
Competition in optimal foraging
Patch-leaving strategies with random arrival times

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Summary. We investigate the optimal behaviour of foragers reaching a patch at random arrival times. In the case where competition is limited to sharing a common resource, we show that the optimal behaviour can be obtained via a Charnov rule with carefully chosen parameters. In the case with interference, we in effect extend the model of [7] to asynchronous arrivals. In order to solve the resulting problem, we need to solve a war of attrition with random end-time. This is done in an appendix. In both cases our analysis holds independant of the arrival law, provided that it be Markov.

1 Introduction

Behavioral Ecology 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, notion conveniently called *fitness*.

In this respect, optimal foraging theory seeks to investigate the behavior of an animal searching for a valuable resource such as food or a host to parasitize. In most 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 judicious 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 [3] introduces the existence of an optimal average intake rate R^* that, if achieved, gives the greatest fitness gain a forager can expect in its environment.

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

Naturally, the question arises to know whether this result holds for foragers competing for a common patchily distributed resource, i.e. if this is an evolutionary stable strategy [6]. The authors of [7] assume that somehow n foragers have reached a patch simultaneously, and they investigate their optimal (or rather equilibrium) patch-leaving rule. Here, we allow for an *a-priori* unlimited number of foragers reaching a patch at random arrival times. We shall refer to these situations as, respectively, synchronous and asynchronous foraging.

In section 2, we develop a mathematical model of the problem at hand and recall Charnov's classical marginal value theorem [3]. In section 3, we investigate the so called "pseudo-interference" case where the only competition between foragers is trough sharing a common resource. In section 4, we investigate the case with actual interference [8]. In order to solve the last problem, we need to extent the classical "war of attrition" game [6] to a case with a random end time. This is done in appendix 7.

2 Model

2.1 Fitness accumulation

A single 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 on the patch.
- $\rho = \frac{p}{q} \in \Sigma_1 = [0,1]$ be the potential 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 $\dot{f} = \frac{\partial f}{\partial \tau}(q,\tau)$ is a known function $r(\rho)$ continuous, strictly increasing and concave; in appendix 6 we derive such a law from an assumption of homogeneous and isotropic 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 $\pi(t)$ of the differential equation

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

and it comes:

Theorem 1. *Our model is given by*

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

It yields: $\forall q$,

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

A single forager on a previously exploited patch

Assume that the forager reaches a patch that has already be 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 following graph:

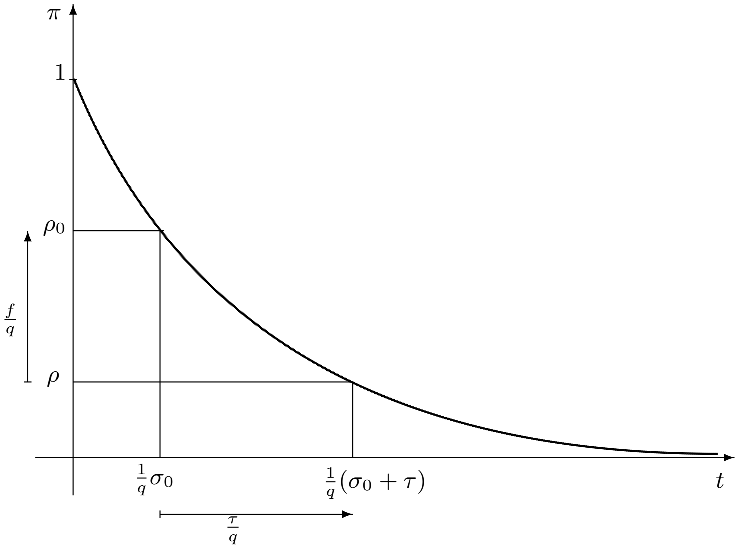

Fig. 1. The reduced graph

Competing foragers

Assume that $n \in \mathbb{N}$ **identical** foragers are on the same patch at time t. Let the sequence of forager arrivals be $\sigma = \{\sigma_1, \sigma_2, \ldots, \sigma_n\}$ and $i \in \{1, 2, \ldots, n\}$. Let μ be a parameter which quantifies interference intensity among foragers; $\mu = 0$ corresponds to pseudo-interference. Let r be allowed to depend not only on ρ anymore but also on n and μ such that

$$\forall \rho\,, n \mapsto r(\rho, n, \mu) \quad \text{is} \begin{cases} \text{strictly decreasing if } \mu \neq 0 \\ \text{invariant if } \mu = 0 \end{cases} .$$

It yields

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

And

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

Hence the fitness accumulated by forager i after a residence time τ_i is

$$f_i(\tau_i, \tau_{-i}, \sigma) = \int_{\sigma_i}^{\sigma_i + \tau_i} \dot{f}_i(t)\,\mathrm{d}t\,,$$

where τ_{-i} stands for the set $\{\tau_j\}\,, j \neq i$, which surely impacts f_i.

2.2 Criterion

The marginal value theorem

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

$$R(\tau(q)) = \frac{\mathbb{E}f(q, \tau(q))}{\bar{\theta} + \mathbb{E}\tau(q)}\,. \tag{2}$$

Theorem 2 (Charnov's marginal value theorem). *The maximizing admissible τ is given as a function of q by the rule*

- *either* $\dfrac{\partial f}{\partial \tau}(q, 0) \leq R^*$ *and* $\tau^* = 0$,
- *or* $\dfrac{\partial f}{\partial \tau}(q, \tau^*) = R^*$.

where R^* is obtained by placing τ^* in (2).

Proof: Call $\mathrm{D}R$ the (Gâteaux) derivative of R in (2). Euler's inequality reads, for any $\delta\tau$ such that $\tau^* + \delta\tau$ be admissible

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

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 [3].

Equivalent criterion

Following [7], we choose an equivalent criterion which is the effective fitness compared to the optimal average one for a given residence time:

$$J_i(\tau_i, \tau_{-i}, \sigma) = f_i(\tau_i, \tau_{-i}, \sigma) - (\bar\theta + \tau_i)R^*\,.$$

We may notice that by definition R^* is such that the maximum expected J is zero.

The previous assumptions yield

- $\forall \tau_{-i}\,, \forall \sigma$,
  - $J_i(0, \tau_{-i}, \sigma) = -\bar\theta R^*$,
  - $\tau_i \mapsto J_i(\tau_i, \tau_{-i}, \sigma)$ is concave
  - $\lim_{\tau_i \to \infty} J_i(\tau_i, \tau_{-i}, \sigma) = -\infty$.
- $\forall \tau_i\,, \forall \sigma\,, \forall j \neq i\,, \tau_j \mapsto J_i(\tau_i, \tau_{-i}, \sigma)$ is non increasing.

3 Pseudo-interfering foragers

3.1 The evolutionary stable strategy

Competition strictly limited to pseudo-interference only takes in account the fact that the resource depletes faster due to simultaneous foraging activities. 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 R^* and must leave at the same time, independently of theirs arrival dates. Hence we claim the following result: let $t_i = \sigma_i + \tau_i$ then

Theorem 3. *A Nash equilibrium of the game in non-anticipative strategies is given by the following Charnov-like rule: leave at t^* given by*

- *either $\rho(\sigma_i) \le \rho^*$ and $t^* = 0$ (i.e. $\tau_i^* = 0$),*
- *or $\rho(t^*) = \rho^* := r^{-1}(R^*)$.*

As the Nash equilibrium is both strict and symmetric, this is indeed an evolutionary stable strategy.

3.2 An analytical expression of R^*

Let us assume that all foragers apply the above patch-leaving rule, i.e. leave when $\dot f = R^*$ 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 $\rho_0 = 1$.

Our purpose now is to give pleasant expressions of both $\mathbb{E}f(t^*)$ and $\mathbb{E}\tau^*$ to be able to compute R^*.

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

$$\text{for } t \in (\sigma_j, \sigma_{j+1})\,, \quad S(t,\sigma) = j(t - \sigma_j) + \sum_{k=1}^{j-1} k(\sigma_{k+1} - \sigma_k)\,. \tag{3}$$

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 subsection 2.1, 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, we get

Lemma 1. *The patch trajectory satisfies*

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

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

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 *central trajectory* of order $\hat{n}$ that particular trajectory where all $\hat{n}$ foragers arrived at time 0. 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. Notice 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,

$$\mathbb{E}_\xi \tau_\xi^* = \sigma_{\hat{n}} - \frac{1}{\hat{n}} \sum_{j=1}^{\hat{n}} \sigma_j + \tau_{\hat{n}}^*\,. \tag{4}$$

Now, τ_n^* is defined by $\pi(\frac{1}{q} S(\sigma_{\hat{n}} + \tau_{\hat{n}}^*, \sigma)) = \rho^*$, i.e., according to equation (3):

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

Notice 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

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

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

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

so that finally

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

Place this in (4), it comes $\mathbb{E}_\xi \tau_\xi^* = \tau_\odot^*$. But this last quantity is independent on σ, so that, for any fixed q and $\hat{n}$,

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

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. The ratio $\frac{q}{\hat{n}}$ is the amount of resource per forager active on that patch. It may be hoped that its mean in the environment can be evaluated. It is a measure of, but not exactly equal to, the amount of resource available per forager.

Taking the expected value overall patch qualities and sequences of arrival, we obtain the following result:

Theorem 4. *Let*

$$q^* = \mathbb{E}\left(\frac{q}{\hat{n}}\right) ,$$

the optimal average intake rate is given by the solution of the equation

$$R^* = \frac{1-\rho^*}{\frac{\bar{\theta}}{q^*} + \pi^{-1}(\rho^*)} = r(\rho^*)$$

Therefore, it is exactly as applying Charnov's marginal value theorem for both deterministic patch quality q^* and travel time $\bar{\theta}$. In this case, it is traditional to compute R^* and the optimal τ^* graphically, as done in figure 2.

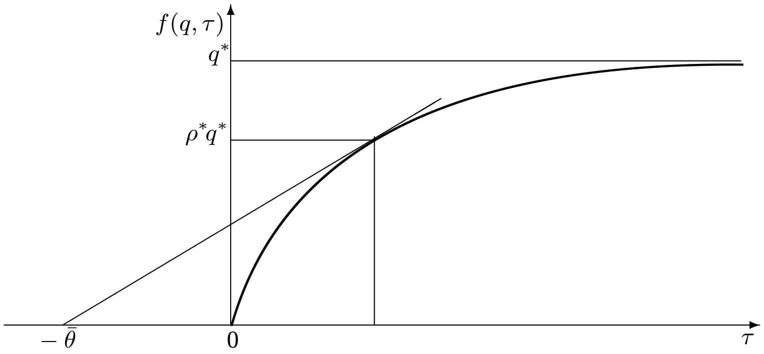

Fig. 2. The marginal value theorem

4 Mutually-interfering foragers

From now on, we assume that, beyond sharing the same resource, competition on a patch decreases the foraging efficiency of all participants. This effect might even increase with the scarcity of the resource. As a consequence, the departure of a forager surely causes an abrupt increase of the intake rate $\dot{f}$ [8]. It implies that the latter does not depend on ρ only anymore, but also on n, the current number of foragers present on the patch. A passive Charnov-like strategy, where the foragers only monitor their own intake rate to decide whether to stay or leave, should no more be optimal.

Indeed, previous papers [7] reveal that synchronous foragers should trigger a war of attrition [6], i.e. leave at random (but optimally distributed) times, except the lucky one which remains alone on the patch, expected to stay to exhaust the patch up to its profitability threshold ρ^*.

The question arises to know whether this result holds for asynchronous foragers or to what extent. The doubt mainly arises from the fact that unexpected newcomers can disrupt the game.

4.1 Generating function

A-priori, we cannot exhibit any Nash equilibrium in pure strategies; hence the need to deal with mixed strategies, say P_i, $i \in \{1, 2, \ldots, n\}$ for n foragers. We shall subscript $-i$ to mean all players except player i.

So our criterion becomes the following generating function:

$$\mathcal{G}_i(P_i, P_{-i}, \sigma) = \mathbb{E}^{P_i, P_{-i}}_{\tau_i, \tau_{-i}} J_i(\tau_i, \tau_{-i}, \sigma)\,. \tag{5}$$

As a consequence,

$$\mathbb{E}\mathcal{G}_i(P^*_i, P^*_{-i}, \sigma) = 0\,.$$

4.2 Dynamic programming

Let us define a stage as a stochastic period during which the number of foragers n remains constant on the patch; notice that in such a stage the intake rate is only affected by ρ. Let it be superscripted by $k \in \mathbb{N}$; $k = 0$ indicates the stage at which the reference forager started the game. As their exists a profitability threshold ρ^*, the patch can not be indefinitely exploited; the total number of stages $K \in \mathbb{N}$ and the total number of players $N \in \mathbb{N}$ are thus finite, but *a-priori* unknown

We define the state at the beginning of stage k as

$$\chi^k = \begin{pmatrix} \rho^k \\ n^k \end{pmatrix} \in \Sigma_1 \times \mathbb{N}\,.$$

For each stage, each player decides of a persistence time $x^k_i \in \mathbb{R}^+$; i.e. if the stage is not yet finished at that time it quits the game and so its own horizon is $K_i = k$. We find it convenient to let the exceptional case where all x_i are equal end the current stage: it means that all players are invited to play again in order to make the patch surely exhausted once visited.

Let us introduce the stochastic variable:

$$\alpha^k = \begin{cases} 1 & \text{if an arrival occured during stage } k \\ -1 & \text{if a departure occured during stage } k \\ 0 & \text{otherwise} \end{cases}\,.$$

It depends on the strategies of the players, but if the arrival times are a Markov process, which we shall assume, as well as the strategies, it remains a Markov process itself.

Let δ^k be the duration of stage k and

$$\kappa^k_i = \begin{cases} 0 & \text{if } x^k_i = \delta^k \,\&\, \max x^k_{-i} > x^k_i \\ 1 & \text{otherwise} \end{cases}\,,$$

i.e. $\kappa^k_i = 1$ if player i remains in the patch beyond the current stage. It yields the following dynamics:

$$\begin{cases} \rho^{k+1} = \rho^k - \varDelta_\rho(\rho^k, n^k, \delta^k) =: \varLambda_\rho(\rho^k, n^k, \delta^k) \\ n^{k+1} = n^k + \alpha^k \end{cases} ,$$

with $\varDelta_\rho(\rho, n, \delta)$ a known function, easy, if boring, to write explicitly from paragraph 2.1.

Each criterion can be expressed as

$$\mathcal{G}_i = \mathbb{E}\left\{ \sum_{k=0}^{K_i} \mathcal{L}(\chi^k, \delta^k) \right\} ,$$

with

$$\mathcal{L}(\chi^k, \delta^k) = \mathcal{L}(\rho^k, n^k, \delta^k) = \frac{q}{n^k} \varDelta_\rho(\rho^k, n^k, \delta^k) - R^* \delta^k .$$

To solve the corresponding dynamic game problem via dynamic programming, we introduce the function $V_i^k(\chi)$ which is the optimal expected total future reward for entering stage k in the state χ. We get the following functional equation of dynamic programming:

$$V_i^k(\chi^k) = \mathbb{E}^* \left[\mathcal{L}(\chi^k, \delta^k) + \kappa_i^k V_i^{k+1}(\chi^{k+1}) \right] \quad \forall k \le K_i , \tag{6}$$

where $\mathbb{E}^*$ means that we look for a set of strategies which yield a Nash equilibrium at each stage. As the game is surely stationary, V_i does not depend on the stage number k and (6) becomes the following implicit equation

$$V_i(\rho, n) = \mathbb{E}^* \left[\mathcal{L}(\rho, n, \delta) + \kappa V_i(\varLambda_\rho(\rho, n, \delta), n + \alpha) \right] \quad \forall \rho > \rho^* .$$

As a consequence, it suffices to solve the game limited to one stage to obtain the Nash-optimal (and so evolutionary stable) strategy in closed loop. Furthermore, this is surely a war of attrition with stochastic stopping time as defined in appendix 7. Indeed the one-stage game can be stated as follows. Let $V_i(\varLambda_\rho(\rho, n, \delta), n) =: \mathcal{V}_i(\delta, n)$ and thus, the game has a utility function

$$U_i(x_i, x_{-i}, \delta) = \mathcal{L}(n, \delta) + \begin{cases} 0 & \text{if } x_i = \delta \,\&\, \max x_{-i} > x_i \\ \mathcal{V}_i(\delta, n) & \text{if } x_i = \delta \,\&\, \max x_{-i} = x_i \\ \mathcal{V}_i(\delta, n+1) & \text{if } \delta < \min\{x_i, x_{-i}\} \\ \mathcal{V}_i(\delta, n-1) & \text{otherwise} \end{cases} .$$

Let $\check{x}$ be such that $\varLambda_\rho(\rho, n, \check{x}) := \rho^*$; it is the time after which a forager, even alone, has no incentive to stay on the patch, i.e. $\mathcal{V}_i(\check{x}, \cdot) = 0$.

Let then $\hat{x} = \arg\max_x \mathcal{L}(n, x)$. (Both $\hat{x}$ and $\check{x}$ depends on ρ and n).

As a consequence, $\forall n \,, \forall x > \hat{x} \,, \mathcal{L}'(n, x) < 0$. Moreover, if there is no departure, the $\mathcal{L}$ function of the next stage is still decreasing. Thus its $\hat{x}$ is zero and according to appendix 7, its value is zero. Hence if $\delta \in [\hat{x}, \check{x}] \,, \mathcal{V}_i(\delta, n) = \mathcal{V}_i(\delta, n+1) = 0$.

We shown in appendix 7 that the value of the game is, as in the classical war of attrition, equal to $\mathcal{L}(\hat{x}, n)$. As a consequence,

$$\mathcal{V}_i(x, n-1) = \max_y \mathcal{L}(\varLambda_\rho(\rho, n, x), n-1, y) =: \mathsf{V}(x, n) .$$

We therefore obtain the following result,

Theorem 5. *The Nash equilibrium of the game (5) is*

$$P^*(x,n) = \begin{cases} 0 & \forall x < \hat{x} \\ 1 - \mathrm{e}^{-\frac{1}{n-1}\int_{\hat{x}}^{x} h(y,n)\,\mathrm{d}y} & \forall x \in [\hat{x}, \check{x}] \\ 1 & \forall x \geq \check{x} \end{cases} ,$$

with

$$h(x,n) = -\frac{\mathcal{L}'(x,n)}{\mathsf{V}(x,n)} .$$

5 Conclusion

Our objective was to determine the evolutionary stable strategy that foragers competing for a common patchily distributed resource should adopt. Compared to [7], the innovation lies in the fact that random arrival times are allowed.

First, we proved that if competition is strictly limited to pseudo-interference the game yields simple Nash-optimal strategies. In other words, a passive Charnov-like strategy is still optimal. Moreover, the optimal average intake rate can be simply computed via the classical graph associated to the marginal value theorem, with carefully chosen parameters. Furthermore, these results are independent on the distribution law of arrival times: the dynamical aspect of the game has essentially been bypassed.

Then we added mutual-interference in the model; it implies that passive strategies can no longer be optimal. We shown that the war of attrition with a random horizon has a solution surprisingly similar to that of the classical problem. In particular, if some conditions prevail, as they do in our problem, the solution is independent on the probability law of the horizon. As a consequence, the solution of the asynchronous foraging problem investigated here, expressed as a closed loop strategy on the number of foragers, is identical of the synchronous problem of [7].

One can notice that, in a war of attrition, the value of the game is the reward which would have been earned without entering the game. Nevertheless, a Nash equilibrium requires to play; the question that arises then is:

If I am not concerned by my opponents' gains, why should I play if my expected gain is not greater than my guaranteed value ?

In the particular case of evolutionary game theory, the answer is obvious: to prevent the proliferation of any mutant that would decide alternatively to stay longer on the patch.

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6 Modelling patch depletion

In our model, the forager is not supposed to explore the patch in a systematic way but is assumed to randomly probe the patch. As a consequence, it finds itself more and more often probing an area already exploited. That is the reason why its efficiency decreases with patch depletion, prompting it to leave in order to find a richer patch elsewhere.

Let us introduce a surface (or volume) resource density D.

Two time constants enter into the model:

- the *exploration time* T_e 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).
- the *handling time* T_h is the extra time it takes to actually retrieve a unit of resource if necessary.

Following most of the literature, we propose here a model where the resource comes as a continuum; indeed, a similar model where the resource is decomposed in discrete units yields similar formulas [1].

Our hypothesis is that a ratio ρ of the patch area is productive so that an area $\mathrm{d}æ$ produces a quantity

$$\mathrm{d}f = \rho D \mathrm{d}æ$$

of resource and the time necessary to gather it is

$$\mathrm{d}t = T_e \mathrm{d}æ + \rho D T_h \mathrm{d}æ\,.$$

Hence we get

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

One can relate this equation to Holling's functional response [5] by substituting T_e by the *attack rate*, a parameter giving the amount of resource attacked per unit time, $a = \frac{D}{Te}$.

7 A war of attrition with stochastic stopping time

Let us consider the following non-zero sum game:

- n players.
- Player i chooses $x_i \in \mathbb{R}^+$.
- ς is a positive stochastic variable (the end time) independent of the players' decisions.
- The criterion of player i is as follows, where x_{-i} stands for $\{x_j\}\,, j \neq i$:

$$U_i(x_i, x_{-i}, \varsigma) = \begin{cases} L_i(x_i) & \text{if } x_i \le \min\{x_{-i}, \varsigma\} \;\&\; \max x_{-i} > x_i \\ D_i(x_i) & \text{if } x_i \le \min\{x_{-i}, \varsigma\} \;\&\; \max x_{-i} = x_i \\ E_i(\varsigma) & \text{if } \varsigma < \min\{x_i, x_{-i}\} \\ W_i(\min x_{-i}) & \text{otherwise} \end{cases} .$$

The hypotheses are: $\forall i$,

- $\exists\,!\,\hat{x} = \arg\max_x L_i(x)$.
- L_i is strictly decreasing for $x > \hat{x}$.
- $W_i(x) > D_i(x) \ge E_i(x) \ge L_i(x)\,\forall x \in [\hat{x}, \check{x})$.
- either $\exists\,\{\check{x} \ge \hat{x}\,|\,\forall x \ge \check{x}\,, L_i(x) = W_i(x)\}$,
- otherwise let $\check{x} = \infty$.

We seek a Nash equilibrium, with $P_i(x)$ the cumulative distribution function of player i. We claim the following

Theorem 6. *A Nash equilibrium set of strategies must satisfy the following properties:*

- *the Nash-optimal probability density function is continuous over $[\hat{x}, \check{x})$ and zero elsewhere but may exhibit a Dirac weight at $\check{x}$.*
- *Let*
$$h_i(x) = -\Big\{\frac{P'_\varsigma(x)}{1 - P_\varsigma(x)}\frac{E_i(x) - L_i(x)}{W_i(x) - L_i(x)} + \frac{L'_i(x)}{W_i(x) - L_i(x)}\Big\}\,,$$
-
$$H_i^*(x) = 1 - \mathrm{e}^{-\int_{\hat{x}}^{x} h_i(y)\,\mathrm{d}y} \quad \forall x \in [\hat{x}, \check{x}]\,,$$
- *and*
$$\mathcal{H}_i(x) := \frac{\prod_{k=1}^{n}[1 - H_k^*(x)]^{\frac{1}{n-1}}}{1 - H_i}\,.$$

- *The unique Nash-optimal strategy is* $\forall i$,

$$P_i^*(x) = \begin{cases} 0 & \forall x < \hat{x} \\ 1 - \mathcal{H}_i(x) & \forall x \in [\hat{x}, \check{x}) \\ 1 & \forall x \geq \check{x} \end{cases} .$$

Proof

The hypotheses made clearly show that everyone share a common *spectrum*, i.e. mixed strategy support, $[\hat{x}, \check{x}]$. Let now P_i, H_i and P_ς be the cumulative distribution functions of respectively $x_i,\ \min x_{-i}$ and ς. The generating function is then

$$G_i(x, H_i, P_\varsigma) = \int_{y \in [\hat{x}\,, \check{x}]} \int_{z \in [\hat{x}\,, \infty)} U_i(x, y, z) \mathrm{d}P_\varsigma(z) \mathrm{d}H_i(y)\,,$$

$$\begin{aligned} G_i(x, H_i, P_\varsigma) = & \int_{y \in [\hat{x}\,, x)} \big[\int_{z \in [\hat{x}\,, y)} E_i(z) \mathrm{d}P_\varsigma(z) + \int_{z \in [y\,, \infty)} W_i(y) \mathrm{d}P_\varsigma(z) \big] \mathrm{d}H_i(y) + \\ & \int_{y \in [x\,, \check{x}]} \big[\int_{z \in [\hat{x}\,, x)} E_i(z) \mathrm{d}P_\varsigma(z) + \int_{z \in [x\,, \infty)} L_i(x) \mathrm{d}P_\varsigma(z) \big] \mathrm{d}H_i(y)\,. \end{aligned}$$

As the optimal strategy is equalizing on the opponents' spectrum, in any open set Ω in $[\hat{x}, \check{x})$, one must have

$$\frac{\partial}{\partial x} G_i(x, H_i^*, P_\varsigma) = 0 \quad \forall x \in \Omega\,.$$

Differentiating $G_i(x, H_i, P_\varsigma)$ yields

$$\begin{aligned} 0 = & [E_i(x) - L_i(x)][1 - H_i^*(x)] P_\varsigma'(x) + \\ & [1 - P_\varsigma(x)] \left\{ L_i'(x)[1 - H_i^*(x)] - [W_i(x) - L_i(x)] H_i^{*\prime}(x) \right\}. \end{aligned}$$

Hence

$$H_i^*(x) = 1 - \mathrm{e}^{-\int_{\hat{x}}^{x} h_i(y)\,\mathrm{d}y} \quad \forall x \in [\hat{x}, \check{x}]\,,$$

with

$$h_i(x) = -\Big\{ \frac{P_\varsigma'(x)}{1 - P_\varsigma(x)} \frac{E_i(x) - L_i(x)}{W_i(x) - L_i(x)} + \frac{L_i'(x)}{W_i(x) - L_i(x)} \Big\}\,.$$

Hence the Nash optimal strategies are given by

$$\forall i\,, 1 - H_i^*(x) = \prod_{j \neq i} [1 - P_j^*(x)]\,,$$

where the H_i's are known.

It implies

$$\prod_i [1 - H_i^*(x)] = \prod_i [1 - P_i^*(x)]^{n-1}\,.$$

Therefore,

$$P_i^*(x) = 1 - \frac{\prod_{k=1}^{n}[1 - H_k^*(x)]^{\frac{1}{n-1}}}{1 - H_i} =: 1 - \mathcal{H}_i(x) \quad \forall x \in [\hat{x}, \check{x})\,.$$

Hence the unique Nash equilibrium such that

$$\forall i\,, P_i^*(x) = \begin{cases} 0 & \forall x < \hat{x} \\ 1 - \mathcal{H}_i(x) & \forall x \in [\hat{x}, \check{x}) \\ 1 & \forall x \geq \check{x} \end{cases}\,.$$

An atom of probability takes place on $\check{x}$. Indeed, a Nash equilibrium requires $G_i(x, H_i^*, P_\varsigma) = G_i^*\, \forall x \in [\hat{x}, \check{x})$, where G_i^* is the value of the game. Up to now, we implicitly assumed that H_i was continuous in $[\hat{x}, \check{x})$. Indeed, let $\tilde{x} \in [\hat{x}, \check{x}]$ and suppose this is a point of discontinuity of amplitude ϵ. As the convention wants, P_i is cadlag. If $\tilde{x} < \check{x}\,, \lim_{x \downarrow \tilde{x}} G_i(x) - G_i(\tilde{x}) = \epsilon(1 - P_\varsigma(\check{x})(W_i(\check{x}) - L_i(\check{x}))$ (if the draw is taken in account, in the case where all other foragers have a Dirac at the same $\check{x}$, $L_i(\check{x})$ is replaced by a convex combination of $L_i(\check{x})$ and $D_i(\check{x})$), therefore a Dirac is impossible for any $\tilde{x} < \check{x}$. Moreover, if a jump occurs in H_i at $\check{x}$, $\lim_{x \uparrow \tilde{x}} G_i(x) - G_i(\tilde{x}) = \epsilon(1 - P_\varsigma(\check{x})(L_i(\check{x}) - D_i(\check{x})) = 0$ by the definition of $\check{x}$. Hence a jump is possible on $\check{x}$. To conclude, it is obvious that, from the previous hypotheses on L_i, $\forall x \notin [\hat{x}, \check{x})\,, G_i(x, H_i^*, P_\varsigma) \leq G_i^*$, as $G_i^* = L_i(\hat{x})$.

Hence, if the game is symmetric,

$$P^*(x) = \begin{cases} 0 & \forall x < \hat{x} \\ 1 - \mathrm{e}^{-\frac{1}{n-1}\int_{\hat{x}}^{x} h(y)\,\mathrm{d}y} & \forall x \in [\hat{x}, \check{x}) \\ 1 & \forall x \geq \check{x} \end{cases}\,.$$

One can notice that, if $\forall x \in [\hat{x}, \check{x}]\,, P_\zeta(x) = 0$, the above solution of the war of attrition coincides with the classical solution [4, 2].

∎