Stochastic patch exploitation model

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A solitary animal is foraging in a patch consisting of discrete prey items. We develop a stochastic model for the accumulation of gain as a function of elapsed time in the patch. The model is based on the waiting times between subsequent encounters with the prey items. The novelty of the model is that it renders possible—via parameterization of the waiting time distributions—the incorporation of different foraging situations and patch structures into the gain process. The flexibility of the model is demonstrated with different foraging scenarios. Dependence of gain expectation and variance of the parameters of the waiting times is studied under these conditions. The model allows us to comment upon some of the basic concepts in contemporary foraging theory.

Keywords: group foraging; individual's benefit; unequal competition; marginal value theorem; assortative grouping

1. INTRODUCTION

Exploitation of prey occurring in patches by foraging animals is one of the central themes of the foraging theory (see, for example, Stephens & Krebs 1986). Diet models concern whether a prey item should be included in the diet or not, whereas the patch models focus on development of gain when the forager is in the patch. Under this domain it is assumed that the forager encounters prey only within patches, and with encounters the gain accumulates. However, because of the forager's success prey availability decreases, and the depletion causes the gain to level-off with increasing time in the patch. Charnov (1976) showed that the optimal time to be spent in a patch depends on the travel time and the gain against time spent in the patch. These elements have become the key determinants for theory on foraging in a patchy environment. The solution for the optimal time in patch by a long-term energy maximizer is known as the marginal value theorem, MVT (Charnov 1976; Charnov *et al.* 1976; Krebs & McCleery 1984; Stephens & Krebs 1986; Kamil *et al.* 1987).

Because of the central role of development of gain against time in a patch, we shall here focus on a forager's success when in a patch of food. Acknowledging that different patch structures call for appropriate models we address the accumulation of foraging gain as a stochastic process. From some basic assumptions concerning the process we shall derive the distribution of gain, and characterize it by expectation and variance. We feel motivated, as—despite the efforts by Oaten (1977), MacNamara (1982) and Stephens & Charnov (1982)—stochastic accumulation of gain has not been explicitly addressed in full detail (see, for example, Stephen & Krebs 1986).

2. PATCH EXPLOITATION MODEL

Let $G(t)$ be the amount of prey obtained by a solitary forager after it has been exploiting a patch of size X for t time units, elapsed from the encounter of the patch. We assume that the prey is of a discrete type, which implies that the possible states of the accumulated gain $G(t)$ are 0, 1, 2, ... X for any time-point t . The stochastic process $G(t)$, $t \geq 0$, is characterized by the probabilities

$$p_k(t) = \Pr(G(t) = k) \quad (1)$$

for $k=0, 1, \dots, X$.

To calculate these probabilities, assume that the process G is in state k at time t , that is, $G(t)=k$. The basic concept of the following reasoning, intensity, is familiar from the Poisson process (Feller 1966; Cox & Isham 1980). Assume that when $G(t)=k$ the probability of finding a new prey item during a time interval $[t, t+h)$ is of the form

$$\lambda_k h + o(h), \quad (2)$$

where $o(h)$ is the symbol for a function with the property that $o(h)/h$ approaches zero as h does. The intensity λ_k , unlike in the Poisson process, now depends on the state of the process, i.e. from the number of prey, k , gained so far. Assumptions in equation (2) means that for short time intervals—with small h —the probability of encountering a new prey item can be approximated by $\lambda_k h$. The expected number of prey items found—the number of incidences—per unit time is thus λ_k . The probability of more than one incidence during the short interval $[t, t+h)$ is approximately zero and thus the probability of no incidence during $[t, t+h)$ is $1 - \lambda_k h$. We thus obtain

$$p_k(t+h) = p_k(t)[1 - \lambda_k h] + p_{k-1}(t)[\lambda_{k-1} h] + o(h), \quad (3)$$

because the gain process can reach the state k at time $t+h$ via two routes: either it is in state k already at time t and

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after that nothing happens before $t+h$, or the process is in state $k-1$ at time t and one incidence takes place before time $t+h$.

Moving terms, dividing by h and letting h approach 0, one obtains from equation (3) the following differential equation for the probability $p_k(t)$:

$$p'_k(t) = -\lambda_k p_k(t) + \lambda_{k-1} p_{k-1}(t). \quad (4)$$

The parameters λ_k , $k=0, 1, \dots, X$ are called the transition intensities as they determine how the gain process moves from a state (k items gained) to the following ($k+1$ items gained). For notational convenience we let the index k run up to X , although one always has $\lambda_X=0$. Note that, naturally, the intensities λ_k depend on the original patch size X . To emphasize this we will sometimes use the notation $\lambda_k = \lambda_k(X)$.

The derivation of equation (4) is heavily based on the assumption that behaviour of the gain process depends only on its state at time t , not from the past behaviour, i.e. not on the way the state $G(t)=k$ was achieved. This means that the process has the property of a Markov process: the past affects the future behaviour of the process only through the current state (Karlin 1966). This type of process may also be called a renewal process (Cox & Isham 1980; McNair 1982).

(a) *Solution of the differential equation*

To solve equation (4), start with $k=0$: obviously one must take $\lambda_{k-1}=0$, and equation (4) reduces to

$$p'_0(t) = -\lambda_0 p_0(t),$$

which, with the natural initial condition $p_0(0)=1$, gives

$$p_0(t) = \exp(-\lambda_0 t). \quad (5)$$

The larger λ_0 is, the faster $p_0(t)$ approaches zero with increasing patch residence time t . With large values of λ_0 , we may expect the gain process to leave the state $G(t)=0$ earlier than would be the case with smaller values of λ_0 .

The probabilities $p_k(t)$ for $k>0$ can now be solved from equation (4) starting with $p_0(t)$ in equation (5). The obvious initial condition for $k>0$ is $p_k(0)=0$. Of course, $p_k(t)=0$ for $k>X$. The recursive formula (Kreyszic 1988) is,

$$p_k(t) = \exp(-\lambda_k t) \left[\int_0^t \lambda_{k-1} p_{k-1}(s) \exp(\lambda_k s) ds \right]. \quad (6)$$

The solution is a linear combination of the exponentials $\exp(-\lambda_k t)$, $k=0, 1, \dots, X$ with rational expressions of the λ_k s as coefficients.

For demonstrative purposes we present below an explicit solution for patch size $X=3$. Assume that the intensities λ_k are all unequal. For $k=1$,

$$p_1(t) = \frac{\lambda_0}{\lambda_1 - \lambda_0} [\exp(-\lambda_0 t) - \exp(-\lambda_1 t)], \quad (7)$$

which is valid for any patch size above 1, and for $k=2$

$$\begin{aligned} p_2(t) = & \frac{\lambda_1 \lambda_0}{(\lambda_2 - \lambda_0)(\lambda_1 - \lambda_0)} \exp(-\lambda_0 t) \\ & - \frac{\lambda_1 \lambda_0}{(\lambda_2 - \lambda_1)(\lambda_1 - \lambda_0)} \exp(-\lambda_1 t) \\ & + \frac{\lambda_1 \lambda_0}{(\lambda_2 - \lambda_1)(\lambda_2 - \lambda_0)} \exp(-\lambda_2 t), \end{aligned} \quad (8)$$

which is valid for any patch size above 2.

The last non-zero probability is

$$p_3(t) = 1 - [p_0(t) + p_1(t) + p_2(t)], \quad (9)$$

which is valid for patch size $X=3$ only.

The transition intensities λ_k have an interpretation in terms of waiting times. From equation (5) one can see that the time from encountering a patch to the finding of the first prey item is exponentially distributed with parameter λ_0 . Analogously, the time from the first to the second encounter is exponential with λ_1 and so on. From the properties of the exponential distribution the expectations or averages of these successive waiting times are $1/\lambda_k$, $k=1, 2, \dots, X-1$.

(b) *On the sequence λ_k*

The sequence λ_k , $k=0, 1, \dots, X$ of transition intensities determines the distribution of the gain $G(t)$ through the differential equation, equation (4). Let us emphasize that different choices of the sequence λ_k correspond to different foraging behaviour, patch structures and prey types. Next, we study some natural choices of λ_k to exemplify its features and flexibility in modelling different foraging scenarios.

First, to obtain a simple form of the gain distribution, take

$$\lambda_k(X) = (X - k)\lambda \quad (10)$$

for $k=0, 1, \dots, X$, where λ is a positive constant. The intensities λ_k are now linearly related to the amount of prey left in the patch. Instead of X parameters we now have only one: λ . It is an easy task to show that the amount of prey eaten $G(t)$ by time t now obeys the binomial distribution (Appendix 1) with parameters X (number of trials) and

$$\pi(t) = 1 - \exp(-\lambda t) \quad (11)$$

(success probability). The value of λ in equation (10) determines the time-scale. The behaviour of the probabilities $p_k(t)$ in equation (1) corresponding to intensities λ_k in equation (10) is explored in figure 1a,b. Nonlinear choices of λ_k —not obtainable from equation (10)—are shown in figure 1c,d.

The linear choice of parameter values, equation (10), is not necessarily very realistic, at least with larger patches. It assumes that the transition intensity, which is linearly related to the probability of finding something during a short interval, decreases by the same amount (λ) when the number of prey items left in the patch decreases irrespective of the amount of prey left in the patch. Therefore, if the amount of prey decreases from 100, say, to 99, this should be different from the situation where the number of prey left changes from two to one. In addition, the

Figure 1. The probabilities $p_k(t)$ for $k=0, 1, 2$ and 3 ; equation (1) with patch size $X=3$. The horizontal axes is the patch residence time. The transition intensities λ_k have been chosen according to equation (10) with $\lambda=1$: fast linear (a) and $\lambda=0.3$: slow linear (b). In (c) the intensities are $\lambda_0=8$, $\lambda_1=0.88$ and $\lambda_2=0.44$ corresponding to a situation where prey is easily found at the patch encounter but gets more difficult after the first item has been obtained. In (d) the situation is the other way round: $\lambda_0=1$, $\lambda_1=1.18$ and $\lambda_2=0.56$. The latter two cases correspond to each other in the sense that the sum of the inverses, $\sum (1/\lambda_k)$, is the same in both cases. This means that the sums of expected waiting times are equal.

capacity of the forager to handle and ingest prey items sets an upper limit to the prey item accumulation intensity, whereas the linear form of equation (10) can increase above any limit with increasing patch size.

Second, study an intensity sequence in which (i) the largest intensity λ_0 is always below a predetermined limit despite the size of the patch; and (ii) the difference $\lambda_{k-1}-\lambda_k$ increases with depleting patch (increasing k), thus creating an effect of depression.

Choose first the upper limit for the intensities (δ , say) and a positive parameter (γ , say), which determines the acceleration in the differences of the intensities. Then define

$$\lambda_k(X) = \delta\{1 - \exp[-\gamma(X-k)]\} \quad (12)$$

for $k=0, 1, \dots, X$. The general sequence of transition intensities λ_k is parameterized using the two parameters, δ and γ . The effect of these two parameters is illustrated in figure 2. With large values of γ , the corresponding λ_k s are almost constant.

Third, an extremely simple case is to take $\lambda_k=\lambda$ for $k=0, 1, \dots, X-1$. The intensity to find prey items is now independent of the amount of prey left in the patch. This choice describes a long and thin sequential patch, resembling a depleting feeder with equally distributed waiting times between the items supplied. An example of this could be a string of eggs laid by females of several fish species (for example, perch (*Perca fluviatilis*)), which are

Figure 2. Different choices of the transition intensity sequence λ_k ($X=25$) as a function of prey already captured k . The linear functions, 1 and 2, correspond to equation (10) with $\lambda=1$ and $\lambda=0.3$. Functions 3, 4 and 5 correspond to equation (12). Function 6 describes the case of hiding prey. Only the first few waiting times are short, but soon they turn long. The function 7 characterizes a case, for example, when prey are covered by a substrate and to unveil most of them takes some time (at the beginning the intensities are low, then they start to increase until depletion takes over).

prey for many foragers, or drift as food for many stream-dwelling fish.

As constant intensities correspond to the Poisson process (Feller 1966), the distribution of the gain, i.e. the probabilities $p_k(t)$ for $k=0, 1, \dots, X-1$ are obtained from the Poisson distribution with parameter λt . The only remaining non-zero probability $p_X(t)$ is obtained through subtraction from 1 (Appendix 1). The distribution is thus a censored Poisson.

Fourth, the linear (equation (10)) and exponential (equation (12)) way of defining the sequence (λ_k) both share the following property:

$$\lambda_k(X) = \lambda_0(X-k). \quad (13)$$

The intensities $\lambda_k(X)$, $k=0, 1, \dots, X$ depend on X and k only through their difference $X-k$ (prey left in the patch) and are determined by the sequence $\lambda_0(X)$ with patch sizes $X=1, 2, 3, \dots$. Equation (13) may be called a 'newly fresh' property as the intensities do not depend on the amount already eaten but only on the amount of prey remaining. A model with this property does not allow the intensity to decrease after the first few items have been eliminated (for

Figure 3. Expected gain (a–c) with corresponding variances (d–f) with different choices of the intensities λ_k ($X=3$), values of λ_k are inserted. (a) Linear sequence of intensities (equation (10)). (b) Nonlinear λ_k (the same as in figure 1c,d). (c) The intensities λ_k have constant value λ_0 . Parameter values in the examples indicated with dashed line are selected so that sums of expected waiting times are equal. Note how the variance approaches zero with time approaching infinity, that is, the patch being depleted up to the end.

example, hiding prey, or increasing satiation of foragers). This kind of effect can be handled by defining the sequence λ_k such that

$$\lambda_k(X) < \lambda_0(X - k). \quad (14)$$

Fifth, the sequences studied above are decreasing with respect to k , the amount already gained. Obviously, with patch depletion the intensities shall finally decrease towards zero, but one may also need models where the intensities increase at the very beginning of patch exploitation. This corresponds to a patch where prey availability initially is low, but increases after some foraging and searching activity (figure 2, last curve), such as woodpeckers seeking insect larvae in dead trees.

Sixth, a 'local' foraging strategy, where you eat what you reach until you have to move to a new place within the patch, may cause fluctuations in the intensities. The main trend is decreasing, but local increasing periods occur. This scenario corresponds, for example, to waxwings feeding on berries in a rowan tree.

(c) Expected gain and variance of gain

The gain function studied in the patch model is actually an average or—in terms of probability theory—expecta-

tion of a random process $G(t)$; see, for example, Stephens & Krebs (1986). We now study the explicit form of the expected gain implicitly determined by the sequence λ_k .

Let us first use the linear choice in equation (10). Because gain $G(t)$ is now binomially distributed (Appendix 1), the expected gain $G_E(t)$ is

$$G_E(t) = X[1 - \exp(-\lambda t)], \quad (15)$$

i.e. the number of trials times success probability. This gain corresponds to a linear depression of the patch. Expectation, equation (15), has been used by many authors in studies in the framework of the MVT, most recently and most explicitly by Livoreil & Giraldeau (1998). Note, that equation (15) fulfils the differential equation

$$(G_E)'(t) = \lambda[X - G_E(t)], \quad (16)$$

i.e. the rate at gain accumulation is linearly related to the amount of prey remaining in the patch. In figure 3a expectation (15) is shown for some values of λ .

For any choice of λ_k the distribution of gain and thus its expectation can be calculated. As can be seen from the case $X=3$ (equations (7)–(9)), the expected gain will be a linear combination of exponential functions $\exp(-\lambda_k t)$,

Figure 4. Expected gain (a) with variance of gain (b) against elapsed time in patch with three different MVT scenarios for optimal time in the patch (broken lines): (i) variance is at the highest, (ii) and (iii) with clearly differing travelling times correspond to situations where variances are matching. The expected gain (and its variance) corresponds to that in figure 3a with $\lambda=1$ and $X=3$. (c) Expected gain (a) and its variance (b) combined into a single graph. (d) A measure of risk, expected gain divided by its standard deviation, graphed against elapsed time in patch.

$k=0, 1, \dots, X-1$. Expected gains corresponding to some choices of the transition intensity sequence are represented in figure 3b. The curve $\lambda=0.5$ (figure 3a) roughly corresponds to both curves in figure 3b in that the sums of the inverses of the intensities, $\sum (1/\lambda_k)$, i.e. the sum at expected waiting times are equal. In addition, in the same sense, each of the three curves in figure 3a has its counterpart in figure 3c, where the value $\lambda_0=0.1$ is additional.

To derive variance for the gain let us again start with the linear choice of intensities in equation (10). Because the gain $G(t)$ is binomially distributed (Appendix 1), it has variance

$$G_V(t) = X[1 - \exp(-\lambda t)] \exp(-\lambda t), \quad (17)$$

which with variances corresponding to some nonlinear choices of the intensity sequence λ_k are studied in figure 3a-c.

3. DISCUSSION

Using a stochastic renewal process we have modelled explicitly the development of gain as a function of elapsed time in a patch of food. That is, we have given an accurate description of what happens in a patch of a given size. The model is based on waiting times between sequential

successful encounters with prey items. Via parameterization of the waiting times the model gains enough flexibility to encompass different foraging scenarios, from depleting food patches and drift of food in streams, to caches of food that are hard to open but yield a rich source of food for rapid depletion. Thus, the gain model renders it possible to analyse a wide variety of different foraging situations.

Our results merit commenting on patch-departure rules (see also, Iwasa *et al.* 1981; Giraldeau 1997). First, when one-parameter exponential gain (equation (15)) is used, it is implicitly assumed that the intake rate is linearly related to the amount of prey left in the patch. If one, for example, estimates the MVT optimal patch time using a one-parameter expected gain, when a more complicated form for the gain function is needed, severe bias may arise. The gains in figure 3b leading to a different MVT optimal patch time (neither of which is achievable using a one-parameter model) serve as a demonstration of this. Therefore, patch structure and its implications to the foraging situation should be carefully analysed before fitting any gain curve.

Second, a notable feature of the variance of the gain is its non-monotony. At the beginning of the patch exploitation variance increases with increasing gain, but with patch depletion it starts to decrease. With increasing

elapsed time in the patch, variance of gain approaches zero. The two variance minima are rather understandable, because at the beginning of the time spent in a patch not much is gained by the forager, and at the point when the patch is depleted of prey nothing remains to be gained. From this it is obvious that a risk-averse forager minimizing variance (Caraco 1981) would face problems. Because of the 'bell' shape of the variance as a function of elapsed time, a given threshold variance is prone to yield two different levels of expected gains. A relevant measure in line with this is the long-term average food-intake rate, i.e. gain divided by the sum of travel times and patch residence times. Variance of gain $G_V(t)$ describes the level of variation in gain obtained from a single patch after time t . Other sources of variation for a solitary forager are, for example, travel time, patch departure rule and patch size. If one assumes constant travel time, linear λ_k sequence (implying constant optimal patch time) and constant patch size (all elements assumed in the MVT), variation in gain, $G_V(t)$, determines variation in average intake rate. This justifies examination of $G_V(t)$. In addition, if the other sources of variation as listed above are also relevant, $G_V(t)$ still remains as one of the sources. Obviously, studying all these sources of variation at the same time is a task in itself, requiring knowledge of $G_V(t)$ too.

The MVT (Charnov 1976) is based on averages. The optimal patch time t_{opt} is such that average intake in the patch after time t in the patch $G_E(t)$ divided by sum of t and average travel time, τ , between patches equals average intake rate in the foraging environment (Charnov 1976; Ranta *et al.* 1995). From this it follows that t_{opt} is constant as long as average intake and average travel time do not change. Despite constant optimal patch time, t_{opt} , there is variation from patch to patch in the amount of gain $G(t_{opt})$ the forager obtains. Variance $G_V(t)$ describes the amount of this variation (figure 4a-c). Thus, one expects other optimization rules—in addition to the average optimization of the MVT—to be valid currencies for foraging animals.

Finally, risk-sensitive foraging behaviour is a foraging strategy which responds both to expected gain (and its costs) and its variance (for examples, see Caraco 1980, 1981; McNamara *et al.* 1991; Caraco *et al.* 1995). Preference of small variance is termed risk-averse behaviour, whereas risk-prone foragers are those preferring high risk. Assuming a foraging environment as above, we can derive a measure of 'risk' against elapsed time in a patch by dividing expected gain by its standard deviation (figure 4d). By definition, risk-averse foragers should prefer the maximum of such a function, whereas risk-prone foragers should prefer the minimum. Under this domain, risk-averse foragers would stay until the patch was completely depleted, whereas risk-prone foragers would be expected to leave the patch soon after consuming the first prey item. This undoubtedly necessitates conceptual clarification of the risk-sensitive foraging behaviour.

APPENDIX 1

Let the intensities be chosen according to equation (10). To show that gain $G(t)$ obeys binomial distribution with X as the number of trials and $\pi(t) = 1 - \exp(-\lambda t)$ as the

success probability we use induction with respect to the number of prey obtained, k . If $k=0$ we have

$$p_0(t) = \exp(-\lambda_0 t) = [1 - \pi(t)]^X \text{ as } \lambda_0 = X\lambda.$$

Assume that $p_k(t)$ is obtained from binomial distribution, i.e.

$$p_k(t) = \binom{X}{k} \pi(t)^k [1 - \pi(t)]^{X-k}. \quad (\text{A1})$$

From the recursive formula (equation (6)) one obtains

$$p_{k+1}(t) = \exp(-\lambda_{k+1} t) \left[\int_0^t \lambda_k p_k(s) \exp(\lambda_{k+1} s) ds \right]. \quad (\text{A2})$$

Inserting $\lambda_k = (X - k)\lambda$, and performing straight integration leads to

$$p_{k+1}(t) = \binom{X}{k+1} \pi(t)^{k+1} [1 - \pi(t)]^{X-k-1}, \quad (\text{A3})$$

which is the binomial probability for $k+1$.

If, instead, the intensities have the form $\lambda_k = \lambda_0$ for $k=0, \dots, X$, one has, in accordance with the Poisson process,

$$p_k(t) = \frac{(\lambda_0 t)^k}{k!} \exp^{-\lambda_0 t} \quad (\text{A4})$$

for $k=0, \dots, X-1$. As the only remaining possible (i.e. having non-zero probability) state of the gain is X , it must have the rest of the probability, i.e.

$$p_X(t) = 1 - \sum_{k=0}^{X-1} \frac{(\lambda_0 t)^k}{k!} \exp^{-\lambda_0 t}. \quad (\text{A5})$$

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