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

2. Interference Competition

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Abstract

Our objective is to determine the evolutionarily stable strategy [13] that is supposed to drive the behavior of foragers competing for a common patchily distributed resource [15]. Compared to [17], the innovation lies in the fact that random arrival times are allowed.

In this second part, we add interference to the model: it implies that a "passive" Charnov-like strategy can no longer be optimal. A dynamic programming approach leads to a sequence of wars of attrition [13] with random end times. This game is solved in Appendix A. Under some conditions that prevail in our model, the solution is independent of 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 to that of the synchronous problem [17].

Finally, we discuss the biological implications such as a possible connection with the genetic variability in the susceptibility to interference observed in [22].

1 Introduction

As the main concepts and notation are introduced in a companion paper [9], we just summarize them hereafter.

"*Nothing in biology makes sense except in the light of evolution*".[1] In this respect, behavioral ecology interprets animal behavior through an evolutionary approach, via estimating its capacity to get through the natural selection process, and to maximize Darwinian *fitness* [12]—a notion analogous to that of "utility" in economics. Typically, in foraging theory or the art of gathering resources in the environment, fitness is related to the quantity of resource gathered. In many cases, the resource is patchily distributed and the utility function on each patch is strictly increasing, concave and bounded with respect to time. As the *intake rate* decreases with the quantity of resource available on the patch, it is likely advantageous to leave a patch not yet exhausted in order to find a new one, in spite of an uncertain *travel time*. Charnov's marginal value theorem reveals that the optimal giving-up time is when the intake rate is equal to the optimal long-term mean rate γ^*—which, if achieved, gives the best fitness a forager can expect in its environment. This famous theoretical model is actually applied to a lone forager that has a monopoly on resources it finds.

Naturally, the question arises of whether this result holds for foragers competing for a common patchily distributed resource, i.e., whether this is an evolutionarily stable strategy [13]. The authors of [17] assume that somehow n foragers have reached a patch simultaneously, and they investigate the 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. We shall refer to these situations as, respectively, synchronous and asynchronous foraging.

In the first part [9], we investigated the *scramble competition* case where the only competition between foragers is in sharing a common resource: Charnov's patch-leaving rule remains qualitatively unchanged. In this second part, we extend that model to take into account actual *interference* [18], i.e., the decline of the intake rate due to competition. The complete solution of the new game is obtained in Section 2, and makes use of the solution of a *war of attrition* [13] with random end time, solved in a more general setup in Appendix A.

We freely refer to the concepts of evolutionarily stable strategy (ESS) and replicator dynamics provided by evolutionary game theory. Appendix B gathers

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[1] Theodosius Dobzhansky, geneticist, 1900–1975.

some basic facts concerning these topics and their relationship to classical game theory.

2 Interference Competition

In this second part, we assume that beyond sharing the same resource, competition on a patch yields a decline of the intake rate of all the contestants [18]. This effect might even increase with the scarcity of the resource. As a consequence, the departure of a forager surely causes an abrupt rise of the intake rate. It implies that the latter does not only depend on the ratio of available resource but also on 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 longer be optimal.

Indeed, previous papers [17] reveal that synchronous foragers should trigger a war of attrition, i.e., the foragers should 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.

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

2.1 Model

Assume that $n \in \mathbb{N}$ identical foragers are on the same patch. Let the sequence of forager arrival times be $\sigma = \{\sigma_1, \sigma_2, \ldots, \sigma_n\}$ and $i \in \{1, 2, \ldots, n\}$. 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 $m \in \mathbb{R}^+$ be a parameter which quantifies interference intensity among foragers [18]; $m = 0$ corresponds to scramble competition. Let $r(\rho, n, m)$ be a known function such that

- $\forall n, m, \quad \rho \mapsto r(\rho, n, m)$ is continuous, strictly increasing and concave,
- $\forall \rho, m, \quad n \mapsto r(\rho, n, m)$ is strictly decreasing if $m > 0$ and invariant otherwise,
- $\forall \rho, n, \quad m \mapsto r(\rho, n, m)$ is strictly decreasing if $n > 1$ and invariant otherwise.

Our basic assumption is that the fitness gathered by forager i is given by the differential equation

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

and

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

Let the fitness accumulated by forager i after a residence time τ_i be $f_i(\tau_i, \tau_{-i}, \sigma_i)$ where τ_{-i} stands for the set $\{\tau_j\}$, $j \neq i$, which surely impacts f_i.

Following [12, 17], we use an equivalent criterion to that of [9] which is the effective fitness compared to the optimal (Nash) average one for a given residence time:

$$J_i(\tau_i, \tau_{-i}, \sigma_i) = f_i(\tau_i, \tau_{-i}, \sigma_i) - (\bar{\theta} + \tau_i)\gamma^*,$$

where $\bar{\theta}$ is the mean travel time. Note that by definition γ^* is such that the maximum expected J is zero.

2.2 The Game

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 use the subscript $-i$ to mean all players except player i.

So our criterion becomes the following generating function:

$$\mathcal{G}_i(P_i, P_{-i}, \sigma_i) = \mathbb{E}_{\tau_i, \tau_{-i}}^{P_i, P_{-i}} J_i(\tau_i, \tau_{-i}, \sigma_i). \tag{1}$$

As a consequence of the above definition of γ^*,

$$\mathbb{E}\mathcal{G}_i(P_i^*, P_{-i}^*, \sigma_i) = 0.$$

Let us define a *stage* as a stochastic period during which the number of foragers n remains constant on the patch; note that in such a stage the intake rate is only affected by ρ. Let the superscript $k \in \mathbb{N}$ denote the number of the stage; $k = 0$ indicates the stage at which the reference forager started the game. As there 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 commits to a *persistence time* $x_i^k \in \mathbb{R}^+$; 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—zero-measure—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:

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

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

Let δ^k be the duration of stage k and

$$\kappa_i^k = \begin{cases} 0 & \text{if } x_i^k = \delta^k \text{ and } \max x_{-i}^k > x_i^k \\ 1 & \text{otherwise} \end{cases},$$

i.e., $\kappa_i^k = 1$ if player i remains in the patch beyond the current stage. This yields the following dynamics:

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

with $\Delta_\rho(\rho, n, \delta)$ a known function that can be derived from the dynamic model of Section 2.1, and which enjoys the following properties:

- $\forall \rho, n, \Delta_\rho(\rho, n, 0) = 0$,
- $\forall \rho, n, \delta \mapsto \Delta_\rho(\rho, n, \delta)$ is increasing and concave,
- $\forall \rho, n, \lim_{\delta\to\infty} \Delta_\rho(\rho, n, \delta) = \rho$.

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

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

Previous assumptions made on Δ_ρ yield

- $\forall \rho, n, \mathcal{L}(\rho, n, 0) = 0$,
- $\forall \rho, n, \delta \mapsto \mathcal{L}(\rho, n, \delta)$ is concave,
- $\forall \rho, n, \lim_{\delta\to\infty} \mathcal{L}(\rho, n, \delta) = -\infty$.

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:

$$V_i^k(\chi^k) = \mathbb{E}^*\left[\mathcal{L}(\chi^k, \delta^k) + \kappa_i^k V_i^{k+1}(\chi^{k+1})\right] \quad \forall k \le K_i, \tag{2}$$

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 (2) becomes the following implicit equation:

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

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

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

Let $\check{x}$ be such that $\Lambda_\rho(\rho, n, \check{x}) := \rho^*$; 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 $\check{x}$ depend 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 A, 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 show in Appendix A that the value of the game is, as in the classical war of attrition, equal to $\mathcal{L}(\hat{x}, n)$. As a consequence,

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

We therefore obtain the following result.

Theorem 2.1. *The Nash equilibrium of the game (1) is*

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

with

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

Hence the solution of the asynchronous foraging problem investigated here, expressed as a closed loop strategy on the number of foragers, is identical to the synchronous problem of [17].

3 Concluding Remarks

3.1 How Does a War of Attrition Influence the Residence Time?

A question that is not addressed by the model is: Does interference, thus a war of attrition, imply that multiple foragers should stay longer on a patch than a lone forager? We cannot answer in a general way.

It is an established fact [17] that a war of attrition causes the forager to stay longer than the "Charnov time." Yet, this Charnov time itself, here $\hat{x}$, depends in a complex fashion on the detailed interference model.

In this respect, the article [7] does not invalidate the theoretical model; on the contrary, this paper seems to corroborate the model of [17], as the larger the number of animals on the patch, the larger is their tendency to leave. First, part of the contestants leave the patch almost immediately; this can be connected to the "$n - K$" of [17]. Then the remaining contestants leave sequentially, as in [17].

3.2 On a Possible Connection with Population Genetics

Up to now, we have focused on mixed strategies in their classical sense: a random strategy x distributed according to a probability density function $p(x)$. Let $p^*(x)$ equalize the opponent's payoff on its spectrum as in a solution of a Nash game.

Note that in a war of attrition, the value of the game is the reward which would have been earned without entering the game. Nevertheless, the Nash solution requires one to play; the question that arises then is: Why should I play if my expected gain is not greater than my guaranteed value? In the context of evolutionary game theory, the answer makes sense: "to prevent the proliferation of any mutant that would alternatively stay longer on the patch." That is, the mutant is equivalent to a cheater in a population commonly and conventionally adopting a simple Charnov-like strategy: by breaking off the convention, it would obtain more fitness and would consequently invade. Note that, in return, adopting such an ESS has no extra cost as the value of the game remains the same.

Evolutionary game theory provides another viewpoint to implement mixed strategies. Instead of considering a monomorphic population playing a common random strategy, let us now consider a polymorphic population in which pure strategies are distributed homogeneously according to p^* (see Appendix B). Since p^* is equalizing, all the individuals of the population can expect the same fitness.

In a population involved in "war of attrition" contests, it simply means that distributing a deterministic persistence time to each individual according to p^* is evolutionarily stable. In other words, a variability in terms of individuals' ability to sustain interference would be expected among the population. Indeed, in this model, interference is taken as a perturbation, not as a decision variable like in a *hawk-dove* contest [5, 6, 13]; interference affects all the contestants equally.

Interestingly, the authors of [22] observed "*the existence of a significant intra-population genetic variability in the susceptibility of females to interference*," acting on the "*time they are willing to invest*." Moreover, there was no significant genetic variability in terms of aggressiveness (unpublished data). Thus these intraspecific interactions seem to be governed by a war of attrition game rather than a hawk-dove one.

However, the connection with these *emigration-threshold genotypes* [15] seems somewhat premature as the stability of the replicator dynamics [10] in a continuous strategy space—as is the case for a war of attrition—is still under investigation [3, 4].

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Appendix A A War of Attrition with a Stochastic End Time

We consider the following nonzero-sum game:

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

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

The hypotheses are: $\forall i$,

- $\exists\,!\,\hat{x} = \arg\max_x L_i(x)$.
- L_i is strictly decreasing for $x > \hat{x}$.
- $W_i(x) > D_i(x) \geq E_i(x) \geq L_i(x)\,\forall x \in [\hat{x}, \check{x})$.
- either $\exists\,\{\check{x} \geq \hat{x} \mid \forall x \geq \check{x}, L_i(x) = W_i(x)\}$,
- 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 A.1. *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*

$$h_i(x) = -\left\{\frac{P'_\epsilon(x)}{1 - P_\epsilon(x)}\frac{E_i(x) - L_i(x)}{W_i(x) - L_i(x)} + \frac{L'_i(x)}{W_i(x) - L_i(x)}\right\},$$

- $$H_i^*(x) = 1 - \mathrm{e}^{-\int_{\hat{x}}^{x} h_i(y)\,\mathrm{d}y} \quad \forall x \in [\hat{x}, \check{x}],$$
- *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 shares a common *spectrum*, i.e., mixed strategy support, $[\hat{x}, \check{x}]$. Let now P_i, H_i and P_ϵ be the cumulative distribution functions of respectively x_i, $\min x_{-i}$ and ϵ. The generating function is then

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

$$G_i(x, H_i, P_\epsilon) = \int_{y \in [\hat{x}, x)} \left[\int_{z \in [\hat{x}, y)} E_i(z)\mathrm{d}P_\epsilon(z) + \int_{z \in [y, \infty)} W_i(y)\mathrm{d}P_\epsilon(z)\right] \mathrm{d}H_i(y)$$
$$+ \int_{y \in [x, \check{x}]} \left[\int_{z \in [\hat{x}, x)} E_i(z)\mathrm{d}P_\epsilon(z) + \int_{z \in [x, \infty)} L_i(x)\mathrm{d}P_\epsilon(z)\right] \mathrm{d}H_i(y).$$

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

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

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

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

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
$$h_i(x) = -\left\{\frac{P_\epsilon'(x)}{1 - P_\epsilon(x)} \frac{E_i(x) - L_i(x)}{W_i(x) - L_i(x)} + \frac{L_i'(x)}{W_i(x) - L_i(x)}\right\}.$$
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.

This 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 we have 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 $G_i(x, H_i^*, P_\epsilon) = G_i^* \,\forall x \in [\hat{x}, \check{x})$, 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 that this is a point of discontinuity of amplitude j—for "jump." Per convention, P_i is cadlag. If $\tilde{x} < \check{x}$, $\lim_{x \downarrow \tilde{x}} G_i(x) - G_i(\tilde{x}) = j(1 - P_\epsilon(\check{x}))(W_i(\check{x}) - L_i(\check{x}))$—if the draw is taken into 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 $\check{x}$, $\lim_{x \uparrow \tilde{x}} G_i(x) - G_i(\tilde{x}) = j(1 - P_\epsilon(\check{x}))(L_i(\check{x}) - D_i(\check{x})) = 0$ 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, $\forall x \notin [\hat{x}, \check{x})$, $G_i(x, H_i^*, P_\epsilon) \leq G_i^*$, as $G_i^* = L_i(\hat{x})$.

Hence, if the game is symmetric,

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

Note that, if $\forall x \in [\hat{x}, \check{x}]$, $P_\epsilon(x) = 0$, the above solution of the war of attrition coincides with the classical solution [1, 2, 8]. □

Appendix B ESS and Classical Game Theory

B.1 Notation and Setup

We consider a compact metric space X as the space of *traits* or *phenotypes* or *pure strategies*. Three cases of interest are

- X is finite (the *finite* case), $X = \{x_1, x_2, \ldots, x_n\}$,
- X is a line segment $[a, b] \subset \mathbb{R}$,
- X is a compact subset of $\mathbb{R}^n$.

We shall use letters x, y for elements of X.

We let $\Delta(X)$ denote the set of probability measures over X. In the finite case, we shall also denote it as Δ_n. We notice that, in the weak topology, $\Delta(X)$ is compact and the mathematical expectation is continuous with respect to the probability law. We shall use letters p, q for elements of $\Delta(X)$.

A population of animals is characterized by the probability $p \in \Delta(X)$ governing the traits of its individuals. There is no need to distinguish whether each individual acts many times, adopting a strategy in $A \subset X$ with probability $p(A)$—the population is then monomorphic and its members are said to use the *mixed strategy p*—or whether each animal behaves in a fixed manner, but in a polymorphic population, where p is the distribution of traits among the population, for any subset $A \subset X$, $p(A)$ is the fraction of the population which has its trait x in A. Then, p also governs the probability that an animal taken randomly in the population behaves a certain way.

We are given a *generating function* $G : X \times \Delta(X) \to \mathbb{R}$ jointly continuous (in the weak topology for its second argument). Its interpretation is that it is the *fitness* gained by an individual with trait x in a population characterized by p.

A case of interest, called hereafter the *linear case*, is when G derives from a function $H : X \times X \to \mathbb{R}$ giving the benefit $H(x, y)$ that an animal with trait x gets when meeting an animal with trait y, according to the expected benefit for trait x:

$$G(x, p) = \int_X H(x, y)\ \mathrm{d}p(y). \tag{B.1}$$

Then G and F below are linear in their second argument. But this is not necessary for many of the results to follow.

The fitness gained by an animal using a mixed strategy q in a population characterized by p is

$$F(q, p) = \int_X G(x, p)\ \mathrm{d}q(x).$$

Note that if $\delta_x \in \Delta(X)$ denotes the Dirac measure at x, $G(x, p) = F(\delta_x, p)$.

The most appealing definition of an ESS is as follows [13].

Definition B.1. The distribution $p \in \Delta(X)$ is said to be an *ESS* if there exists $\varepsilon_0 > 0$ such that for any positive $\varepsilon < \varepsilon_0$,

$$\forall q \neq p^*, \quad F(p, (1-\varepsilon)p + \varepsilon q) > F(q, (1-\varepsilon)p + \varepsilon q).$$

Using only the linearity, it coincides with the original definition of [14].

Theorem B.1. *If F is linear in its second argument, Definition B.1 is equivalent to Definition B.2 below.*

Definition B.2. The distribution $p \in \Delta(X)$ is said to be an ESS if

(I) $\forall q \in \Delta(X), \quad F(q, p) \le F(p, p),$
(II) $\forall q \neq p, \quad F(q, p) = F(p, p) \Rightarrow F(q, q) < F(p, q).$

B.2 Relation to Classical Game Theory

Consider a two-player game between, say, player 1 and player 2. Both choose their action, say, q_1 and q_2, in $\Delta(X)$. Let their respective reward functions, that they seek to maximize, be

$$\begin{aligned} J_1(q_1, q_2) &= F(q_1, q_2), \\ J_2(q_1, q_2) &= F(q_2, q_1). \end{aligned}$$

We have the obvious proposition.

Proposition B.1.

- *Condition B.2 of Definition B.2 is equivalent to the statement that (p, p) is a Nash equilibrium of this game. For that reason, any p satisfying that condition is called a* Nash point.
- *If (p, p) is a strict Nash equilibrium, p is an ESS.*

We immediately have the following, by a theorem due to Von Neumann [21, assertion (17:D) p. 161] in the finite case, and noticed at least since the early 1950s in the infinite case.[2]

Theorem B.2. *Let p be an ESS, then*

(I) $\forall x \in X,\ G(x, p) \le F(p, p)$,

(II) *let* $N = \{x \in X \mid G(x, p) < F(p, p)\}$, *then* $p(N) = 0$.

A proof completely similar to —but slightly distinct from— the existence proof of the Nash equilibrium lets one state the following result, which applies here.

Theorem B.3. *Let P be a compact space, and let $F : P \times P \to \mathbb{R}$ be a continuous function, concave in its first argument. Then there exists at least one $p \in P$ satisfying condition (I) of Definition B.2.*

B.3 Further Analysis of the Linear Finite Case

B.3.1 Characterization in Terms of the Game Matrix

In the finite linear case, the problem is entirely defined by the matrix $A = (a_{ij})$ with $a_{ij} = H(x_i, x_j)$, as

$$G(x_i, p) = (Ap)_i, \quad F(q, p) = \langle q, Ap\rangle = q^t Ap.$$

We rephrase Theorem B.2 in that context. To do so, introduce the notation **1** to mean a vector—of appropriate dimension—the entries of which are all ones, and

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[2] Von Neumann's proof applies to zero-sum games. Its extension to a Nash equilibrium is trivial and can be found, e.g., without claim of novelty, in [11].

the notation for vectors u and v of same dimension $u < v$ to mean that the vector $v - u$ has all its coordinates strictly positive.

We obtain the following more or less classical results.

Theorem B.4. *In the finite linear case, the two conditions of Definition B.2 are respectively equivalent to (I) and (II) below.*

(I) There exists a partition $X = X_1 \cup X_0$, $|X_1| = n_1$, $|X_0| = n_0$, *such that, reordering the elements of* X *in that order and partitioning* $\mathbb{R}^n$ *accordingly, there exists a vector* $p_1 \in \Delta_{n_1}$, *a real number* α *and a vector* $h \in \mathbb{R}^{n_0}$ *such that*

$$p = \begin{pmatrix} p_1 \\ 0 \end{pmatrix}, \quad Ap = \begin{pmatrix} \alpha\mathbf{1} \\ h \end{pmatrix}, \quad h < \alpha\mathbf{1}. \tag{3}$$

(II) Partitioning A *accordingly in*

$$A = \begin{pmatrix} A_{11} & A_{10} \\ A_{01} & A_{00} \end{pmatrix},$$

$$\forall q_1 \in \Delta_{n_1}\backslash\{p_1\}, \quad \langle q_1 - p_1, A_{11}(q_1 - p_1)\rangle < 0. \tag{4}$$

Note that the vectors $\mathbf{1}$ in the second and third expression of (3) do not have the same dimension. Note also that p_1 may still have some null coordinates.

Proof. For condition (I), this is just a rephrasing of Theorem B.2. Concerning condition (II), the vectors $q \in \Delta(\mathbb{R}^n)$ such that $F(q, p) = F(p, p)$ are all the vectors of the form

$$q = \begin{pmatrix} q_1 \\ 0 \end{pmatrix}, \quad q_1 \in \Delta_{n_1}.$$

As a matter of fact, for all such vectors, $\langle q, Ap\rangle = \alpha$. Thus condition (I) of Definition B.2 says that $\forall q_1 \in \Delta_{n_1}\backslash\{p_1\}$, $\langle q_1 - p_1, A_{11}q_1\rangle < 0$. But we have seen that $\langle q_1 - p_1, A_{11}p_1\rangle = 0$. Therefore, we may subtract that quantity to get (II) above. □

Theorem B.3 says that there always exists at least one solution of equations (3). The question thus is to know whether that solution satisfies condition (II) of the definition. To further discuss that question, let $p_2 \in \mathbb{R}^{n_2}$ be the vector of the nonzero entries of p_1, so that, reordering the elements of X_1 if necessary,

$$p_1 = \begin{pmatrix} p_2 \\ 0 \end{pmatrix}.$$

Let also A_{22} be the corresponding submatrix of A, and for $i = 1, 2$, define $B_i := A_{ii} + A_{ii}^t$ and the $n_i \times (n_i - 1)$-dimensional matrices Q_i obtained by deleting one column from the symmetric projector matrix $P_i := [I - (1/n_i)\mathbf{1}\mathbf{1}^t]$. The condition that the restriction of the quadratic form to the orthogonal subspace to $\mathbf{1}$ be negative definite translates into the following.

Corollary B.1.

- *A necessary condition for a solution of equation (3) to be an ESS is that* $Q_2^t B_2 Q_2 < 0$ *(negative definite).*
- *A sufficient condition is that* $Q_1^t B_1 Q_1 < 0$*, and a fortiori that* $B_1 < 0$*.*

We may note the following fact.

Proposition B.2. *Matrices* B_i*,* $i = 1, 2$ *that satisfy the conditions of Corollary B.1 have at most one nonnegative eigenvalue.*[3]

Another easy corollary is that the number of ESSs is bounded by n. More precisely, we have the following statement.

Corollary B.2. *If there is an ESS in the relative interior of a face, there is no other ESS in that face, and in this statement* Δ_n *is itself an* $n-1$*-dimensional face.—In particular, if there is an ESS in the relative interior of* Δ_n*, it is* the *unique ESS.*

B.3.2 Stability of the Replicator Dynamics

Some authors ([19, 20]) define an ESS—in the finite case—as a stable point p of the replicator dynamics

$$\dot{q}_i = q_i[G(x_i, q) - F(q, q)]. \tag{5}$$

Notice first that a consequence of (5) is that

$$q_i(t) = q_i(0) \exp\left(\int_0^t [G(x_i, q(s)) - F(q(s), q(s))] \, \mathrm{d}s\right)$$

so that if all $q_i(0)$ are non-negative, this is preserved over time. Moreover, one sees that $\sum_i \dot{q}_i = \sum_i q_i G(x_i, q) - (\sum_i q_i) F(q, q) = (1 - \sum_i q_i) F(q, q) = 0$, so that the hyperplane $\{q \mid \sum_i q_i = 1\}$ is invariant. The conclusion of these two remarks is the following:

Proposition B.3. *Under the replicator dynamics,*

- $\Delta(X)$ *is invariant, as well as its interior,*
- *the faces of* $\Delta(X)$ *are invariant as well as their interiors.*

It is known (see, e.g., [16] for a much more detailed analysis) that in the finite linear case, the relationship between these two concepts is as in the next theorem. Note that in the continuous case, the situation is far more complex and still open. In the later case, the evolution equation in $\mathbb{R}^n$ is replaced by one in a measure space, so that the definition of stability depends on the topology used—and the Lyapunov function used here is not continuous in the natural weak topology.

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[3] Some authors have mistakenly replaced *at most one* by *exactly one*.

Theorem B.5. *In the finite linear case, every asymptotically stable point of (5) is a Nash point. Every ESS is a locally*[4] *asymptotically stable point of (5), and its attraction basin contains the relative interior of the lowest dimensional face of* $\Delta(X)$ *it lies on.*

Two particular cases of this theorem are as follows.

Corollary B.3. *In the finite linear case:*

- *If an ESS is an interior point of* $\Delta(X)$ *it is globally stable in the interior of* $\Delta(X)$.
- *Every pure strategy, whether an ESS or not, is a rest point of (5). The above theorem implies nothing more for a pure ESS.*

Proof of the theorem. To prove the necessity, assume p is not a Nash point, so that there is an index k such that $p_k = 0$, but $G(x_k, p) > F(p, p)$. Take an initial q with $q_k > 0$. Then it is impossible that $q(t) \to p$, as this would require that $q_k(t) \to 0$, and hence that

$$\int_0^t [G(x_k, q(s)) - F(q(s), q(s))] \, \mathrm{d}s \to -\infty,$$

while in a neighborhood of p the integrand would be positive.

For the sufficiency, restrict the attention to the subspace $\mathbb{R}^{n_2}$ of Corollary B.1, where all coordinates of p are strictly positive, and further to $\Delta := \Delta_{n_2}$. And consider the Lyapunov function

$$V(q) = \sum_i p_i \ln \frac{p_i}{q_i}.$$

It is zero at p. It can be written $V(q) - \sum_i p_i \ln(q_i/p_i)$, and using the fact that $\ln x < x - 1$ as soon as $x \neq 0$, $V(q) > -\sum_i p_i(q_i/p_i - 1) = 0$ as soon as $\mathrm{D} \ni q \neq p$. Thus its restriction to Δ is indeed a valid Lyapunov function. And trivially, on a trajectory,

$$\frac{\mathrm{d}V(q(t))}{\mathrm{d}t} = -\sum_{i=1}^{n_2} p_i[G(x_i, q) - F(q, q)] - F(p, q) + F(q, q)$$

which is by hypothesis negative on Δ_{n_2}. □

As a matter of fact, one can prove more, using the following fact, the proof of which (based upon compactness) we omit.

Definition B.3. A strategy $p \in \Delta_n$ is called *locally superior* if there exists a neighborhood $\mathcal{N}$ of p in Δ_n such that, for any $q \in \mathcal{N}$, $q \neq p$, $F(q, q) < F(p, q)$.

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[4] Relative to the face we are referring to.

Theorem B.6. *In the finite linear case, p is an ESS if and only if it is locally superior.*

Corollary B.4. *In the finite linear case, the basin of attraction of an ESS contains a neighborhood in Δ_n of the relative interior of the lowest dimensional face of Δ_n on which that ESS lies.*

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