Foraging Under Competition: Evolutionarily Stable Patch-Leaving Strategies with Random Arrival Times.

1. Scramble Competition

Frédéric Hamelin
CNRS and University of Nice Sophia Antipolis–I3S
École Polytechnique de l'Université de Nice Sophia Antipolis
930 Route des Colles, B.P.145
06903 Sophia Antipolis, France
hamelin@polytech.unice.fr

Pierre Bernhard
CNRS and University of Nice Sophia Antipolis–I3S
École Polytechnique de l'Université de Nice Sophia Antipolis
930 Route des Colles, B.P.145
06903 Sophia Antipolis, France
bernhard@polytech.unice.fr

Philippe Nain
INRIA
2004 Route des Lucioles
06902 Sophia Antipolis, France
philippe.nain@sophia.inria.fr

Éric Wajnberg
INRA
400 Route des Chappes, B.P. 167
06903 Sophia Antipolis Cedex, France
wajnberg@antibes.inra.fr

Abstract

Our objective is to determine the evolutionarily stable strategy [14] that is supposed to drive the behavior of foragers competing for a common patchily distributed resource [16]. Compared to [18], the innovation lies in the fact that random arrival times are allowed.

In this first part, we investigate scramble competition: the game still yields simple Charnov-like strategies [4]. Thus we attempt to compute the optimal long-term mean rate γ^* [11] at which resources should be gathered to achieve the maximum expected fitness: the assumed symmetry among foragers allows us to express γ^* as a solution of an implicit equation, independent of the probability distribution of arrival times.

A digression on a simple model of group foraging shows that γ_N^* can be simply computed via the classical graph associated to the marginal value theorem—N is the size of the group. An analytical solution allows us to characterize the decline in efficiency due to group foraging, as opposed to foraging alone: this loss can be relatively low, even in a "bad world," provided that the handling time is relatively long.

Back to the original problem, we then assume that the arrivals on the patch follow a Poisson process. Thus we find an explicit expression of γ^* that makes it possible to perform a numerical computation: Charnov's predictions still hold under scramble competition.

Finally, we show that the distribution of foragers among patches is not homogeneous but biased in favor of bad patches. This result is in agreement with common observation and theoretical knowledge [1] about the concept of ideal free distribution [12,22].

1 Introduction

Behavioral ecology [13] attempts to assert to what extent the natural selection process could have carved animal behavior. This evolutionary approach focuses on optimal strategies in terms of capitalizing on genetic inheritance through generations; as a common currency between survival ability and reproductive success, we shall use the term—Darwinian—*fitness* [15], analogous to the concept of "utility" in economics.

In this respect, optimal foraging theory [20] seeks to investigate the behavior of an animal searching for a valuable resource such as food or a host to parasitize. In many cases, these resources are spread in the environment as distant *patches* of various *qualities*. Moreover, the resource *intake rate* suffers from patch depletion. As a consequence, it is likely advantageous to leave a patch not yet exhausted in order to find a richer one, in spite of an uncertain *travel time*. Hence the need to determine the optimal leaving rule.

In this context, Charnov's marginal value theorem [4] provides a way to gather resources at an optimal long-term mean rate γ^* that gives the best fitness a forager can expect in its environment.

Actually, this famous theoretical model is applied to a lone forager that has a monopoly on the resources it finds; it predicts that each patch should be left when the intake rate on that patch drops below γ^*, independently of either its quality or on the time invested to reach it.

Naturally, the question arises of whether this result holds for foragers competing for a common patchily distributed resource [16], i.e., whether this is an evolutionarily stable strategy [14]. The authors of [18] assume that somehow n foragers have reached a patch simultaneously, and they investigate their evolutionarily stable giving-up strategy. Our innovation lies in the fact that an a priori unlimited number of foragers reaching a patch at random arrival times is allowed.

In Section 2, we develop a mathematical model of the problem at hand and recall Charnov's classical marginal value theorem. In Section 3, we investigate the *scramble competition* case, where the only competition between foragers is in sharing a common resource.

In a companion paper [9], we extend the model to take into account actual *interference*; i.e., a decline of the intake rate due to competition.

2 Model

We consider a population of independent animals foraging freely in an environment containing a patchily distributed resource, assumed to be stationary; i.e., the spatial and qualitative statistical distributions of the patches remain constant over time. In other words, there is no environment-wide depletion but only local depletion; an ad hoc renewal process of the resource is then implicitly assumed, although it might not necessarily be an appropriate modeling shortcut [2,3]. We then focus on a single forager evolving in this environment, among its conspecifics.

2.1 Local Fitness Accumulation

2.1.1 A Lone Forager on an Initially Unexploited Patch

We consider the case of a single forager acquiring some fitness from a patch of resource. We let

- $q \in \mathbb{R}^+$ be the quality of the patch, i.e., the potential fitness it initially offers,
- $p \in \mathbb{R}^+$ be the current state of the patch, i.e., the amount of fitness remaining,
- $\rho = p/q \in \Sigma_1 = [0, 1]$ be the fitness remaining on the patch relative to its quality.

Let $f(q, \tau)$ be the fitness gathered in a time τ on a patch of quality q. Our basic assumption is that the intake rate $\dot{f} = \partial f(q, \tau)/\partial \tau$ is a known function $r(\rho)$ continuous, strictly increasing and concave. In Appendix A.3 we derive such a law from an assumption of random probing on a patch. It yields

$$\dot{f} = r(\rho), \quad f(0) = 0,$$

resulting in

$$q\dot{\rho} = -r(\rho), \quad \rho(0) = 1. \tag{1}$$

We find it convenient to introduce the solution $\phi(t)$ of the differential equation

$$\dot{\phi} = -r(\phi), \quad \phi(0) = 1.$$

Theorem 2.1. *Our model is given by*

$$f(q, \tau) = q\left[1 - \phi\left(\frac{\tau}{q}\right)\right]. \tag{2}$$

It yields: $\forall q$,

- $f(q, 0) = 0$,
- $\tau \mapsto f(q, \tau)$ *is strictly increasing and concave,*
- $\lim_{\tau \to \infty} f(q, \tau) = q$.

2.1.2 A Lone Forager on a Previously Exploited Patch

Assume that the forager reaches a patch that has already been exploited to some extent by a conspecific. The patch is characterized by its initial quality q and its ratio of available resource ρ_0 at arrival time. The dynamics are still (1) initialized at $\rho(0) = \rho_0$, and the fitness gathered is

$$f(q, \rho_0, \tau) = p_0 - p(\tau) = q[\rho_0 - \rho(\tau)].$$

This is depicted on the reduced graph, Figure 1.

2.1.3 Several Foragers on a Patch

Assume that $n \in \mathbb{N}$ identical foragers are on the same patch. Let the sequence of forager arrivals times be $\sigma = \{\sigma_1, \sigma_2, \ldots, \sigma_n\}$ and $i \in \{1, 2, \ldots, n\}$. By definition, scramble competition lets the intake rate be independent of n, thus

$$\forall i,\ \dot{f_i} = \dot{f} = r(\rho), \quad f_i(\sigma_i) = 0.$$

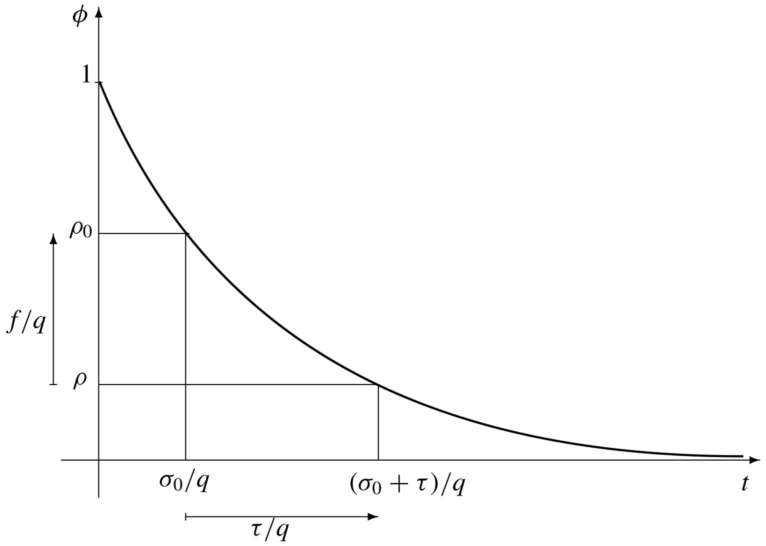

Figure 1: The reduced graph.

Nevertheless, the speed of depletion is multiplied by n:

$$\dot{p} = q\dot{\rho} = -n\dot{f}, \quad \rho(0) = \rho_0.$$

2.2 Global Fitness Accumulation

2.2.1 The Marginal Value Theorem

In order to optimally balance the residence times on the differing patches, a relevant criterion is the average fitness acquired relative to the time invested: assume the quality q of the patch visited is a random variable with cumulative distribution function $\mathcal{Q}(q)$. We allow the residence time to be a random variable, measurable on the sigma algebra generated by q. We also assume that the travel time θ is a random variable of known distribution and let $\bar{\theta} = \mathbb{E}\theta$. It yields

$$\gamma = \frac{\mathbb{E}f(q,\tau)}{\bar{\theta} + \mathbb{E}\tau}. \tag{3}$$

Theorem 2.2. *Charnov's marginal value theorem: the maximizing admissible τ is given as a function of q by the rule*

- *either $\frac{\partial f}{\partial \tau}(q, 0) \le \gamma^*$ and $\tau^* = 0$,*
- *or τ is such $\frac{\partial f}{\partial \tau}(q, \tau^*)$ that γ^*,*

where γ^* is obtained by placing τ^* in (3).

Proof. Call $\mathrm{D}\gamma$ the Gâteaux derivative of γ in (3). Euler's inequality reads, for any $\delta\tau$ such that $\tau^* + \delta\tau$ is admissible,

$$\mathrm{D}\gamma.\delta\tau = \frac{1}{\bar{\theta} + \mathbb{E}\tau^*} \int_{\mathbb{R}^+} \left[\frac{\partial f}{\partial \tau}(q, \tau^*) - \gamma^*\right] \delta\tau(q)\ \mathrm{d}\mathcal{Q}(q) \le 0.$$

The increment $\delta\tau$ may have any sign if τ^* is strictly positive, but it must be positive if τ^* is zero. Hence the result. This is a marginal improvement over Charnov's marginal value theorem. □

2.2.2 A Lone Forager Evolving in Our Model

As in the classical model, we consider in this subsection a lone forager which has a monopoly on resource it finds. Under the main modeling assumption of Section 2.1.1, the criterion becomes

$$\gamma = \mathbb{E}\left\{q\left[1 - \phi\left(\frac{\tau(q)}{q}\right)\right]\right\} \Big/ \left[\bar{\theta} + \mathbb{E}q\frac{\tau(q)}{q}\right].$$

Charnov's optimal patch-leaving strategy is to leave when $\dot{f} = \gamma^*$. In our model, the intake rate of a lone forager only depends on ρ, hence an equivalent

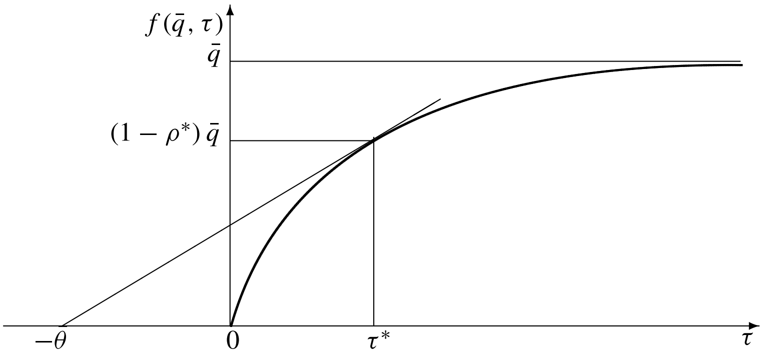

Figure 2: The marginal value theorem.

threshold is $\rho^* = r^{-1}(\gamma^*)$. Note that any unexploited patch should be attacked independently of its quality since, for every q, $(\partial f/\partial\tau)(q,0) = r(1)$ and $r(1) > \gamma^*$ by construction.

A simple property of our model—see equation (2)—is that $\tau^*(q)/q$ is a constant, say z, $z = \phi^{-1}(\rho^*)$, for any q. Hence the following expression of γ^*, if we let $\bar{q} = \mathbb{E}q$:

$$\gamma^* = \frac{1-\phi(z)}{\bar{\theta}/\bar{q} + z}.$$

Therefore, one can compute the optimal value of ρ^*, or equivalently γ^*, via the well-known graph in Figure 2. One can notice the duality between $\bar{q}$ and $\bar{\theta}$: multiplying the average level of resource by n is equivalent to dividing the average travel time by n.

As a consequence, the patches should be relatively less depleted in a *good world* [6]—with rich and easy to find patches—than in a bad one—with scarce patches offering few resources.

Thus, in our particular case, only $\bar{q}$ is relevant: "it suffices to know $\bar{q}$—rather than $\mathcal{Q}(q)$—to be able to behave optimally." Hence this model stands if the resource is "only" stationary in a weak sense; i.e., if the **means** of the qualitative and spatial[1] statistical distributions of the patches remain constant over time.

2.2.3 An Explicit Formula for ρ^*

We now make use of the particular form of the function r of Appendix A.3: it allows the function $\phi(t)$ to be inverted into

$$\phi^{-1}(\rho) = h(1-\rho) - \alpha\ln(\rho). \tag{4}$$

---

[1] More precisely, this is the mean travel time which has to remain stationary.

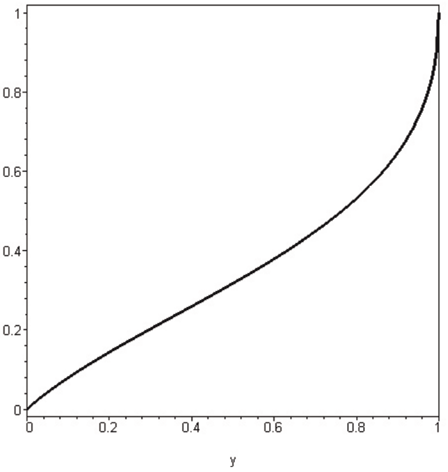

Figure 3: The function $\rho^*(y)$.

It yields an analytical solution, simply by performing an optimization in ρ as $\rho^* = \arg\max_\rho \gamma(\rho)$ with

$$\gamma(\rho) = \frac{1-\rho}{\bar{\theta}/\bar{q} + \phi^{-1}(\rho)}, \quad \rho \in \Sigma_1.$$

Hence

$$\rho^* = -1/W_{-1}(-e^{-(1+x)}), \tag{5}$$

where $x = \bar{\theta}/(\alpha\bar{q})$ and W_{-1} is the Lambert W function as defined in [7]—this is indeed the "*nonprincipal*" branch of this multi-valued function that contains the solution as $\rho^* \in \Sigma_1 \Rightarrow W \leq -1$.

Thus ρ^* depends on $1+x$, a sort of inverse duty cycle as $\alpha\bar{q}$ is the time needed to cover an average patch in a systematic way; note that ρ^* does not depend on the handling time h although γ^* does. Let $y = 1/(1+x) = \alpha\bar{q}/(\alpha\bar{q}+\bar{\theta})$; the function $\rho^*(y)$ is plotted in Figure 3.

As expected, in a bad world the patches should be relatively more depleted than in a good one—high "duty cycle" y—where the forager would be harder to please.

3 Scramble Competition

Scramble competition only takes into account the fact that the resource depletes faster due to simultaneous foraging activities on the patch. As a consequence, the departure of a forager only slows down the depletion. Hence there is no hope to see ρ, or equivalently the intake rate, increase. Moreover, as foragers are assumed to be identical, they surely share the same optimal long-term mean rate γ^* and thus must leave at the same time, independently of their arrival times. Hence adopting commonly the Charnov's patch-leaving strategy given by Theorem 2.2 provides a Nash equilibrium in nonanticipative strategies among the population. As this latter is both strict and symmetric, this is indeed an evolutionarily stable strategy—this is detailed in Appendix B of the second part [9].

3.1 An Attempt to Get an Analytical Expression of γ^*

Let us assume that all foragers apply Charnov's patch-leaving strategy, i.e., they leave when $\dot{f} = \gamma^*$ or equivalently when $\rho = \rho^*$. As a consequence, when a patch is left, it is at a density ρ^* which makes it unusable for any forager. Hence all admissible patches encountered are still unexploited, with $\rho_0 = 1$.

Let t be the time elapsed since the patch was discovered. For a fixed ordered sequence of σ_j's, $j \in \{1, 2, \dots, n\}$, let us introduce a "forager second"—as one speaks of "man month"—$s = S(t, \sigma)$ defined by

$$\dot{s} = j \quad \text{if } \sigma_j \le t < \sigma_{j+1}, \quad s(0) = 0.$$

Equivalently

$$\text{for } t \in (\sigma_j, \sigma_{j+1}), \quad S(t, \sigma) = j(t - \sigma_j) + \sum_{k=1}^{j-1} k(\sigma_{k+1} - \sigma_k). \tag{6}$$

The function $t \mapsto S(t, \sigma)$ is strictly increasing. It therefore has an inverse function denoted $t = S_\sigma^{-1}(s)$, easy to write explicitly in terms of the $s_j = S(\sigma_j, \sigma)$:

$$\text{for } s \in (s_j, s_{j+1}), \quad S_\sigma^{-1}(s) = \frac{1}{j}(s - s_j) + \sum_{k=1}^{j-1} \frac{1}{k}(s_{k+1} - s_k).$$

According to Section 2.1.3, the dynamics of the patch are now

$$\dot{p} = q\dot{\rho} = -jr(\rho), \quad \text{for } t \in (\sigma_j, \sigma_{j+1}).$$

As a consequence, the patch trajectory satisfies

$$\rho(t) = \phi\left(\frac{1}{q}S(t, \sigma)\right).$$

We shall also let t^* be such that $\rho(t^*) = \rho^*$, i.e., to be explicit, if not clearer, $t^* = S_\sigma^{-1} \circ (q\phi^{-1}) \circ r^{-1}(\gamma^*)$.

Let us regroup possible combinations of σ's by the maximum number of foragers reached before they all leave the patch, say $\hat{n}$. When they leave, they have retrieved an amount $\sum_i f_i = q(1 - \rho^*)$ of the resource. By symmetry, the expectation of fitness acquired is, for each of them,

$$\mathbb{E}_\sigma f = \frac{q}{\hat{n}}(1 - \rho^*).$$

Moreover, this is exactly the amount of resource each would have acquired if they all had arrived simultaneously, since in that case they all acquire the same amount of resource.

Let us call a *central trajectory* of order $\hat{n}$ that particular trajectory where all $\hat{n}$ foragers arrived at time zero. We denote with an index $\odot$ the corresponding quantities. Hence, for all $\hat{n}$, $\mathbb{E}_\sigma(f) = f_\odot$.

Now, for a given ordered sequence σ of length $\hat{n}$, the reference forager may have occupied any rank, from 1 to $\hat{n}$. Let ξ be this rank. Call τ_ξ^* its residence time depending on ξ. Note that since they all leave simultaneously,

$$\forall \hat{n},\ \forall \xi \in \{1, \dots, \hat{n}\}, \quad \tau_\xi^* = \sigma_{\hat{n}} - \sigma_\xi + \tau_{\hat{n}}^*.$$

Again, for reasons of symmetry,

$$\mathbb{E}_\xi \tau_\xi^* = \sigma_{\hat{n}} - \frac{1}{\hat{n}} \sum_{j=1}^{\hat{n}} \sigma_j + \tau_{\hat{n}}^*. \tag{7}$$

Now, τ_n^* is defined by $\phi(S(\sigma_{\hat{n}} + \tau_{\hat{n}}^*, \sigma)/q) = \rho^*$, i.e., according to equation (6):

$$\hat{n}[(\tau_{\hat{n}}^* + \sigma_{\hat{n}}) - \sigma_{\hat{n}}] + \sum_{j=1}^{\hat{n}-1} j(\sigma_{j+1} - \sigma_j) q \phi^{-1}(\rho^*).$$

Note that

$$\sum_{j=1}^{\hat{n}-1} j(\sigma_{j+1} - \sigma_j) = \hat{n}\sigma_{\hat{n}} - \sum_{j=1}^{\hat{n}} \sigma_j.$$

Hence we get

$$\tau_{\hat{n}}^* = \frac{q}{\hat{n}} \phi^{-1}(\rho^*) - \sigma_{\hat{n}} + \frac{1}{\hat{n}} \sum_{j=1}^{\hat{n}} \sigma_j.$$

On the central trajectory of order $\hat{n}$, it holds that $s = \hat{n}t = \hat{n}\tau$, so that

$$\tau_\odot^* = \frac{q}{\hat{n}} \phi^{-1}(\rho^*),$$

so that finally

$$\tau_{\hat{n}}^* = \tau_\odot^* - \sigma_{\hat{n}} + \sum_{j=1}^{\hat{n}} \sigma_j.$$

Place this in (7), and we obtain $\mathbb{E}_\xi \tau_\xi^* \tau_\odot^*$. But this last quantity is independent of σ, so that, for any fixed q and $\hat{n}$,

$$\mathbb{E}_\sigma \tau^* = \tau_\odot^* = \frac{q}{\hat{n}} \phi^{-1}(\rho^*).$$

The random variables q and $\hat{n}$ are surely correlated, as the foragers stay a longer time on better patches, and are thus likely to end up more numerous. Similarly, $\hat{n}$ surely depends on ρ^*; hence we use $\mathbb{E}^*$ to mean that we take the expected value over all patch qualities and sequences of arrival under the optimal scenario. Let then $q^* = \mathbb{E}^*(q/\hat{n})$. We obtain the fixed point equation:

$$r(\rho^*) = \gamma^* = \frac{1-\rho^*}{\bar{\theta}/q^* + \phi^{-1}(\rho^*)}. \tag{8}$$

Yet, it remains a partial result as long as we do not know how to express q^* as a function of ρ^*.

3.1.1 A Digression on a Simple Model of Group Foraging

In this subsection we relax the assumption of independent foragers provided that they are identical—all we need up to now is symmetry among foragers.

Thus let us consider a group of N identical individuals foraging "patch-by-patch"; i.e., the travel times are assumed to be too long to allow the group to cover two patches simultaneously. In this "*information-sharing*" model [8], once a patch is discovered by any member of the group, the others are assumed to join it sequentially. That is, we assume that the group spread itself in a radius [17] that allows every member to benefit from the poorest patch, as a function of the optimal profitability threshold ρ^* computed below. This assumption results in $\hat{n}$ equal to N independently of q and ρ^*. Therefore, the formula (8) is exactly the same as applying Charnov's marginal value theorem for both deterministic patch quality $\bar{q}/N$ and travel time $\bar{\theta}$. One can compute γ^* graphically, as done in Figure 4.

Obviously, foraging in a group is less[2] efficient in term of fitness gathering than foraging alone, if no advantage [5] is taken into account. However, it does not imply that the individual efficiency $\gamma^*(N) =: \gamma_N^*$ is an homogeneous function of

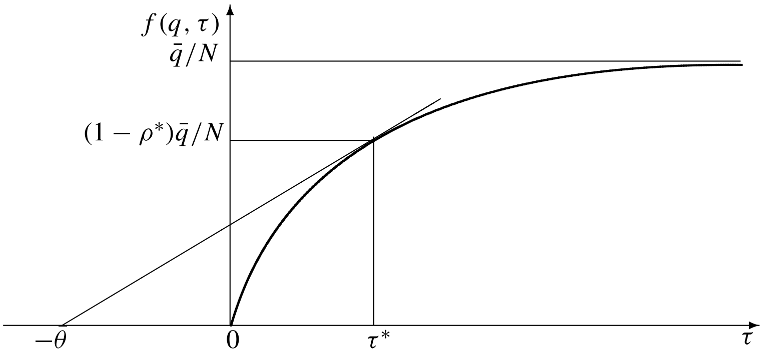

Figure 4: The marginal value theorem.

---

[2] At best equal, if ever the mean travel time was divided by N while foraging in a group [5].

degree -1; indeed, the relation $\gamma_N^* = \gamma_1^*/N$ would be true if the individuals were acting as if they were alone.

If we make use of the particular form of the function r of Appendix A.3, $N \mapsto \rho^*(N)$ is given by equation (5) with $x = N\bar{\theta}/(\alpha\bar{q})$; as $\gamma^* = r(\rho^*)$, the function $N \mapsto \gamma^*(\rho^*(N))$ is easily obtained. Let $\beta = \alpha/h$, $\mu = \bar{\theta}/(\alpha\bar{q})$ and

$$\Gamma(N) := \gamma_1^*/\gamma_N^* = \left[1 - \beta W_{-1}\left(-\mathrm{e}^{-(1+N\mu)}\right)\right]/\left[1 - \beta W_{-1}\left(-\mathrm{e}^{-(1+\mu)}\right)\right].$$

Let $\kappa = \beta/\left[(1 - \beta W_{-1}\left(-\mathrm{e}^{-(1+\mu)}\right)\right]$ and $\Gamma'(N) := \mathrm{d}\Gamma(N)/\mathrm{d}N$; we obtain

$$\Gamma'(N) = \kappa\mu W_{-1}\left(-\mathrm{e}^{-(1+N\mu)}\right)/\left[1 + W_{-1}\left(-\mathrm{e}^{-(1+N\mu)}\right)\right] > 0.$$

Let $\Gamma''(N) := \mathrm{d}\Gamma(N)/\mathrm{d}N^2$. We have

$$\Gamma''(N) = -\mu^2\kappa W_{-1}\left(-\mathrm{e}^{-(1+N\mu)}\right)\Big/\left\{\left[1 + W_{-1}\left(-\mathrm{e}^{-(1+N\mu)}\right)\right]^3\right\} < 0.$$

Thus $\Gamma(N)$ is strictly increasing but concave. Therefore, foraging in a group should yield more than only an Nth of what a lone forager would get, provided that the strategy is adapted to the size of the group.

Moreover, it is easy to see that $\lim_{N\to\infty}\Gamma(N) = \infty$, that $\lim_{N\to\infty}\Gamma'(N) = \kappa\mu$ and that $\Gamma''(N)$ increases abruptly in the vicinity of zero. Hence $\Gamma(N)$ can be approximated by an affine function of slope $\kappa\mu$: let $\tilde{\Gamma}(N) := (1 - \kappa\mu) + N\kappa\mu \sim \Gamma(N)$. The "duty cycle" is now $y = 1/(1 + \mu)$. Figure 5 approximately characterizes the decline in individual efficiency resulting from foraging in a group, as opposed to foraging alone. We see that even in a bad world, the loss can be relatively small if the handling time is relatively long.

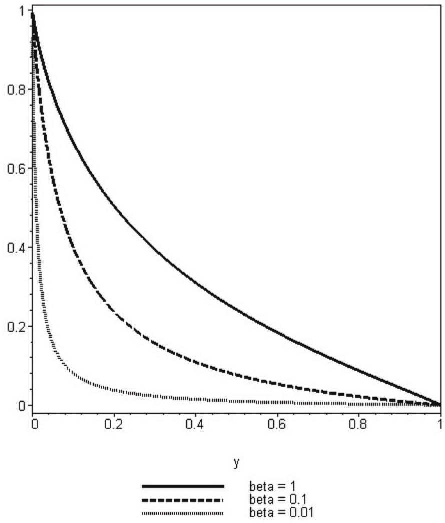

Figure 5: The function $y \mapsto \kappa\mu$.

3.1.2 Back to the Original Problem

As $q^* = \mathbb{E}_q \mathbb{E}^*(q/\hat{n}|q) = \mathbb{E}_q q \mathbb{E}^*(1/\hat{n}|q)$, we shall first consider that q is fixed.

Let ζ_1 be the time a lone forager would stay on a patch of quality q if not disturbed by an intruder: $\zeta_1 := \tau^*_{\odot}\hat{n} = q\phi^{-1}(\rho^*)$. In order to perform an optimization in ρ as in Section 2.2.3, our purpose is now to compute the function $\zeta_1 \mapsto \mathbb{E}^*(1/\hat{n})$. Let the successive arrival times on a patch be a Poisson process with intensity $\lambda > 0$. This means that the successive interarrival times form a sequence of mutually independent random variables $\{w_n\}$, exponentially distributed with mean $1/\lambda$.

Once a first intruder has arrived, the maximum—in the absence of further intruders—remaining time to deplete the patch up to ρ^* is divided by two as the depletion speed doubles; more generally, after the nth arrival, the maximum remaining residence time is reduced by a factor $(n-1)/n$. Our aim is now to express the cumulative distribution function of $\hat{n}$ in closed form as a function of ζ_1, from which we will deduce $\mathbb{E}^*(1/\hat{n})$.

A way to formulate the problem is the following one: let ζ_n be the remaining effort in "forager seconds" when the nth forager arrives. Clearly

$$\zeta_{n+1} = \zeta_n - n w_n, \quad n \geq 1.$$

Note that the mapping $n \to \zeta_n$ is nonincreasing. Therefore, the random variable $\hat{n}$ is characterized by $\zeta_{\hat{n}+1} \leq 0 < \zeta_{\hat{n}}$.

We have

$$\begin{aligned} P(\hat{n} > M) &= P(\zeta_2 > 0, \ldots, \zeta_{M+1} > 0), \\ &= P(\zeta_1 > w_1 + 2w_2 + \cdots + M w_M). \end{aligned}$$

This is equivalent to finding the probability distribution of $\sum_{n=1}^{M} n w_n$. As the probability density function of the sum of independent random variables is given by the convolution product of their density functions, one can obtain it by inverting the product of the Laplace–Stieltjes transforms of their probability distributions. This is done in Appendix B and it yields

$$\mathbb{E}^*(1/\hat{n}|q) = 1 - \sum_{l=1}^{\infty} (1 - e^{-\lambda\zeta_1/l}) e^{-l} \frac{l^{l-1}}{l!}.$$

Hence

$$q^* = \mathbb{E}^*(q/\hat{n}) = \bar{q} - \sum_{l=1}^{\infty} \left[\left(\bar{q} - \int_0^{\infty} \mathrm{e}^{-\lambda\zeta_1/l} q \,\mathrm{d}\mathcal{Q}(q) \right) e^{-l} \frac{l^{l-1}}{l!} \right].$$

We now make use of the particular form of $\phi^{-1}(\rho)$ given by equation (4); it yields $\zeta_1 = q[h(1-\rho) - \alpha \ln(\rho)]$.

As the Laplace transform of $q(\mathrm{d}\mathcal{Q}(q)/\mathrm{d}q)$ is the derivative of the Laplace transform of $-\mathrm{d}\mathcal{Q}(q)/\mathrm{d}q$, it yields

$$\int_0^{\infty} q\,\mathrm{d}\mathcal{Q}(q)\mathrm{e}^{-\lambda\zeta_1/l} - \mathcal{L}'(\hat{\nu}),$$

with $\hat{\nu} = \lambda[h(1-\rho) - \alpha\ln(\rho)]/l$, where $\mathcal{L}(\nu)$ is the Laplace–Stieltjes transform of q and $\mathcal{L}'(\nu) = \mathrm{d}\mathcal{L}(\nu)/\mathrm{d}\nu$.

Hence

$$q^* = \bar{q} - \sum_{l=1}^{\infty}\left\{[\bar{q} + \mathcal{L}'(\hat{\nu})]e^{-l}\frac{l^{l-1}}{l!}\right\}.$$

Although we now get an explicit expression of $\gamma(\rho)$ as, according to equation (8),

$$\gamma(\rho) = \frac{(1-\rho)}{\bar{\theta}/q^* + \phi^{-1}(\rho)},$$

this expression does not allow us to find an analytical expression for $\rho^* = \arg\max_{\rho}\gamma(\rho)$.

However, one can perform some numerical computations, as done in Figure 6. We took α as a time unit, $\beta = \alpha$, a unique $q = 200$ units of fitness, $\theta = 50\alpha$ and $L = 100$ for numerical computations, as suggested in Appendix B. At $\lambda \sim 0$, the mean interarrival time is infinite, thus we took $\forall\rho, \mathbb{E}(1/\hat{n}) = 1$. $\lambda = 0.05$ is

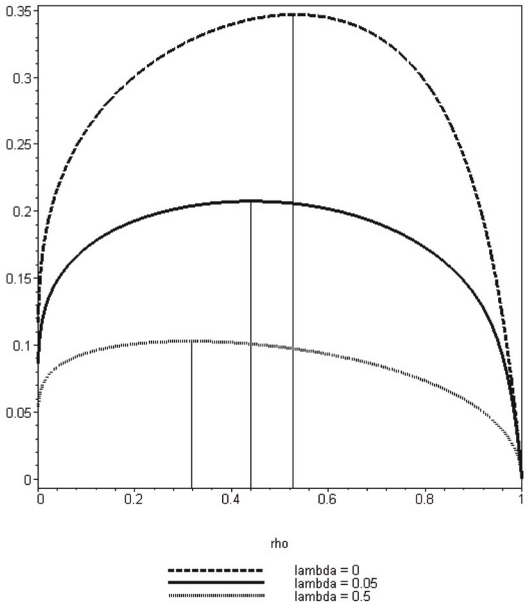

Figure 6: The function $\gamma(\rho)$.

a fair intensity as the mean interarrival time equal to 20α. $\lambda = 0.5$ is an extreme intensity as the mean interarrival time is equal to 2α.

In agreement with Charnov's model, the patches should be more depleted in a bad world—now in terms of the possible presence of competitors.

4 Concluding Remarks

Unavoidably, the consideration of the number of foragers reaching a patch as a function of its quality raises the issue of the relation with another central concept in foraging theory: the *ideal free distribution* [12,22]. It focuses on the distribution that corresponds to a Nash equilibrium among the foragers; i.e., into such a configuration, no one can individually improve its intake rate by moving instantaneously elsewhere. Hence the intake rates of identical foragers should be permanently equalized.

A simple property of our model—see equation (2)—is that a homogeneous and synchronous distribution of foragers yields a permanent equalization of their intake rates; i.e., if the number of foragers on any patch is proportional to patch quality and if they all reach their respective patch at the same time, their intake rates would remain equalized as all patch densities would decrease at the same speed.

Compared to that distribution, the calculations of Appendix B let one compute $\zeta_1 \mapsto \mathbb{E}^*\hat{n}$, the expected maximum number of foragers as a function of patch quality where now ρ^* is fixed and thus ζ_1 is proportional to q:

$$\mathbb{E}^*(\hat{n}) = 1 + \sum_{l=1}^{\infty}(1 - e^{-\lambda\zeta_1/l})e^{-l}\frac{l^{l-1}}{l-1!}.$$

It can be easily shown that the function $\zeta_1 \mapsto \mathbb{E}^*\hat{n}$ is increasing but concave, so good patches seem under matched relative to the "ideal free" distribution mentioned above. This deviation is in agreement with the common observation [21] and previous theoretical results [1] regarding the effect of perturbations such as nonzero travel time—or equivalently the foragers' asynchrony here.

Acknowledgments

This work is part of GDR 2155 "Écologie Comportementale" (CNRS commission 29), and the ESF/BEPAR scientific programme. We thank Minus van Baalen, Carlos Bernstein, Joel S. Brown, Michel de Lara, Jean-Sébastien Pierre, and an anonymous referee for their comments.

Appendix A Modeling Patch Depletion

A.1 Discrete Foraging

We consider in this subsection a situation where the resource comes as a finite number of tokens. We let $q \in \mathbb{N}$—for *quality*—be the initial number of tokens in the unvisited patch.

In our model, a token of resource remains on the patch once exploited, as an empty token. The forager is assumed to search for tokens at random—it is not supposed to search the patch in a systematic way—so that the distribution of depleted resource tokens among the patch will be assumed to be uniform at all times. Thus the forager finds itself more and more often probing a possible resource that turns out to be void. As a result, its efficiency decreases, prompting it to usually leave the patch before it is completely depleted. The decision parameter in the theory of patch use is the time τ that the forager spends on the patch before leaving it, or the *residence time*. We let α be the time it takes to move to a new token and probe it and h, the *handling time*, be the time it takes to actually exploit a token of resource. Let t_k be the time at which the kth valid resource token is found. It is actually exploited at time $t_k + h$. Let p_k be the amount of resource remaining on the patch *after* the kth unit is taken, i.e., $p_k = q - k$—and hence $p_0 = q$. Let also $\rho_k = p_k/q$ be the density of good resource tokens. We seek the law for t_{k+1}.

The forager finds a potential item of resource, possibly already exploited, every α units of time. For a given $t = t_k + h + \ell\alpha$, the event $t_{k+1} = t$ is equivalent to the fact that the items found at times $t_k + h + \alpha, t_k + h + 2\alpha, \ldots, t_k + h + (\ell - 1)\alpha$ were already exploited, and the one found at time $t_k + h + \ell\alpha$ was not. During that time, ρ does not change, so that, assuming these events are independent—the patch is attacked in a homogeneous fashion—the probability of this event is

$$P_{k,\ell} = (1 - \rho_k)^{\ell-1}\rho_k.$$

Therefore, the expected time t_{k+1} is given by

$$\mathbb{E}(t_{k+1} - t_k - h) = \sum_{\ell=1}^{\infty}(1 - \rho_k)^{\ell-1}\rho_k\ell\alpha = \frac{\alpha}{\rho_k}.$$

Hence

$$\mathbb{E}(t_{k+1} - t_k) = \frac{\alpha + \rho_k h}{\rho_k}. \tag{A.1}$$

Deriving from there the law f, i.e., the expectation of the number of good resource tokens found in a given time τ, is done in Appendix A.2. One computes, for $n \le q$,

$$P_k^n := P\{t_n = k\alpha + (n - 1)h\},$$

and finds that it can be expressed in terms of products a_m^n of combinatorial coefficients

$$a_m^n = (-1)^{n-1}\binom{q-1}{n-1}(-1)^m\binom{n-1}{m},$$

as (equation(A.3))

$$P_k^n = \sum_{m=0}^{n-1} a_m^n \left(\frac{m}{q}\right)^{k-1}.$$

Then, let $k_n = \mathrm{Int}[(\tau - nh)/\alpha]$. The expected harvest is

$$f(q,\tau) = \sum_{n \le q} n P^n_{k_n}.$$

A.2 Combinatorics of Discrete Foraging

We have seen, from equation (A.1), that

$$P\{t_{k+1} - t_k - h\ell\alpha\} =: P_{k,\ell} = (1-\rho_k)^{\ell-1}\rho_k.$$

From there, we compute the full law for the residence time τ_n as follows. Let $P^n_k := P\{t_n = k\alpha + (n-1)h\}$. It is the probability that k attempts were necessary to find n items. It is the probability that $t_0 + (t_1 - t_0 - h) + \cdots + (t_n - t_{n-1} - h) = k\alpha$. The characteristic function of the sum of independent random variables is the product of their characteristic functions. Let therefore

$$\hat{P}_k(z) = \sum_{\ell=1}^{\infty} P_{k,\ell} z^{-\ell} \frac{\rho_k}{z - (1-\rho_k)}.$$

The characteristic function of t_n is therefore

$$\begin{aligned}\hat{P}^n(z) &= \hat{P}_0(z)\hat{P}_1(z)\cdots\hat{P}_{n-1}(z),\\ &= \frac{\rho_0\rho_1\ldots\rho_{n-1}}{[z-(1-\rho_0)][z-(1-\rho_1)]\ldots[z-(1-\rho_{n-1})]}.\end{aligned}$$

If, now, $\rho_0 = 1$ and $\rho_\ell = 1 - \ell/q$, we obtain

$$\hat{P}^n(z)\frac{\left(1-\frac{1}{q}\right)\left(1-\frac{2}{q}\right)\cdots\left(1-\frac{n-1}{q}\right)}{z\left(z-\frac{1}{q}\right)\cdots\left(z-\frac{n-1}{q}\right)}. \tag{A.2}$$

It remains to expand this rational fraction in powers of z^{-1} to compute the probability sought: $P^n_k = P\{t_n = k\alpha + (k-1)h)\}$. This is done through a decomposition in simple elements and expansion of each. If we let

$$\hat{P}^n(z) = \sum_{m=0}^{n-1} \frac{a^n_m}{z - \frac{m}{q}},$$

we obtain, for $n \le q$,

$$a^n_m = (-1)^{n-m-1}\frac{(q-1)!}{(q-n)!\,m!\,(n-m-1)!}(-1)^{n-m-1}\binom{q-1}{n-1}\binom{n-1}{m},$$

and the expansion yields, still for $n \le q$:

$$P^n_k = \sum_{m=0}^{n-1} a^n_m \left(\frac{m}{q}\right)^{k-1}, \tag{A.3}$$

with the convention that $0^0 = 1$, which is useless in practice, since for $k > 1$, the only interesting case, the term $m = 0$ can clearly be omitted.

It can be directly shown that the above formulas enjoy the desired properties that for any fixed $n \leq q$, the P_k^n are null if $k < n$, and add up to one:

$$\forall k < n, P_k^n = 0, \quad \text{and} \quad \sum_{k=n}^{k=\infty} P_k^n = 1.$$

A.3 Continuous Foraging

Following most of the literature, we shall use a continuous approximation of the above theory, assuming that the resource is, somehow, a continuum: now, $q \in \mathbb{R}^+$. Let us introduce a surface—or volume—resource density D.[3] Two time constants enter into the model:

- α is the time it takes for the forager to explore a unit area that could contain a quantity D of resource, if it were not yet exploited.
- h is the extra time, or *handling time*, it takes to actually retrieve a unit of resource if necessary.

Our hypothesis is that a ratio ρ of the patch area is productive so that an area dæ produces a quantity

$$\mathrm{d}f = \rho D \mathrm{d}æ$$

of resource and the time necessary to gather it is

$$\mathrm{d}t = \alpha \mathrm{d}æ + \rho D h \mathrm{d}æ.$$

Hence we get

$$\dot{f} = \frac{\rho D}{\alpha + \rho D h} := r(\rho).$$

One can relate this equation to Holling's equation [10] by substituting α by the *attack rate*, a parameter giving the amount of resource attacked per unit time, $a = D/\alpha$.

Appendix B Evaluating a Probability Distribution

Let $w_1, \ldots, w_n$ be mutually independent random variables with common probability distribution $P(w_j < x) = 1 - \exp(-\lambda x)$. Define $Y_k = w_1 + 2w_2 + \cdots + kw_k$. The Laplace–Stieltjes transform (LST) of Y_k is given by

$$f_k(s) := \mathbb{E}(e^{-sY_k}) = \prod_{j=1}^{k} \frac{\lambda}{\lambda + js}.$$

---

[3] In the body of this chapter, we assume that the unit of area chosen is such that $D = 1$ or, equivalently, α is the time required to probe one unit of resource.

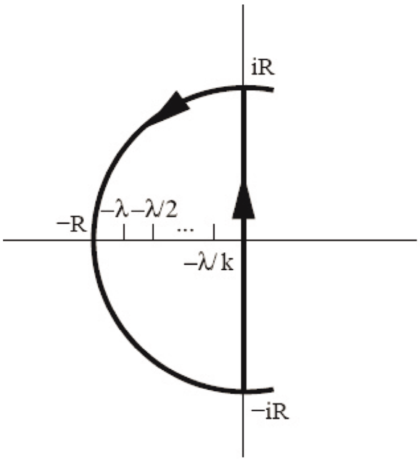

Figure B.1: The contour C_R.

Denote by $g_k(t)$ the density function of Y_k, namely, $g_k(t) = dP(Y_k < t)/dt$. The function $g_k(t)$ may be computed by inverting the LST $f_k(s)$. This gives

$$g_k(t) = \frac{1}{2\pi i} \int_{\gamma - i\infty}^{\gamma + i\infty} e^{st} f_k(s) ds,$$

where γ is any real number chosen so that the line $s = \gamma$ lies to the right of all singularities of $f_k(s)$ [19]. The function $f_k(s)$ has only k simple poles, located at points $s = -\lambda/j$ for $j = 1, \ldots, k$. We may therefore take $\gamma = 0$.

The usual way of computing the complex integral $\int_{-i\infty}^{i\infty} e^{st} f_k(s) ds$ is first to consider the complex integral $I(R) := \int_{C_R} e^{st} f_k(s) ds$, where C_R is the contour defined by the half circle in the left complex plane centered at $s = 0$ with radius R, and the line $[-iR, iR]$ on the imaginary axis. R is any real number such that $R > 1/\lambda$ so that all poles of $f_k(s)$ are located inside the contour C_R; see Figure B.1. By applying the residue theorem we see that

$$I(R) = 2\pi i \sum_{l=1}^{k} \text{Residue } (e^{st} f_k(s); s = -\lambda/l).$$

Since the residue of the function $e^{st} f_k(s)$ at $s = -\lambda/l$ is equal to $e^{-\lambda t/l}(\lambda/l) \times \prod_{\substack{j=1 \\ j \neq l}}^{k} l/(l-j)$, we find that

$$I(R) = 2\pi i \sum_{l=1}^{k} e^{-\lambda t/l} \frac{\lambda}{l} \prod_{\substack{j=1 \\ j \neq l}}^{i} \frac{l}{l-j}. \tag{B.1}$$

At this point we have shown that

$$\begin{aligned} g_k(t) &= \frac{1}{2\pi i} \lim_{R\to\infty} \int_{-iR}^{iR} e^{st} f_k(s)ds, \\ &= \frac{1}{2\pi i} \lim_{R\to\infty} I_R - \frac{1}{2\pi i} \lim_{R\to\infty} \int_{\Gamma_R} e^{st} f_k(s)ds, \\ &= \sum_{l=1}^{k} e^{-\lambda t/l} \frac{\lambda}{l} \prod_{\substack{j=1 \\ j\neq l}}^{k} \frac{l}{l-j} - \frac{1}{2\pi i} \lim_{R\to\infty} \int_{\Gamma_R} e^{st} f_k(s)ds, \end{aligned}$$

by using (B.1), where $\Gamma_R = C_R - [-iR, iR]$.

One can find constants $K > 0$ and $a > 0$ such that $|f_k(s)| < K/R^a$ when $s = Re^{i\theta}$ for R large enough,[4] so that the integral in the latter equation vanishes as $R \to \infty$ [19, Theorem 7.4].

In summary, the density function $g_k(s)$ of the r.v. Y_k is given by

$$g_k(t) = \sum_{l=1}^{k} e^{-\lambda t/l} \frac{\lambda}{l} \prod_{\substack{j=1 \\ j\neq l}}^{k} \frac{l}{l-j}. \tag{B.2}$$

Let us now come back to the original problem. Define with $\zeta > 0$

$$n = \inf\{k \geq 1 : \zeta - (w_1 + 2w_2 + \cdots + kw_k) \leq 0\},$$

or equivalently

$$n = \inf\{k \geq 1 : \zeta - Y_k \leq 0\}.$$

We are interested in $\mathbb{E}(1/n)$. We have

$$\begin{aligned} P(n > M) &= P(\zeta - Y_1 > 0, \ldots, \zeta - Y_M > 0), \\ &= P(Y_1 < \zeta, \ldots, Y_M < \zeta), \\ &= P(Y_M < \zeta). \end{aligned} \tag{B.3}$$

Since $P(n = M) = P(n > M - 1) - P(n > M)$ we see from (B.3) that for $M \geq 2$,

$$\begin{aligned} P(n = M) &= P(Y_{M-1} < \zeta) - P(Y_M < \zeta) \\ &= \int_0^\zeta g_{M-1}(t)dt - \int_0^\zeta g_M(t)dt \qquad \text{(B.4)} \\ &= \sum_{l=1}^{M-1} (1 - e^{-\lambda\zeta/l}) \prod_{\substack{j=1 \\ j\neq l}}^{M-1} \frac{l}{l-j} - \sum_{l=1}^{M} (1 - e^{-\lambda\zeta/l}) \prod_{\substack{j=1 \\ j\neq l}}^{M} \frac{l}{l-j}, \end{aligned}$$

where the latter equality follows from (B.2).

---

[4] Hint: Always true if $f_k(s) = P(s)/Q(s)$, where P and Q are polynomials and the degree of P is strictly less than the degree of Q.

The right-hand side of (B.4) can be further simplified, to give

$$P(n = M) = \sum_{l=1}^{M} (1 - e^{-\lambda\zeta/l})(-1)^{M-1-l} \frac{M}{(M-l)!} \frac{l^{M-2}}{(l-1)!}, \tag{B.5}$$

for $M \geq 2$. It remains to determine $P(n = 1)$. Clearly,

$$P(n = 1) = P(Y_1 > \zeta) = e^{-\lambda\zeta}. \tag{B.6}$$

Therefore,

$$\begin{aligned}
\mathbb{E}(1/n) &= \sum_{M=1}^{\infty} \frac{1}{M} P(n = M) \\
&= 1 + \sum_{M=1}^{\infty} \sum_{l=1}^{M} (1 - e^{-\lambda\zeta/l})(-1)^{M-1-l} \frac{1}{(M-l)!} \frac{l^{M-2}}{(l-1)!} \\
&= 1 + \sum_{l=1}^{\infty} (1 - e^{-\lambda\zeta/l}) \frac{1}{(l-1)!} \sum_{M=l}^{\infty} (-1)^{M-1-l} \frac{l^{M-2}}{(M-l)!} \\
&= 1 - \sum_{l=1}^{\infty} (1 - e^{-\lambda\zeta/l}) e^{-l} \frac{l^{l-1}}{l!}.
\end{aligned} \tag{B.7}$$

Similarly, we find

$$\mathbb{E}(n) = 1 + \sum_{l=1}^{\infty} (1 - e^{-\lambda\zeta/l}) e^{-l} \frac{l^{l-1}}{l-1!}. \tag{B.8}$$

Remark

A way to avoid the calculation of the infinite series in the right-hand side of (B.7), or similarly that of (B.8), is to split the series in two parts: $\sum_{l=1}^{L}(1-e^{-\lambda\zeta/l})e^{-l}l^{l-1}/l!$ and $\sum_{l>L}(1-e^{-\lambda\zeta/l})e^{-l}l^{l-1}/l!$ for some arbitrary—but carefully chosen—integer $L > 1$. The first—finite— series can be evaluated without any problem for moderate values of L, and the second one can be approximated by using Stirling's formula as shown below. Indeed, if we use the standard approximation $l! \sim \sqrt{2\pi l}\, l^l\, e^{-l}$, then it follows that

$$\sum_{l>L} (1 - e^{-\lambda\zeta/l}) e^{-l} \frac{l^{l-1}}{l!} \sim 1 - \frac{1}{\sqrt{2\pi}} \sum_{l>L} (1 - e^{-\lambda\zeta/l}) l^{-3/2}.$$

We can further approximate the infinite series $\sum_{l>L}(1 - e^{-\lambda\zeta/l})l^{-3/2}$ by the integral $\int_L^\infty (1 - e^{-\lambda\zeta/x})x^{-3/2}\, dx$, which gives

$$\sum_{l>L}^{\infty} (1 - e^{-\lambda\zeta/l}) l^{-3/2} \sim \frac{2}{\sqrt{L}} - \sqrt{\frac{\pi}{\lambda\zeta}} \operatorname{erf}\left(\sqrt{\frac{\lambda\zeta}{L}}\right),$$

where the error function erf is defined by erf $:= 2/\sqrt{\pi} \int_0^x e^{-t^2} dt$.

References

[1] Bernstein C., Kacelnik A., Krebs J.R.: Individual decisions and the distribution of predators in a patchy environment II: the influence of travel costs and structure of the environment. *Journal of Animal Ecology*, **60**:205–225, 1991.

[2] Brown J.S.: Patch use as an indicator of habitat preference, predation risk and competition. *Behavioral Ecology and Sociobiology*, **22**:37–47, 1988.

[3] Brown J.S., Rosenzweig M.L.: Habitat selection in slowly regenerating environments. *Journal of Theoretical Biology*, **123**:151–171, 1986.

[4] Charnov E.L.: Optimal foraging: the marginal value theorem. *Theoretical Population Biology*, **9**:129–136, 1976.

[5] Clark C.W., Mangel M.: The evolutionary advantages of group foraging. *Theoretical Population Biology*. **30**:45–75, 1986.

[6] Clark C.W., Mangel M.: Dynamic state variable models in Ecology, methods and applications. Oxford Series in Ecology and Evolution. Oxford University Press, New York, USA, 2000.

[7] Corless R.M., Gonnet G.H., Hare D.E.G., Jeffrey D.J., Knuth D.E.: On the Lambert W function. *Advances in Computational Mathematics*, **5**:329–359, 1996.

[8] Giraldeau, L.-A., Beauchamp, G.: Food exploitation: searching for the optimal joining policy. *Trends in Ecology and Evolution*, **14**:102–106, 1999.

[9] Hamelin F., Bernhard P., Shaiju A.J., Wajnberg E.: Foraging under competition: evolutionarily stable patch-leaving strategies with random arrival times. 2. Interference competition. *Annals of Dynamic Games, this volume, Birkhauser*, pp. 349–366, 2007.

[10] Holling C.S.: Some characteristics of simple types of predation and parasitism. *The Canadian Entomologist*, **91**:385–398, 1959.

[11] Houston A.I., McNamara J.M.: Models of adaptive behavior: an approach based on state. Cambridge University Press, Cambridge, UK, 1999.

[12] Kacelnik A., Krebs J.R., Bernstein C.: The ideal free distribution and predator-prey populations. *Trends in Ecology and Evolution*, **7**:50–55, 1992.

[13] Krebs J.R., Davies N.B., editors: Behavioural ecology: an evolutionary approach. Blackwell Science, Oxford, UK, 1997.

[14] Maynard Smith J.: Evolution and the theory of games. Cambridge University Press, Cambridge, UK, 1982.

[15] McNamara J.M., Houston A.I., Collins E.J.: Optimality models in Behavioral Biology. *SIAM Review*. **43**: 413–466, 2001.

[16] Parker G.A., Stuart R.A.: Animal behaviour as a strategy optimizer: evolution of resource assessment strategies and optimal emigration thresholds. *The American Naturalist*, **110**:1055–1076, 1976.

[17] Ruxton G.D., Fraser C., and Broom M.: An evolutionarily stable joining policy for group foragers. *Behavioral Ecology*, **16**:856–864, 2005.

[18] Sjerps M., Haccou P.: Effects of competition on optimal patch leaving: a war of attrition. *Theoretical Population Biology*, **3**:300–318, 1994.

[19] Spiegel M.R.: Shaum's outline of theory and problems of Laplace transforms, Shaum's Outline Series, McGraw-Hill Book Company, New York, USA, 1965.

[20] Stephens D.W., Krebs J.R.: Foraging theory. Monographs in Behavior and Ecology, Princeton University Press, Princeton, New Jersey, USA, 1986.

[21] Sutherland W.J.: From individual behavior to population ecology. Oxford Series in Ecology and Evolution. Oxford University Press, New York, USA, 1996.

[22] Trezenga T.: Building on the ideal free distribution. *Advances in Ecological Research*, **26**:253–302, 1995.