

The Value of Information in Central-Place Foraging.

Research Report

E. J. Collins ^{*} A. I. Houston [†] J. M. McNamara ^{*}

22 February 2006

Abstract

We consider a central place forager with two qualitatively different types of food sources; type 1 sources are always available whereas type 2 sources become available intermittently and this availability is signalled by information present at the central place. Source 1 is modelled using a standard patch foraging model whereas source 2 is modelled somewhat schematically in terms of the presence of information, the time spent at the source and the average reward received. The only decision in the model is the time spent by the forager at source 1 on each trip. We characterise the optimal foraging time and the optimal overall reward rate under the two source model and compare it with the corresponding quantities for a single source model. We show that, in general, the potential for information transfer has a marked effect on the forager's behaviour, and that a forager behaving optimally should return to check for new information with what might, under a single source model, seem to be a strictly submaximal load. We consider the dependence of the optimal foraging time and the optimal overall reward rate on the source 2 model parameters, and also show that our qualitative results hold for a variety of models for the time spent on source 2.

^{*}Centre for Behavioural Biology, School of Mathematics, University of Bristol, University Walk, Bristol BS8 1TW, UK

[†]Centre for Behavioural Biology, School of Biological Sciences, University of Bristol, Woodland Road, Bristol BS8 1UG, UK

1 Introduction

We consider a central place forager with two qualitatively different types of food sources. The essential difference is that type 1 sources are always available whereas type 2 sources become available intermittently and this availability is signalled by information present at the central place. Amongst other things, our analysis highlights the effect the availability of this information has on the behaviour of the forager on standard type 1 sources.

Type 1 sources are modelled using a standard patch foraging model (Charnov 1976, Stephens & Krebs 1986). We write $r(t) > 0$ for the rate at which the forager gains food when the current time on a patch is t and we assume $r(t)$ is either constant or is decreasing with t . We write τ for the travelling time for a single round trip from the central place to a patch and back. As is usual with such models, we assume either that $r(t)$ is constant, reflecting a resource that offers a constant supply of food (Model 1) or that $r(t)$ is strictly decreasing with t , reflecting a resource that gets depleted over each foraging period (Model 2).

To allow for a variety of interpretations and applications, source 2 is modelled somewhat more schematically in terms of the presence of information, the time spent at the source and the average rewards received. We assume that each time the forager returns from source 1, there is a certain probability that information will be present indicating the availability of source 2. This probability will generally depend on the length of time the forager has been away. We write $P(s)$ for the probability that such information is present when the forager returns from a round trip of total length s to source 1. For clarity of presentation we will initially assume that source 2 becomes available at some constant rate $\lambda > 0$, so that $P(s) = 1 - e^{-\lambda s}$ and $1/\lambda$ can be interpreted as the expected time until source 2 is again available. However in Section 5 we show that our results extend directly to a wider class of models for $P(s)$ (ref!!).

If a forager arrives at the central place and no information is present, then it immediately returns to source 1. If information is present, then the forager exploits source 2 for a time with expected length $T > 0$, until the source is no longer available. This may include several trips by the forager. It then recommences foraging at source 1, irrespective of the current information state. We write γ for the overall rate at which food is gained at source 2, so the expected total food gained from the source at each

exploitation is γT . Note that the only decision in the model is the time spent by the forager at source 1 on each trip.

Finally, we note an alternative interpretation in terms of a ‘foraging-recovery’ model, which can be viewed as complementary to previous treatments of diving models with convex-increasing un-rewarded recovery times (Houston & McNamara 1985, Houston & McNamara 1999). Consider a model under which each foraging round trip of total length $t + \tau$ is automatically followed by a recovery period of length $P(t + \tau)T$ during which the forager receives a reward at rate γ . Assume the recovery time is a bounded increasing concave function of the total trip time and is zero if the total trip time is zero, i.e. that $P(t)$ is a bounded increasing concave function of t with $P(0) = 0$. The average reward under this model, for a policy with foraging time t and journey time τ , is exactly the same as under the original model. To distinguish between models we refer to this version as the ‘foraging-recovery’ model and refer to the original model as the ‘foraging-information’ model.

For a given choice of t , the ‘foraging-recovery’ model evolves deterministically as a sequence of reward cycles, each of fixed total length $t + \tau + P(t + \tau)T$, while the ‘foraging-information’ model evolves stochastically, with each reward cycle comprising a random number of foraging trips to source 1 followed by a single visit to source 2. However, although conceptually different, the models are operationally equivalent in that for the same choice of parameter values they lead to the same optimal choice of foraging time and the same optimal reward. While it was natural under the ‘foraging-information’ model to focus on the case $\gamma > \gamma_1^*$, for the ‘foraging-recovery’ model it may be more natural to consider the case $\gamma < \gamma_1^*$.

2 Review of the single-source model

Previous authors (Charnov 1976, Stephens & Krebs 1986) have considered the ‘single-source’ case where information is not included in the model and the forager exclusively uses sources of type 1. The foraging process is modelled as a standard renewal reward process with renewal points at the epochs when the forager starts out on a new foraging trip. Assume each time the forager makes a trip, it stays for a time t on a source before

returning. Write $G(t)$ for the total food received in that time, then

$$G(t) = \int_0^t r(v)dv$$

and the reward rate over a round trip to source 1 with foraging time s and total travel time τ is

$$\frac{G(t)}{t + \tau}.$$

In line with standard foraging theory we restrict attention to the following models.

Assumption 2.1

We assume $r(s)$ is defined on $s \geq 0$, is positive and either

(i) $r(s) = r_0$ is constant (Model 1), or

(ii) $r(s)$ is strictly decreasing in s (Model 2). □

Define

$$\sigma_G(s) = (G(s)/G'(s)) - s,$$

so that $\sigma_G(s)$ as the distance from the origin to the point where the tangent to the curve $G(s)$ at s intersects the x -axis. In particular, $\sigma_G(s)$ can be interpreted as the travel time for which the foraging time s would be optimal for the single-source model, and thus can be a useful tool for developing intuition about the optimal foraging time for the single source model (Charnov 1976, Stephens & Krebs 1986).

Now let t^* be the optimal foraging time for this single source model and denote the corresponding optimal reward by

$$\gamma_1^* = \sup_t \frac{G(t)}{t + \tau}.$$

The following two lemmas follow summarise results for the single source case, and follow from standard treatments of central place foraging or by direct calculation.

Lemma 2.2 *If $r(s)$ is strictly decreasing then:*

(i) $G(s)$ is strictly concave and strictly increasing in s with $G(0) = 0$ and $G'(s) = r(s)$.

(ii) $G(s)/(s + \tau)$ is maximised at a finite value t^* , and $\gamma_1^* = G(t^*)/(t^* + \tau) = r(t^*)$.

(iii) $\sigma_G(s)$ is strictly increasing in s with $\sigma_G(0) = 0$ and $\sigma_G(t^*) = \tau$. □

Lemma 2.3 *If $r(s)$ is constant (say r_0) then:*

(i) $G(s) = r_0 s$ and $\sigma_G(s) = 0$ for all $s \geq 0$.

(ii) $G(s)/(s + \tau) = r_0 s/(s + \tau)$ is strictly increasing in s for all $s \geq 0$, so $\gamma_1^* = r_0$.

In this case we write $t^* = \infty$. □

3 Two source model with information

Under the two-source model with information, a forager that arrives at the central place when no information is present immediately returns to source 1. If information is present, then the forager makes a single visit to source 2 of length T and then recommences foraging at source 1, irrespective of the information state when the forager finished on source 2. For a given fixed foraging time s , the number of visits to source 1 between each visit to source 2 has a Geometric distribution with mean $1/P(s + \tau)$. Consider a reward cycle that starts each time the forager returns from source 2 and ends the next time the forager returns from source 2. During the cycle the forager will make on average $1/P(s + \tau)$ trips to source 1, each with a total trip time (foraging plus journey) of $s + \tau$ and each earning reward $G(s)$, and will make one visit to source 2 of total time T and total reward γT . Then the expected length of the cycle is $(s + \tau)/P(s + \tau) + T$ and the expected reward during the cycle is $G(s)/P(s + \tau) + T\gamma$.

Write $\Gamma(s)$ for the average reward rate for this fixed foraging time $s \geq 0$. Then

$$\Gamma(s) = \frac{G(s)/P(s + \tau) + T\gamma}{(s + \tau)/P(s + \tau) + T} = \frac{G(s) + P(s + \tau)T\gamma}{s + \tau + P(s + \tau)T}. \quad (1)$$

Now for $s \geq 0$ we define

$$\sigma_P(s) = (P(s)/P'(s)) - s,$$

Just as $\sigma_G(s)$ was useful in studying the single source model, characterising properties of $P(s)$ in terms of $\sigma_P(s)$ can provide useful information in the two source model. In particular, we can interpret $\sigma_P(s)$ as the distance from the origin to the point where the tangent to the curve $P(s)$ at s intersects the x -axis and $P'(s)\sigma_P(s)$ as the height from the origin to the point where it intersects the y -axis.

For ease of presentation we have assumed that information about the availability of source 2 becomes present at rate λ , so $P(s)$ has the Exponential distribution with

parameter λ . In fact, all that is really necessary for existence and uniqueness of an optimal foraging time is that $P(s)$ is strictly concave and strictly increasing in s . This will certainly be true for the Exponential distribution where $P(s) = 1 - e^{-\lambda s}$, but is also true, for example, for the Pareto distribution where $P(s) = 1 - (c/(c+s))^\lambda$. Some properties that follow from this assumption are summarised in the following lemma.

Lemma 3.1 *Assume $P(s)$ is defined on $s \geq 0$ and is strictly concave and strictly increasing in s , with $P(0) = 0$ and with $P(s) \rightarrow 1$ as $s \rightarrow \infty$. Then:*

- (i) $P'(s)$ is positive and strictly decreasing in s with $P'(s) \rightarrow 0$ as $s \rightarrow \infty$.
- (ii) $\sigma_P(s)$ is strictly increasing in s with $\sigma_P(0) = 0$ and $\sigma_P(s) \rightarrow \infty$ as $s \rightarrow \infty$.
- (iii) $P'(s)\sigma_P(s)$ is strictly increasing in s and $P'(s)\sigma_P(s) \rightarrow 1$ as $s \rightarrow \infty$.

Proof The properties easily follow by direct calculation. For example, the last property follows from $\frac{d}{ds}[P'(s+\tau)\sigma_P(s+\tau)] = \frac{d}{ds}[P(s+\tau) - (s+\tau)P'(s+\tau)] = P'(s+\tau) - P''(s+\tau)(s+\tau) - P'(s+\tau) = -P''(s+\tau)(s+\tau) > 0$ by strict concavity of P . \square

In many cases the optimal foraging time under the two source model can be characterised by application of the following lemma.

Lemma 3.2 *The derivative of $\Gamma(s)$ has the same sign as the expression*

$$r(s)(\tau - \sigma_G(s)) - (\gamma - r(s)) \frac{TP'(s+\tau)\sigma_P(s+\tau)}{1 + TP'(s+\tau)}. \quad (2)$$

Proof $\Gamma(s)$ has derivative $[(G'(s) + P'(s+\tau)T\gamma)(s+\tau + P(s+\tau)T) - (G(s) + P(s+\tau)T\gamma)(1 + TP'(s+\tau))]/[s+\tau + P(s+\tau)]^2$. Simplifying, using the facts that $G(s) = (s + \sigma_G(s))G'(s)$, $P(s+\tau) = (s+\tau + \sigma_P(s+\tau))P'(s+\tau)$ and $G'(s) = r(s)$, we deduce that the derivative has numerator $r(s)(\tau - \sigma_G(s))(1 + TP'(s+\tau)) - (\gamma - r(s))TP'(s+\tau)\sigma_P(s+\tau)$ and so overall the derivative has the same sign as the expression above. \square

We will see below that the first term in the expression (2)(i.e. $r(s)(\tau - \sigma_G(s))$) is often monotone decreasing for all $s \geq 0$, and is positive at $s = 0$ and is zero at $s = t^*$. Conversely, the second term (i.e. $(\gamma - r(s))[TP'(s+\tau)\sigma_P(s+\tau)]/[1 + TP'(s+\tau)]$) is often monotone increasing for all $s \geq 0$ and is positive at $s = t^*$. In such cases there exists a unique finite value s^* such that $\Gamma(s)$ is monotone decreasing for $s > s^*$ and monotone increasing for $s < s^*$ (if $s^* > 0$), and this value represents the optimal

foraging time under the model. Some intuition about the situation can be derived from the schematic diagram in Fig 1. In general, we will see that $s^* < t^*$, implying that potential information transfer has a marked effect on the forager's behaviour, and that a forager behaving optimally should return to check for new information with what might, under a single source model, seem to be a strictly submaximal load.

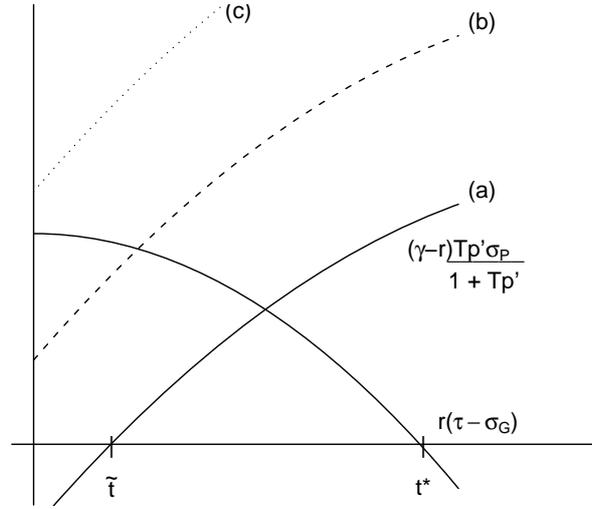


Figure 1: Here γ, T and τ are constants, r denotes $r(s)$, σ_G denotes $\sigma_G(s)$, P' denotes $P'(s + \tau)$ and σ_p denotes $\sigma_P(s + \tau)$. Case (a) $\gamma < r(0)$; case (b) $r(0) < \gamma < \bar{\gamma}$; case (c) $\bar{\gamma} < \gamma$.

Now set

$$\bar{\gamma} = r(0)[1 + \tau(1 + TP'(\tau))/(TP'(\tau)\sigma_P(\tau))] \quad (3)$$

if $r(0)$ is finite, and set $\bar{\gamma} = \infty$ otherwise. Under both models for $r(s)$ we have that for each fixed s , $G(s)/(s + \tau) \leq r(0)s/(s + \tau) \leq r(0)$, so $\gamma_1^* \leq r(0) \leq \bar{\gamma}$. We will see that γ_1^* and $\bar{\gamma}$ represent upper and lower bounds on the values of γ for which the ‘foraging-information’ model is applicable in practice. For $\gamma < \gamma_1^*$ the rate of reward at source 2 is less than the maximal reward rate for foraging on source 1, contradicting our interpretation of source 2 as the more attractive. Conversely, we will see that for $\gamma \geq \bar{\gamma}$ the optimal foraging time under the model is zero, reflecting the attractiveness

of gaining information about the availability source 2 and the fact that the forager would be better off returning straight away from source 1 without spending any time foraging.

Lemma 3.3 For $r(s)$ is strictly decreasing in s and $\gamma \geq \gamma_1^*$, $\Gamma(s)$ is maximised over $s \geq 0$ at a unique finite value s^* , where

- (a) $s^* = 0$ if and only if $\gamma \geq \bar{\gamma}$;
- (b) $0 < s^* < t^*$ if and only if $\gamma_1^* < \gamma < \bar{\gamma}$;
- (c) $s^* = t^*$ if and only if $\gamma = \gamma_1^*$.

Proof

Assume $r(s)$ is positive and strictly decreasing with s , so $\sigma_G(s)$ is strictly increasing, with $\sigma_G(0) = 0$ and $\sigma_G(t^*) = \tau$. Hence $r(s)(\tau - \sigma_G(s))$ is strictly decreasing on $(0, \infty)$, is positive at $s = 0$ and is zero at $s = t^*$.

Similarly $\gamma - r(s)$ is strictly increasing, while $P'(s+\tau)\sigma_P(s+\tau)$ is positive and strictly increasing and $P'(s)$ is positive and strictly decreasing, so $TP'(s+\tau)\sigma_P(s+\tau)/(1+TP'(s+\tau))$ is positive and strictly increasing. Hence $(\gamma - r(s))TP'(s+\tau)\sigma_P(s+\tau)/(1+TP'(s+\tau))$ is strictly increasing and its minimum value is taken at $s = 0$. Moreover, its value at $s = t^*$ is positive if $\gamma > \gamma_1^* = r(t^*)$ and zero if $\gamma = \gamma_1^* = r(t^*)$, and its value at $s = 0$ is less than $r(0)(\tau - \sigma_G(0))$ only if $\gamma < \bar{\gamma}$.

Thus if $\gamma_1^* < \gamma < \bar{\gamma}$ expression (2) is strictly decreasing, is positive at $s = 0$ and is negative at $s = t^*$. In this case there exists a unique value s^* at which the expression is zero and this value lies in the interval $(0, t^*)$. Since the derivative of $\Gamma(s)$ has the same sign as the expression, s^* is also the unique stationary point for $\Gamma(s)$ and $\Gamma(s)$ is increasing for $s < s^*$ and decreasing for $s > s^*$, so s^* is the unique maximising value for $\Gamma(s)$. However, if $\gamma = \gamma_1^*$, then expression (2) is strictly decreasing and is zero at $s = t^*$, so $\Gamma(s)$ is maximised at $s^* = t^*$, while if $\gamma \geq \bar{\gamma}$ then expression (2) is strictly decreasing and never positive, so $\Gamma(s)$ is maximised at $s^* = 0$. \square

For the single source model with $r(s)$ strictly decreasing in s , we have seen in Lemma 2.2 that $\gamma_1^* = G(t^*)/(t^* = \tau) = r(t^*)$. It follows from the characterisation of s^* as the unique zero of expression (2) that the corresponding relationship for the two source model is:

$$\Gamma(s^*) = r(s^*) \left[1 + \frac{\tau - \sigma_G(s^*)}{\sigma_P(s^* + \tau)} \right] \quad (4)$$

displaying clearly the effect of T and $P(s)$ on the optimal overall reward rate.

Consider now the case (Model 1) where $r(s) = r_0$ is constant. We will see that if γ is close to γ_1^* ($\gamma_1^* \leq \gamma \leq r_0(T + \tau)/T$), then the optimal foraging time on source 1 for the two source model is infinite. However, for most values of γ the possible presence of information at the nest ensures that s^* is finite even when $r(s)$ is constant. This contrasts sharply with the situation without potential information transfer, where the optimal time at the food source is $t^* = \infty$.

Note also that when $r(s)$ is constant (say r_0) for the single source model, the rate of reward is a strictly increasing function of the foraging time, so $\gamma_1^* = r_0$ and $t^* = \infty$.

Lemma 3.4

For $r(s) = r_0$ constant (so $t^* = \infty$) and $\gamma > r_0(T + \tau)/T$, $\Gamma(s)$ is maximised over $s \geq 0$ at a unique finite value s^* , where

(a) $s^* = 0$ if and only if $\gamma \geq \bar{\gamma}$;

(b) $s^* > 0$ if and only if $r_0(T + \tau)/T < \gamma < \bar{\gamma}$.

For $r(s) = r_0$ constant and $\gamma_1^* \leq \gamma \leq r_0(T + \tau)/T$, $\Gamma(s)$ is strictly increasing over $s \geq 0$ and we write $s^* = \infty$.

Proof

(i) We start with the second statement of the Lemma. The proof follows closely that of Lemma 4.2. Here $r(s)$ is constant and $\sigma_G(s) = 0$ so the first term in expression (2) is constant with value $r_0\tau > 0$. If $\gamma = \gamma_1^* = r_0$, then the second term is zero, in which case expression (2) is always positive and $\Gamma(s)$ is strictly increasing for all $s \geq 0$. If $\gamma > \gamma_1^* = r_0$, then $\gamma - r(s)$ is constant, with value $\gamma - r_0 > 0$, while $P'(s + \tau)\sigma_P(s + \tau)$ is positive and strictly increasing with limiting value 1 and $P'(s)$ is positive and strictly decreasing with limiting value 0. Hence $(\gamma - r(s))TP'(s + \tau)\sigma_P(s + \tau)/(1 + TP'(s + \tau))$ is positive and strictly increasing with limiting value $(\gamma - r_0)T$. If $\gamma_1^* < \gamma \leq r_0(T + \tau)/T$ then $(\gamma - r_0)T \leq r_0\tau$, so expression (2) is again always positive and $\Gamma(s)$ is strictly increasing for all $s \geq 0$.

For the first statement, note that $\bar{\gamma} = r_0 + r_0\tau(1 + TP'(\tau))/(TP'(\tau)\sigma_P(\tau)) > r_0 + r_0\tau/T = r_0(T + \tau)/T$. Thus if $r_0(T + \tau)/T < \gamma < \bar{\gamma}$ expression (2) is strictly decreasing, is positive at $s = 0$ and is negative for sufficiently large s . In this case there exists a unique finite value $s^* > 0$ at which expression (2) is zero and $\Gamma(s)$ is maximised. However, if $\gamma \geq \bar{\gamma}$ then expression (2) is strictly decreasing and never positive, so $\Gamma(s)$ is maximised at $s^* = 0$. \square

Finally in this section we note the following (obvious) bounds on the optimal overall reward rate.

Lemma 3.5

Let $\Gamma^* = \sup_s \Gamma(s)$. Then $\gamma_1^* \leq \Gamma^* \leq \gamma$.

Proof

Recall first that for any positive constants a, b, c, d ,

$$\frac{a}{b} \leq \frac{c}{d} \implies \frac{a}{b} \leq \frac{a+c}{b+d} \leq \frac{c}{d} \tag{5}$$

with strict inequalities throughout if the first inequality is strict.

For $\gamma > \gamma_1^*$, the definition of γ_1^* implies that for any finite s , $G(s)/(s + \tau) \leq \gamma_1^* \leq \gamma$. Since $\gamma = [P(s + \tau)T]\gamma/[P(s + \tau)T]$, applying equation(5) gives $G(s)/(s + \tau) \leq [G(s) + P(s + \tau)T\gamma]/[s + \tau + P(s + \tau)] \leq \gamma$. Thus $\gamma_1^* = \sup_s G(s)/(s + \tau) \leq \sup_s [G(s) + P(s + \tau)T\gamma]/[s + \tau + P(s + \tau)] \leq \gamma$ and so $\gamma_1^* \leq \Gamma^* \leq \gamma$. \square

Note that that $\gamma_1^* < \gamma$ does not always imply that $\gamma_1^* < \Gamma^* < \gamma$. For example, for constant $r(s) = r_0$ and $\gamma_1^* = r_0 < \gamma < r_0(T + \tau)/T$, it follows from Lemma 3.4 that $\gamma_1^* = r_0 = \Gamma^* < \gamma$.

4 Sensitivity analysis

Our model results in particularly clear predictions about the dependence of the optimal foraging time and the optimal overall reward rate on the source 2 model parameters γ, T and λ . In general, for cases where $0 < s^* < \infty$, the optimal foraging time s^* on source 1 is strictly decreasing with each of the parameters γ, T and λ and the optimal overall reward rate is strictly increasing in γ, T and λ (in each case for fixed values of the other two parameters). Thus a forager acting optimally will spend strictly less time per trip on source 1, and will do strictly better overall, as each parameter increases – and in particular will forage for less time per trip on source 1 and do strictly better overall than under a single source model where only source 1 is available.

These results make intuitive sense. As γ increases, the reward rate on source 2 becomes more attractive; as T increases, source 2 effectively becomes more valuable since it is

available for longer; as λ increases, the frequency of availability of source 2 increases. In each case, information indicating the availability of source 2 becomes more valuable or is more likely to be present, and foraging time on source 1 is sacrificed as a result. Indeed, Lemmas 3.3 and 3.4 predict that if source 2 is particularly rewarding in terms of the reward rate γ or the expected duration of availability T , the forager spends no appreciable time at source 1, but returns immediately to check for the presence of information.

Note that in the cases $T = 0$ and/or $\lambda = 0$ the duration and/or the frequency of availability of source 2 is zero and the model predicts that the forager behaves as if only source 1 was available. Similarly, if $\gamma = \gamma_1^*$ so the rate of reward on source 2 is exactly equal to the maximum rate of reward on source 1, then again Lemmas 3.3 and 3.4 imply that $s^* = t^*$ and $\Gamma^* = \gamma_1^*$, so that the forager's optimal behaviour is the same as under the single source model and the optimal reward rate is also the same.

More precise statements, covering also the cases where $s^* = 0$ and $s^* = t$ are given in the lemmas below. We note first for reference the following property of the Exponential distribution.

Lemma 4.1

Assume $P(s) = 1 - e^{-\lambda s}$ for $s \geq 0$. Write $P(s, \lambda)$ and $\sigma_P(s, \lambda)$ to make clear the dependence of these quantities on λ . Then $P'(s, \lambda)\sigma_P(s, \lambda)/(1 + TP'(s, \lambda))$ is strictly increasing with λ .

Proof The proof follows either by direct calculation or as a particular application of Lemma 5.2 below.

Lemma 4.2

Consider those cases when $0 < s^ < t^*$ or $s^* = t^* = \infty$ (From Lemmas 3.3 and 3.4 these are the cases where either (a) $r(s)$ is strictly decreasing in s and $\gamma_1^* \leq \gamma < \bar{\gamma}$, or (b) $r(s) = r_0$ is constant and $r_0 = \gamma_1^* < r_0(T + \tau)/T < \gamma < \bar{\gamma}$). Then for fixed values of the other two parameters:*

- (i) s^* is strictly decreasing in each of γ, T and λ .
- (ii) Γ^* is strictly increasing in each of γ, T and λ .

Proof

- (i) In the cases considered here, s^* is the unique value at which expression (2) is zero.

For fixed T and λ , the second term in the expression increases with γ for each fixed s while the first term stays constant. Thus if the expression was zero at $s > 0$ for a given γ then it will be negative at s for a small increase in the parameter to, say, $\gamma' > \gamma$ and the new zero will be at $0 < s' < s$. Thus s^* decreases with increasing γ .

Similarly, for fixed γ and λ , the second term in expression (2) increases with T for each fixed s while the first term stays constant, so the same argument shows that s^* decreases with increasing T .

Finally, for fixed γ and T , Lemma 4.1 shows that $P'(s, \lambda)\sigma_P(s, \lambda)/(1 + TP'(s, \lambda))$ increases with λ so again the second term in expression (2) increases with λ for each fixed s while the first term stays constant, so again s^* decreases with increasing λ .

(ii) First consider γ increasing. Write $\Gamma(s, \gamma)$ for the overall reward rate corresponding to foraging for time s on source 1 for the given value of γ , write s_γ for the corresponding optimal foraging time on source 1, and write Γ_γ for the corresponding optimal overall reward rate.

For fixed T and λ , the derivative of $\Gamma(s, \gamma)$ w.r.t. γ is strictly positive, so, for each fixed s , $\Gamma(s, \gamma)$ is strictly increasing in γ . Thus for $\gamma' > \gamma$, $\Gamma(s_\gamma, \gamma) < \Gamma(s_\gamma, \gamma')$. Moreover, $\Gamma(s_\gamma, \gamma') < \Gamma(s_{\gamma'}, \gamma')$ from Lemma 3.3, since $s_{\gamma'} < s_\gamma$ from above and $s_{\gamma'}$ is the unique maximising value for $\Gamma(s, \gamma')$. Thus $\Gamma(s_\gamma, \gamma) < \Gamma(s_\gamma, \gamma') < \Gamma(s_{\gamma'}, \gamma')$ implying that the optimal overall reward rate Γ_γ is strictly increasing in γ .

Similarly, in appropriate notation, for fixed γ and λ and for each fixed s , the derivative of $\gamma(s, T)$ w.r.t. T has the same sign as $\gamma - [G(s)/(s + \tau)]$, which is strictly positive as $\gamma > \gamma_1^* \geq G(s)/(s + \tau)$. Thus exactly the same method can be used to show that for $T' > T$, $\Gamma(s_T, T) < \Gamma(s_T, T') < \Gamma(s_{T'}, T')$ implying that the optimal overall reward rate Γ_T is strictly increasing in T .

Finally, again in appropriate notation, for each fixed γ and T and for each fixed s , $P(s, \lambda)$ is strictly increasing in λ , so the derivative of $\Gamma(s, \lambda)$ w.r.t. λ has once again the same sign as $\gamma - [G(s)/(s + \tau)]$, and so is strictly positive. Thus the same method also shows that for $\lambda' > \lambda$, $\Gamma(s_\lambda, \lambda) < \Gamma(s_\lambda, \lambda') < \Gamma(s_{\lambda'}, \lambda')$ implying that the optimal overall reward rate Γ_λ is strictly increasing in λ . \square

Lemma 4.3

Assume $s^ = 0$ and consider increasing values of each of γ, T and λ for fixed values of the other two parameters. Then:*

- (i) the optimal foraging time remains constant at $s^* = 0$.
- (ii) the optimal overall reward rate Γ^* is strictly increasing.

Proof

(a) From Lemma 3.3 and Lemma 3.4, $s^* = 0$ if and only if $\gamma \geq \bar{\gamma}$.

Consider fixed values of γ, T and λ , for which $\gamma \geq \bar{\gamma}$. If γ increases to γ' while T and λ remain constant, then $\gamma' > \gamma \geq \bar{\gamma}$, so the optimal foraging time will still be $s^* = 0$.

Now consider T increasing to $T' > T$ while γ and λ remain constant. Write $\bar{\gamma}(T)$ to denote the dependence of $\bar{\gamma}$ on T . From the definition of $\bar{\gamma}$ in (3), the derivative of $\bar{\gamma}(T)$ w.r.t. T is strictly negative, so $\bar{\gamma}(T)$ is strictly decreasing in T . Thus $\gamma \geq \bar{\gamma}(T) \Rightarrow \gamma \geq \bar{\gamma}(T')$, so the optimal foraging time will still be $s^* = 0$.

Similarly, from Lemma 4.1, $[1 + TP'(\tau, \lambda)]/[P'(\tau, \lambda)\sigma_P(\tau, \lambda)]$ is strictly decreasing in λ , so (in obvious notation) $\bar{\gamma}(\lambda)$ is also strictly decreasing in λ . As for T above, it follows that the optimal foraging time remains constant at zero if λ increases to λ' .

Finally, $\Gamma(s, \gamma)$ is strictly increasing in each of γ, T and λ for fixed s and fixed values of the other two parameters. Since the optimal foraging time remains constant at $s^* = 0$, $\Gamma_\gamma = \Gamma(0, \gamma) < \Gamma(0, \gamma') = \Gamma_{\gamma'}$ and the optimal overall reward rate is increasing in γ . Similar arguments apply for increasing T and λ . \square

Lemma 4.4

Assume $s^* = t^* = \infty$ and $\gamma_1^* < \gamma < r_0(T + \tau)/T$ and consider increasing values of each of γ, T and λ for fixed values of the other two parameters. Then:

- (i) the optimal foraging time remains constant at $s^* = \infty$;
- (ii) the optimal overall reward rate Γ^* remains constant at $\Gamma^* = r_0$.

Proof

From Lemma 3.4, $s^* = t^* = \infty$ if and only if $r(s) = r_0$ is constant and $r_0 = \gamma_1^* \leq \gamma \leq r_0(T + \tau)/T$, and in this case the optimal reward rate is r_0 .

Consider fixed values of γ, T and λ for which $\gamma_1^* \leq \gamma < r_0(T + \tau)/T$. This inequality will still be satisfied for sufficiently small increases in γ and/or T , and will clearly still be satisfied if λ increases, so in each case it will still be true that $s^* = \infty$ and the optimal reward rate is r_0 . \square

Lemma 4.5

Assume $s^* = t^* = \infty$ and $\gamma = r_0(T + \tau)/T$. Then as λ increases for fixed values of

the other two parameters:

- (i) the optimal foraging time remains constant at $s^* = 0$;
- (ii) the optimal overall reward rate Γ^* remains constant at $\Gamma^* = r_0$.

However, as each of γ and T increase for fixed values of the other two parameters:

- (i) the optimal foraging time s^* is strictly decreasing and finite;
- (ii) the optimal overall reward rate Γ^* is strictly increasing.

Proof

Consider fixed values of γ, T and λ for which $\gamma_1^* < \gamma = r_0(T + \tau)/T$. Again, this inequality is independent of λ , so as λ increases it will still be true that $s^* = \infty$ and the optimal reward rate is r_0 .

However, if γ increases to $\gamma' > \gamma$ for fixed T and λ , then $\gamma' > r_0(T + \tau)/T$. Denote the new optimal overall reward rate by $\Gamma_{\gamma'}$ and the new optimal foraging time by $s_{\gamma'}$. Now choose γ'' with $r_0(T + \tau)/T < \gamma'' < \gamma'$. Then from Lemma 3.4, $s_{\gamma'} < s_{\gamma''} < \infty$ and from Lemma 4.2 $\Gamma_{\gamma'} > \Gamma_{\gamma''}$. However, for any fixed s , $G(s)/(s + \tau) < \gamma_1^*$, and here $\gamma_1^* = r_0 < r_0(T + \tau)/T < \gamma''$. Thus, as in Lemma 3.5, $G(s)/(s + \tau) < [G(s) + TP(s + \tau)]/[s + \tau + TP(s + \tau)] = \Gamma(s, \gamma'') \leq \Gamma_{\gamma''}$, so $r_0 = \gamma_1^* = \sup_s G(s)/(s + \tau) \leq \Gamma_{\gamma''} < \Gamma_{\gamma'}$. Thus as γ increases to γ' , the optimal foraging time s^* strictly decreases and becomes finite and the optimal overall reward rate Γ^* strictly increases from r_0 to $\Gamma_{\gamma'} > r_0$.

Finally, since $r_0(T + \tau)/T$ decreases with increasing T , if T increases to $T' > T$ for fixed γ and λ , then $\gamma > r_0(T' + \tau)/T'$ and an exactly similar argument applies. \square

5 General models for $P(s)$

The models described so far have restricted attention to the simple case where source 2 becomes available at a constant rate λ , so that $P(s) = 1 - e^{-\lambda s}$. In this section we will show that, under appropriate assumption, all the results above carry over to more general models for $P(s)$.

For concreteness, assume the function P can be parameterised by a parameter λ , with $0 \leq \lambda < \infty$, and write $P(s, \lambda)$ to indicate the dependence on both the argument s and the parameter λ . Simple standard examples include the Exponential distribution, where $P(s, \lambda) = 1 - e^{-\lambda s}$, and the Pareto distribution, where $P(s, \lambda) = 1 - (c/(c + s))^\lambda$.

We noted with Lemma 3.1 that the existence and uniqueness of the optimal foraging time depended only on the fact that $P(s)$ was strictly concave and strictly increasing in s . One indicator of concavity is the function $\sigma_P(s)$, which in this extended notation becomes $\sigma_P(s, \lambda) \equiv (P(s, \lambda)/P'(s, \lambda)) - s$. To show that the optimal foraging time and the optimal overall reward rate are monotone functions of the source 2 model parameters, we need to make the following additional assumptions about $P(s, \lambda)$ and $\sigma_P(s, \lambda)$.

Assumption 5.1

- (i) $P(s, \lambda)$ is defined on $s \geq 0$ and is strictly concave and strictly increasing in s , with $P(0, \lambda) = 0$ and $P(s, \lambda) \rightarrow 1$ as $s \rightarrow \infty$.
- (ii) As λ increases from 0 to ∞ $P(s, \lambda)$ is strictly increasing from 0 to 1.
- (iii) $\frac{\partial}{\partial \lambda} P'(s, \lambda) \sigma_P(s, \lambda) > 0$.
- (iv) $\frac{\partial^2}{\partial \lambda \partial s} \sigma_P(s, \lambda) > 0$. □

These assumptions are satisfied for several distributions of interest, including the Exponential and Pareto cases. For example, in the Exponential case $P(s, \lambda) = 1 - e^{-\lambda s}$ and $P(s, \lambda) - sP'(s, \lambda) = 1 - e^{-\lambda s} - \lambda s e^{-\lambda s}$ so $\frac{\partial}{\partial \lambda} [P(s, \lambda) - sP'(s, \lambda)] = s e^{-\lambda s} - s e^{-\lambda s} + s^2 \lambda e^{-\lambda s} > 0$. Similarly $P(s, \lambda)/P'(s, \lambda) = (e^{\lambda s} - 1)/\lambda$ so $\frac{\partial}{\partial \lambda} [P(s, \lambda)/P'(s, \lambda)] = [\lambda s e^{\lambda s} - (e^{\lambda s} - 1)]/\lambda^2 = [1 + (\lambda s - 1)e^{\lambda s}]/\lambda^2 > 0$ since the function $[1 + (x - 1)e^x]$ is zero at $x = 0$ and is positive for $x > 0$.

One might also hypothesis that $\frac{\partial}{\partial \lambda} P'(s, \lambda) < 0$ but this is not always true for the distributions of interest. For example, in the Exponential case, $\frac{\partial}{\partial \lambda} P'(s, \lambda) = (1 - \lambda s)e^{-\lambda s}$. This is positive for $\lambda < s$, so $P'(s, \lambda)$ increases with λ until $\lambda = s$.

Lemma 5.2

Assume $\frac{\partial}{\partial \lambda} P'(s, \lambda) \sigma_P(s, \lambda) > 0$ and $\frac{\partial^2}{\partial \lambda \partial s} \sigma_P(s, \lambda) > 0$.
Then $P'(s, \lambda) \sigma_P(s, \lambda)/(1 + TP'(s, \lambda))$ is strictly increasing with λ .

Proof

Write $P'(s, \lambda)$ for $\frac{\partial}{\partial s} P(s, \lambda)$ and $P_\lambda(s, \lambda)$ for $\frac{\partial}{\partial \lambda} P(s, \lambda)$. Since $\sigma_P(s, \lambda) = P(s, \lambda)/P'(s, \lambda) - s$, the assumptions above imply that $\frac{\partial}{\partial \lambda} [P(s, \lambda) - sP'(s, \lambda)] > 0$ and $\frac{\partial}{\partial \lambda} [P(s, \lambda)/P'(s, \lambda)] >$

0. Thus $P_\lambda(s, \lambda) - sP'_\lambda(s, \lambda) > 0$ and $P_\lambda(s, \lambda)P'(s, \lambda) - P(s, \lambda)P'_\lambda(s, \lambda) > 0$, which gives

$$\begin{aligned}
& \frac{\partial}{\partial \lambda} \left[\frac{P'(s, \lambda)\sigma_P(s, \lambda)}{1 + TP'(s, \lambda)} \right] \\
&= \frac{\partial}{\partial \lambda} \left[\frac{P(s, \lambda) - sP'(s, \lambda)}{1 + TP'(s, \lambda)} \right] \\
&= \frac{[(P_\lambda(s, \lambda) - sP'_\lambda(s, \lambda))(1 + TP'(s, \lambda)) - (P(s, \lambda) - sP'(s, \lambda))TP'_\lambda(s, \lambda)]}{[1 + TP'(s, \lambda)]^2} \\
&= \frac{[(P_\lambda(s, \lambda) - sP'_\lambda(s, \lambda)) + T(P_\lambda(s, \lambda)P'(s, \lambda) - P(s, \lambda)P'_\lambda(s, \lambda))]}{[1 + TP'(s, \lambda)]^2} \\
&> 0.
\end{aligned}$$

□

The only properties of $P(s, \lambda)$ that were assumed in deriving the results in the previous sections were (in Lemma 3.1) that $P(s)$ was defined on $s \geq 0$ and was strictly concave and strictly increasing in s , with $P(0) = 0$ and with $P(s) \rightarrow 1$ as $s \rightarrow \infty$, and (Lemma 4.1) that $P'(s, \lambda)\sigma_P(s, \lambda)/(1 + TP'(s, \lambda))$ was strictly increasing with λ . Thus all those results hold for any model for $P(s, \lambda)$ which satisfies Assumption 5.1

6 Limiting Models

As T increases monotonically over the interval $[0, \infty)$, we can again show that the condition (3) for the optimal foraging time to be positive changes monotonically to the T -independent condition:

$$\gamma \leq r(0)[1 + \tau/\sigma_P(\tau)], \quad (6)$$

which we assume is satisfied for a non-degenerate problem.

For $T = 0$ the reward function again reduces to that for the single source model, since each visit to source 2 only lasts for a zero amount of time, so again $s_0^* = t^*$ and $\Gamma_0^* \equiv \Gamma(s_0^*, 0) = \gamma_1^*$. As T increases monotonically in the interval $(0, \infty)$, it is clear from the form of $\Gamma(s)$ in (1) that $\Gamma(s)$ is bounded above by γ and increases to γ for each fixed s . Hence Γ_T^* converges to γ as T increases to ∞ . It might also seem that, as T increases, the optimal foraging time will tend to zero, in particular if $\gamma > r(0)$. However, for γ satisfying (6), we can show that as T increases monotonically

in the interval $(0, \infty)$, $\Gamma(s^*(T), T)$ increases monotonically to γ but $s^*(T)$ decreases monotonically to a positive limiting value s_∞^* , where s_∞^* is the unique solution of the equation

$$r(\tau - \sigma_G(s)) = (\gamma - r(s))\sigma_P(s + \tau).$$

This is precisely the equation for the optimal foraging time on source 1 in an average cost semi-Markov decision process where the forager has probability $P(s + \tau)$ of moving to source 2 at the end of each round trip to source 1, and then stays on source 2 indefinitely.

As λ increases monotonically over the interval $[0, \infty)$, we can show that the non-degeneracy condition from (3) for the optimal foraging time to be positive becomes monotonically modified to the λ -independent condition:

$$\gamma \leq r(0)[1 + \tau/T], \quad (7)$$

which we assume is satisfied for a non-degenerate problem.

As λ increases to ∞ , the problem reduces to one in which source 2 is certain to be on each time the forager returns (or equivalently, in the ‘foraging-information’ version, the recovery time is constant and independent of the foraging trip time).

Let s_∞^* be the optimal foraging time for this limiting problem, and let Γ_∞^* be the optimal reward for the limiting problem. We can show that, as λ increases monotonically over the interval $[0, \infty)$, s_λ^* decreases monotonically to s_∞^* where s_∞^* is the unique solution of the equation

$$r(s)(\tau - \sigma_G(s)) = (\gamma - r(s))T.$$

Furthermore, Γ_λ^* increases monotonically to $\Gamma_\infty^* < \gamma$, where at $s = s_\infty^*$ (by comparison with (4)) $\Gamma(s, \lambda)$ satisfies the equation

$$\Gamma(s, \infty) = r(s) \left[1 + \frac{\tau - \sigma_G(s)}{\sigma_P(s + \tau)} \right].$$

References

Charnov, E. (1976), ‘Optimal foraging, the marginal value theorem’, *Theoretical Population Biology* **9**, 129–136.

Houston, A. I. & McNamara, J. M. (1985), 'A general theory of central place foraging for single-prey loaders', *Theoretical Population Biology* **28**, 233–262.

Houston, A. I. & McNamara, J. M. (1999), *Models of Adaptive Behaviour*, Cambridge University Press, Cambridge.

Stephens, D. W. & Krebs, J. (1986), *Foraging theory*, Princeton University Press, Princeton.