but, rather, α and β. Another pattern which emerges from these results is that learning proceeds faster in poor than in rich environments. In rich environments the long term intake rate is high and, as a consequence, the quitting threshold Q is also high: foragers leave patches after taking very few food items and can only poorly estimate the richness of the visited patches. As a consequence, they gather information about the environmental distribution of resources very slowly. In very poor environments, on the other hand, patches are exploited virtually to depletion. When leaving a patch, foragers have very good estimates of the number of items that were initially in the patch and they can get a precise idea of the environmental properties in very few visits (Fig. 3).

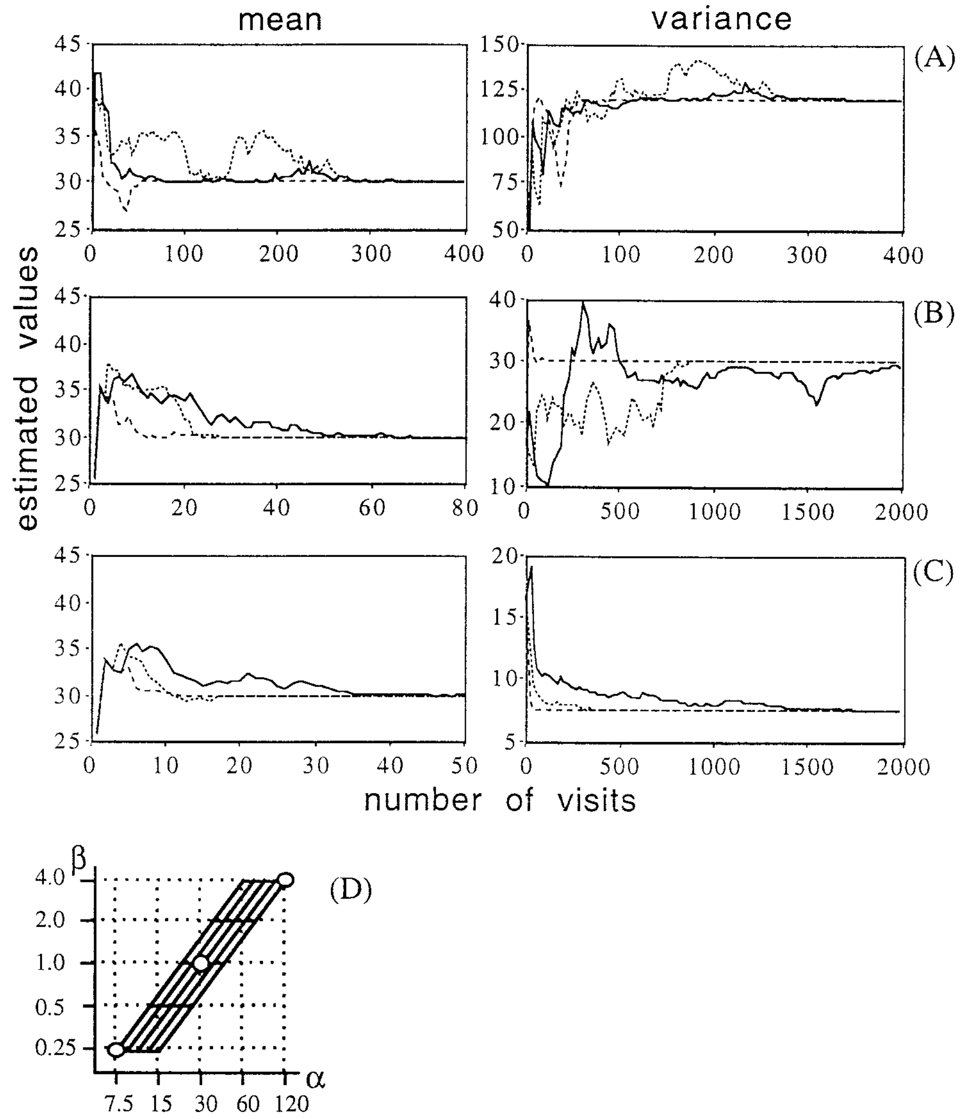

FIG. 3. Estimated values of mean and variance of the gamma distribution of resources as a function of the number of patches visited. Three different resource distributions were simulated, all with an actual mean of 30 food items per patch and variances 120 (A), 30 (B), and 7.5 (C). For each distribution three different values of overall resource richness were considered, each varying in the average travel time between patches: 0.02 (solid curves), 0.2 (dotted curves), and 2.0 (dashed curves). Time units are arbitrarily chosen so that the searching efficiency (Eq. (1)) was $A = 1$. The prior distribution for a and b at the beginning of the simulation was $r(a, b) = \frac{1}{25}$ if (a, b) was one of the intersection points of the solid-line grid presented in (D) and $r(a, b) = 0$ otherwise. The empty circles in (D) represent the three environments simulated. The integral in Eq. (8) was replaced by a summation over the 25 possible discrete combinations of a and b.

GENERAL DISCUSSION

As we have shown, a Bayesian learning foraging rule can lead to markedly different density-dependent resource harvesting relationships depending on the environmental food distribution. When the difference between the mean and variance of the conditional probability that there are k food items left in a patch has the same sign no matter how long the forager has been exploiting the patch and how many food items it has removed, this sign governs the pattern of resource harvesting: a variance larger than the mean will lead to positive density dependent resource harvesting, and vice versa, while equality of mean and variance leads to density independence. When the sign of the difference between mean and variance changes during patch exploitation, however, the Bayesian strategy will result in a convex relationship between resource harvesting and initial patch richness. It had previously been argued that the domed relationships found in host–parasitoid systems must be a consequence of physiological constraints on the parasitoids, such as egg and time limitations (Lessells, 1985). In view of our results, there seems to be no need to postulate such constraints, since a parsimonious imperfect information hypothesis can make the same prediction in an appropriate environment.

Although prey mortality is not uniquely determined by predator behavior, a foraging strategy leading to a type-3 functional response (Holling, 1965) can contribute to stability because prey at higher densities experience higher predation rate and therefore low density patches may constitute prey refuges. This aggregative response of foragers is well known to contribute to prey population stability (Hassell, 1978). When prey are distributed in a negative binomial fashion or equivalent gamma distribution, as in the biologically common clumped distribution (Southwood, 1978), the harvesting behavior of a Bayesian forager produces an aggregative response and therefore may constitute a stabilizing factor. Although the foraging strategy summarized by Eq. (2) is not optimal when the distribution of prey-per-patch is negative binomial, the significance of this result is enhanced by the fact that the optimal strategy produces a similar density dependence pattern of patch exploitation.

As we have seen, the Bayesian rule can be used to acquire information about the patch currently being exploited and about the environment as a whole. In particular, this ability would allow foragers to keep track of fluctuating resource densities and to forage efficiently throughout the seasons. It should be pointed out that, despite the convergence of the simulations shown in Fig. 3 to the real values of the environment, we have no general proof of convergence. McNamara and Houston (1985) propose another case of learning while foraging in which convergence is assured, but in this more complex setting such convergence is not guaranteed and it is possible that, in some circumstances. foragers may "learn" the wrong parameter values.

The flexibility of possible outcomes from a Bayesian foraging strategy and the fact that it could, in principle, explain the most commonly observed types of density-dependent relationships are encouraging. They do not prove, however, that most foragers use Bayesian strategies, since other foraging rules might well lead to similar predictions. The determination of the foraging rules actually used remains an experimental task. Valone and collaborators (Valone and Brown, 1989; Valone, 1991, 1992) have already done some progress in this direction, but the method they employ must be revised in the light of our results. This method consists in offering the foragers pairs of experimental patches of known food density (Brown, 1988; Mitchell and Brown, 1990). From the giving-up density observed it can be calculated the density-dependent relationship of their foraging strategy and whether they overuse or underuse rich patches relative to poor ones. Since different foraging strategies predict different patterns for these two quantities, the foraging strategy that the species under study is using can be inferred from them. The problem with this approach lies in the fact that, as we have seen, a Bayesian foraging strategy does not make, in itself, any prediction about the type of relationship that must exist between initial number of food items in the patch and giving-up density. Studies like the ones by Valone and Brown (1989) or Alonso *et al.* (1995) must therefore be complemented by studies of food distribution. Nevertheless, we believe that the approach of studying giving-up density by using experimental patches is a promising one, as it has already been demonstrated by a variety of studies (e.g., Brown, 1988; Kotler, 1992; Bowers *et al.* 1993: Brown *et al.*, 1994: Hughes *et al.*, 1994; Vásquez, 1994).

At this point, it could be argued that the spatial distribution of most species is well fitted by a negative binomial distribution (or any gamma distribution with parameter $\beta < 1$; see Pielou, 1977; Southwood, 1978). Since a Bayesian foraging strategy in this type of environment would result in a positively density-dependent relationship between the initial number of food items and resource harvesting, it may be claimed that Bayesian foraging strategies will typically result in positive density dependency and that different relationships between the initial number of food items and resource harvesting imply that the forager is not using a Bayesian rule (Valone and Brown, 1989; Valone 1991, 1992). The weakness of this argument lies in the fact that the spatial distribution of food items does not have so much of an effect on the foraging rule as the distribution of number of food items per patch. The difference between these two cannot be overstressed. The model proposed by Iwasa *et al.* (1981) and used throughout this paper assumes that the forager lives in a patchy environment, and therefore that the spatial distribution of food items is clumped. The distribution of the numbers of food items per patch refers to how many food items a forager is likely to find in any one identifiable foraging patch, while the statement that most species follow a negative binomial distribution refers to their spatial distribution, regardless of the variability of density between clumps (Pielou, 1977; Southwood, 1978).

APPENDIX A

The instantaneous intake rate in the patch (McNamara, 1982), $R(n, t)$, can be defined as

$$R(n, t)=\lim_{\delta\to 0^+}\frac{P(\text{capture one prey within time } \delta)}{\delta}. \tag{A1}$$

Let $p_k(n, t)$ be the probability that there are k food items left in the patch after consuming n of them in a time t and let $P(\delta \mid k)$ be the probability of capturing at least one item. From Eq. (1),

$$P(\delta \mid k)=1-e^{-A\cdot k\cdot\delta}, \tag{A2}$$

so that

$$\begin{aligned} R(n, t)&=\lim_{\delta\to 0^+}\frac{\sum_{k\geqslant 0} p_k(n, t)\cdot(1-e^{-A\cdot k\cdot\delta})}{\delta}\\ &=A\cdot\sum_{k\geqslant 0} p_k(n, t)\cdot k \end{aligned} \tag{A3}$$

and, from the definition of $r(n, t)$ (Iwasa *et al.*, 1981),

$$r(n, t)=\sum_{k\geqslant 0} p_k(n, t)\cdot k, \tag{A4}$$

equation (A3) can be rewritten as

$$R(n, t)=A\cdot r(n, t). \tag{A5}$$

APPENDIX B

We know from Iwasa *et al.* (1981) that the probability that there are k food items left in the patch given that the forager has consumed n items in a time t is given by

$$p_k(n, t)=\frac{p_{k+n}\binom{k+n}{n}e^{-A\cdot t\cdot k}}{\sum\limits_{q\geqslant 0} p_{q+n}\binom{q+n}{n}e^{-A\cdot t\cdot q}} \tag{A6}$$

and the expected number of food items remaining in the patch is given by

$$r(n, t)=\frac{\sum\limits_{k\geqslant 0} k\cdot p_{k+n}\binom{k+n}{n}e^{-A\cdot t\cdot k}}{\sum\limits_{q\geqslant 0} p_{q+n}\binom{q+n}{n}e^{-A\cdot t\cdot q}}. \tag{A7}$$

If we define

$$\mu(n, t)=r(n, t)=\sum_{k\geqslant 0} k\cdot p_k(n, t) \tag{A8}$$

and

$$\sigma^2(n, t)=\sum_{k\geqslant 0}(k-\mu(n, t))^2\cdot p_k(n, t) \tag{A9}$$

then, since

$$p_k(n+1, t)=\frac{(k+1)\ p_{k+1}(n, t)}{\sum_{q\geqslant 0}(q+1)\ p_{q+1}(n, t)}, \tag{A10}$$

we can write

$$\begin{aligned} \Delta r(n, t)&\equiv r(n+1, t)-r(n, t)\\ &=\sum_{k\geqslant 0} k\cdot p_k(n+1, t)-\sum_{q\geqslant 0} q\cdot p_q(n, t)\\ &=\frac{\sum_{k\geqslant 0} k(k+1)\cdot p_{k+1}(n, t)}{\sum_{k'\geqslant 0}(k'+1)\cdot p_{k'+1}(n, t)}-\sum_{q\geqslant 0} q\cdot p_q(n, t)\\ &=\frac{1}{\sum_{k'\geqslant 0}(k'+1)\cdot p_{k'+1}(n, t)}\\ &\quad\times\Bigg(\sum_{k\geqslant 0} k(k+1)\cdot p_{k+1}(n, t)\\ &\quad-\sum_{k'\geqslant 0}(k'+1)\cdot p_{k'+1}(n, t)\sum_{q\geqslant 0} q\cdot p_q(n, t)\Bigg)\\ &=\frac{1}{c(n, t)}\Bigg(\sum_{k\geqslant 0} k(k+1)\cdot p_{k+1}(n, t)-\sum_{k'\geqslant 0}(k'+1)\\ &\quad\times p_{k'+1}(n, t)\sum_{q\geqslant 0} q\cdot p_q(n, t)\Bigg), \end{aligned} \tag{A11}$$

where

$$c(n, t)=\sum_{k'\geqslant 0}(k'+1)\cdot p_{k'+1}(n, t)>0. \tag{A12}$$

Using the standard transformation

$$\sum_{k\geqslant 0} f(k)=\sum_{k\geqslant 1} f(k-1) \tag{A13}$$

and noticing that

$$f(k=0)=0\Rightarrow\sum_{k\geqslant 1} f(k)=\sum_{k\geqslant 0} f(k), \tag{A14}$$

we can rewrite Eq. (A11) as

$$\begin{aligned} c(n, t) \cdot \Delta r(n, t) &= \sum_{k \geqslant 0} k(k-1) \cdot p_k(n, t) \\ &\quad - \sum_{k' \geqslant 0} k' \cdot p_{k'}(n, t) \sum_{q \geqslant 0} q \cdot p_q(n, t) \\ &= \sum_{k \geqslant 0} k^2 \cdot p_k(n, t) - \left(\sum_{k \geqslant 0} k \cdot p_k(n, t) \right)^2 \\ &\quad - \sum_{k \geqslant 0} k \cdot p_k(n, t) \\ &= \sigma(n, t)^2 - \mu(n, t) \qquad \text{(A15)} \end{aligned}$$

which proves Eq. (9).

APPENDIX C

Bayes formula tells us that

$$P(X \mid Y) = \frac{P(X \cap Y)}{P(Y)}, \qquad \text{(A16)}$$

where $P(X \mid Y)$ is the probability of event X given that Y is true, $P(X \cap Y)$ is the probability that both X and Y are simultaneously true and $P(Y)$ is the probability of event Y. We are interested in the particular case:

$X \equiv$ the parameters of the gamma distribution that best approximates the distribution of number of food items per patch in the environment are α and β.

$Y \equiv$ the forager has collected n food items from a patch in a time t.

$P(X \cap Y) = P(\alpha, \beta \cap n, t)$ is, hence, the probability of taking n food items after a time t in a gamma distributed environment with parameters α and β, multiplied by the probability that the environment is actually described by α and β (i.e., the forager's prior distribution):

$$P(\alpha, \beta \cap n, t) = P(n, t \mid \alpha, \beta) \cdot \rho(\alpha, \beta). \qquad \text{(A17)}$$

The first term of r.h.s. is

$$P(n, t \mid \alpha, \beta) = \sum_{k \geqslant n} P_{\alpha, \beta}(k) \cdot P(n, t \mid k), \qquad \text{(A18)}$$

where $P(n, t \mid k)$ is the probability of taking n food items in a time t from a patch initially containing k items ($k \geqslant n$). Some algebra and Eq. (1) readily lead to

$$P(n, t \mid k) = A^n \frac{k!}{(k-n)!} e^{-A \cdot k \cdot t + A \cdot f(n, \bar{t})}, \qquad \text{(A19)}$$

with f being a function of the number of food items collected and the times required to collect individual items. Substituting Eqs. (A18) and (A19) into Eq. (A17) gives

$$\begin{aligned} P(\alpha, \beta \cap n, t) = \sum_{k \geqslant n} P_{\alpha, \beta}(k) \frac{k!}{(k-n)!} e^{-A \cdot k \cdot t} \\ \times A^n \cdot e^{A \cdot f(n, \bar{t})} \cdot \rho(\alpha, \beta). \qquad \text{(A20)} \end{aligned}$$

Since $P(Y) = P(n, t)$ is only the integral of $P(\alpha, \beta \cap n, t)$ over all possible values of α and β, we have (substituting Eq. (A20) in Eq. (A16))

$$P(\alpha, \beta \mid n, t) = \frac{\sum_{k \geqslant n} P_{\alpha, \beta}(k) \frac{k!}{(k-n)!} e^{-A \cdot k \cdot t} \cdot A^n \cdot e^{A \cdot f(n, \bar{t})} \cdot \rho(\alpha, \beta)}{\left[\begin{array}{c} \iint_{\alpha', \beta'} \sum_{k \geqslant n} P_{\alpha', \beta'}(k) \frac{k!}{(k-n)!} e^{-A \cdot k \cdot t} \\ \times A^n \cdot e^{A \cdot f(n, \bar{t})} \cdot \rho(\alpha', \beta') \cdot d\alpha' \cdot d\beta' \end{array} \right]}, \qquad (21)$$

which simplifies to Eq. (13).

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