

# DIET SELECTION AS A DIFFERENTIAL FORAGING GAME

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**Abstract.** An important issue addressed by Behavioural Ecology is that of the evolutionary relevance of foraging strategies adopted by animals in quest of a patchily distributed resource, both in terms of diet selection and patch-leaving decisions under competition.

We revisit the classical model of diet selection concerning an isolated —not subject to competition— forager; it yields a zero-one rule —a type of resource should be always accepted, or always rejected— that appears to be more the exception than the rule, as partial preferences are commonly observed in many species. Thus arises the question of its robustness to uncertainties concerning the time available to enjoy a patch before a perturbing event occurs. We mean any event that would affect its gain with respect to what it would obtain by enjoying alone the patch as long as it wants. For instance, the sudden presence of a predator could force it to flee the patch or the arrival of a conspecific would deprive it of some good resources.

By taking into account the potentially imminent arrival of a conspecific —but also any event that would suddenly shorten patch exploitation—, we show that the classical policy of diet selection no longer holds —as it changes the qualitative aspect of the optimal foraging strategies. Qualitatively, the optimal strategy is close to, but less greedy than, the evolutionarily stable strategy that concerns foragers actually competing for resources. It consists in accepting only the most profitable resource until it is depleted down to a given level, after which time both resources are accepted.

The underlying mathematical technique involves the solution of non-zero-sum differential games and synthesis techniques.

**Key words.** Differential Games, Evolutionarily Stable Strategies, Optimal Foraging Theory, Behavioural Ecology.

**AMS subject classifications.** 91A23, 91A22.

**1. Introduction.** “*Nothing in biology makes sense except in the light of evolution*”<sup>1</sup>. In this respect, Behavioural Ecology [18] interprets animal behavior through an evolutionary approach, via estimating its capacity to get through the natural selection process, thus to maximize Darwinian *fitness* [22] —a notion analogous to that of “utility” in Economics. Typically, in foraging theory [33] or the art of gathering resources in the environment, fitness is related to the amount 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 [6] reveals that the optimal giving up time is when the intake-rate is equal to the optimal long-term mean rate  $\gamma^*$  —that, if achieved, gives the best fitness a forager can expect in its environment.

This famous theoretical model was originally designed for lone foragers in quest of a singular patchily distributed resource. In parallel, another branch of the theory started by focusing on the optimal diet selection [5, 17, 31] when the environment offers a plural resource, varying both in profitability and abundance, but spatially reg-

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<sup>1</sup>Theodosius Dobzhansky, geneticist, 1900–1975.

ularly and homogeneously distributed. The authors of [23] merged these two theories afterwards.

Naturally, the question arises of whether this theory holds for foragers competing for a common patchily distributed resource, i.e. whether this is an evolutionarily stable strategy [20]; for instance, it might have implications in terms of population dynamics [34, 37].

Concerning the singular resource case, Charnov’s patch-leaving rule remains qualitatively unchanged under scramble competition —when the only competition between foragers is in sharing a common resource [32, 8];  $\gamma^*$  is clearly affected by the number of potential competitors, but the patch-leaving rule is unchanged. However, if there is *interference*, i.e. a decline in intake-rate due to competition, the game results in a *war of attrition* [32, 9] or random patch-leaving strategies.

In the present paper, our aim is to determine the evolutionarily stable strategy that non-interfering foragers competing for a plural and depleting resource should adopt, both in terms of diet selection and patch-leaving decision [3, 33].

The remainder of the paper is organized as follows. In Section 2, we reformulate the optimal diet selection policy for a lone forager free to leave the current patch of resources at any time. On our way, we solve the optimal diet selection problem for a single forager with a fixed end time; this is done in appendix A. In Section 3, we investigate the foraging game involving several foragers arriving simultaneously on a patch containing two distinct types of resources. Section 4 focuses on an asynchronous two forager game, where the inter-arrival time is assumed deterministic. Finally, the game considered in Section 5 lets the possible arrival of an opponent be a Poisson variable<sup>2</sup>.

**2. Foraging alone.** It is well-known [5, 16] that a lone forager should accept a unit of resource  $i$  if its —energy— value  $e_i$  is worth the time required to retrieve it: the *handling-time*  $h_i$ . Indeed, Charnov’s marginal value theorem [6, 22] prohibits the intake-rate from falling under a critical threshold  $\gamma^*$ . Hence the rule is to accept this resource if and only if  $\gamma^* \leq e_i/h_i$ . We shall define *profitability* of resource  $i$  as the ratio  $e_i/h_i$ . We shall also let  $\delta_i := e_i - \gamma^*h_i$ .

However, let us recall this result in order to introduce our modeling and solution approaches —the latter is close to that of [26].

Let  $x$  be the state vector containing the ratios  $x_i \in [0, 1]$  of each type of resource available in the patch. Let  $u$  be the control vector containing the controls  $u_i \in [0, 1]$  deciding the acceptance rate<sup>3</sup> of each type of resource available in the patch. Let  $\dot{x} := dx/dt$ , where  $t$  stands for the *residence time*.

Proceeding as in [14, 8] and most of the literature, an assumption of random probing on a patch yields the following dynamics:

$$(2.1) \quad \forall i \in \{1, \dots, N\}, \quad q\dot{x}_i = -\frac{u_i x_i}{\alpha + \sum_{j=1}^N u_j x_j h_j}, \quad x_i(0) = x_i^0; \quad \sum_{i=1}^N x_i^0 = 1,$$

where  $\alpha$  is the time required to probe an area of the patch that could contain a unit of resource and  $q$  is the quality of the patch or the quantity of resources it initially contains.

<sup>2</sup>A particular case of that game is that of a single player with an exponential random end time, such as the possible occurrence of a predator.

<sup>3</sup>Or equivalently the probability to accept a given type of resource when encountered.

Following [22], we want to maximize the criterion:

$$(2.2) \quad J = \int_0^{t^*} L(x, u) dt \quad \text{with} \quad L(x, u) = - \sum_{j=1}^N e_j q \dot{x}_j - \gamma^*,$$

where  $t^*$  is a free final time.

We claim the following result:

**THEOREM 2.1.** *The optimal policy in the problem stated by equations (2.1) and (2.2) is given by*

- $\forall t \in [0, t^*]$ , take  $u_i = \begin{cases} 1 & \text{if } \gamma^* < e_i/h_i \\ \text{arbitrary in } [0, 1] & \text{if } \gamma^* = e_i/h_i \\ 0 & \text{if } \gamma^* > e_i/h_i \end{cases}$
- and leave as soon as  $\sum_{j=1}^N u_j x_j (e_j - \gamma^* h_j) - \gamma^* \alpha \leq 0$ .

*Proof.* Let  $s$  be such that  $dt = qDds$  with  $D := \alpha + \sum_{j=1}^N h_j u_j x_j$ . Let  $\dot{x} := dx/ds$  and  $f(x, u) := \dot{x}$ . The dynamics become:

$$\dot{x}_i = -u_i x_i, \quad x_i(0) = x_i^0.$$

Our criterion can now be expressed as follows: let

$$\mathcal{J} := J/q = \int_0^{s^*} \mathcal{L}(x, u) ds \quad \text{with} \quad \mathcal{L}(x, u) = \sum_{j=1}^N u_j x_j e_j - \gamma^* D.$$

It directly yields that the optimal end time is such that  $\mathcal{L}$  be zero on the optimal trajectories, since  $\partial \mathcal{J} / \partial s^* = \mathcal{L}(x(s^*), u(s^*)) = 0$ ; this corresponds to Charnov's patch leaving rule. Hence the claim of the theorem.

Let  $\lambda$  be the adjoint vector. It yields the Hamiltonian:

$$\mathcal{H} = \mathcal{L}(x, u) + \langle \lambda, f(x, u) \rangle = \sum_{j=1}^N (\delta_j - \lambda_j) u_j x_j - \alpha \gamma^*.$$

According to Pontryagin's maximum principle [30], if a policy  $u^*(s)$  generating a trajectory  $x^*(s)$  is optimal, then there exists an adjoint trajectory  $\lambda(s)$  such that

$$\left\{ \begin{array}{l} \dot{\lambda} = -\nabla_x \mathcal{H}(\lambda, u^*, x^*) \\ \lambda(s^*) = 0 \\ \mathcal{H}(s^*) = 0 \\ \left| \begin{array}{l} \forall s \in [0, s^*] \text{ where } u^*(\cdot) \text{ is continuous,} \\ \mathcal{H}(\lambda(s), u^*(s), x^*(s)) = \max_{u \in [0, 1]^n} \mathcal{H}(\lambda(s), u, x^*(s)) \end{array} \right. \end{array} \right. .$$

The last condition above translates into the switch-functions

$$\sigma_i := \partial \mathcal{H} / \partial u_i = (\delta_i - \lambda_i) x_i,$$

and the *bang-bang* optimal policy:

$$u_i^* = \begin{cases} 1 & \text{if } \sigma_i > 0 \\ 0 & \text{if } \sigma_i < 0 \end{cases} .$$

The singular case  $\sigma_i = 0$  allows the focal forager to either accept or reject the less profitable resource indifferently.

We also have

$$\dot{\lambda}_i = -\partial\mathcal{H}/\partial x_i = -(\delta_i - \lambda_i)u_i, \quad \lambda_i(s^*) = 0.$$

It yields  $\dot{\sigma}_i = 0$ . Hence the sign of  $\sigma_i$  never changes, and therefore the optimal policy is:

$$\forall t \in [0, t^*], \quad u_i = \begin{cases} 1 & \text{if } \gamma^* < e_i/h_i \\ 0 & \text{if } \gamma^* > e_i/h_i \end{cases}.$$

As already mentioned in [23], the reason why the author of [26] found another result is that he —consciously— considered, as a constraint, an arbitrarily predetermined residence time<sup>4</sup>. It has to be noticed that in this simple model, *partial preferences* [21] should only occur in the non generic case  $\gamma^* = e_i/h_i$ .  $\square$

Given the optimal policy as a function of  $\gamma^*$ , it is possible to compute both  $\gamma^*$  and the corresponding optimal diet, as done in [23], where the authors provide an algorithm that converges to the solution.

**3. The synchronous foraging game.** The authors of [15] argue that when “a large number” of foragers are competing for a plural and depleting resource, they should maximize their intake-rate. Thus the evolutionarily stable policy consists of being *selective* first and, after a while, being *opportunistic*<sup>1</sup>. The results of both [26, 35] are in agreement with [15] except that they found “earlier” switch-times, for a relatively low number of competitors. However, both approaches point to a convergence of the switch-time towards the intake-rate maximizing one as the number of foragers increases.

Our aim is now to determine the evolutionarily stable policy via an approach similar to that of [26], except that we do not set any arbitrarily predetermined residence time or final patch state.

Following Section 2, we now restrain the resource range to those which would be included in the diet of a lone forager:  $\forall i \in \{1, 2\}, \delta_i \geq 0$  —the resource types rejected by a lone forager should a-fortiori be rejected under competition. We shall also let  $\zeta := e_1h_2 - e_2h_1 \geq 0$  as  $e_2/h_2 \leq e_1/h_1$  by hypothesis.

Proceeding as in [26], we look for the optimal policy against a strategy assumed commonly adopted by the opponents. If it leads to the latter, this is indeed an evolutionarily stable strategy —as this is a strict and symmetric Nash equilibrium [13, 9]. However, to be consistent, we need to assume a state feedback strategy for the opponents. Hence we must use a regular synthesis technique in order to recover the co-state vector as a function of the current state, and construct a switch-manifold in the state space. This, in turn, induces discontinuities in the adjoint variables of the focal player and other difficulties that we must take into account. Throughout our reasoning, we shall refer to figure 3.1, which represents the state-space  $(x_1, x_2)$ .

Let  $n$  be the number of foragers on the patch. Let  $u$  be the decision variable of the focal forager, i.e. the acceptance rate of resource 2 —as resource 1, the most profitable one, should, of course, always be accepted. Similarly, let  $v$  be the decision variable of its opponents.

Let  $D(u) := \alpha + h_1x_1 + uh_2x_2$ . The dynamics are now:

$$(3.1) \quad \begin{cases} q\dot{x}_1 = -x_1/D(u) - (n-1)x_1/D(v), & x_1(0) = x_1^0 \\ q\dot{x}_2 = -ux_2/D(u) - v(n-1)x_2/D(v), & x_2(0) = x_2^0 \end{cases}.$$

<sup>4</sup>This issue is addressed in appendix A.

<sup>1</sup>The author of [10] also mentioned this “*expanding-specialist*” strategy under competition.

The criterion of the focal forager is:

$$(3.2) \quad J = \int_0^{t^*} L(x, u) dt \quad \text{with} \quad L(x, u) = e_1 x_1 / D(u) + u e_2 x_2 / D(u) - \gamma^*$$

and where  $t^*$  is a free final time.

We claim the following result —see figure 3.1:

**THEOREM 3.1.** *The unique pure symmetric state feedback Nash Equilibrium in the game stated by equations (3.1) and (3.2) corresponds to:*

- take  $\begin{cases} u = 0 & \text{as long as } S(x) \leq 0 \\ u = 1 & \text{as soon as } S(x) > 0 \end{cases}$ , where  $S(x)$  is given by equation (3.9)
- and leave as soon as  $\delta_1 x_1 + \delta_2 x_2 - \gamma^* \alpha \leq 0$ .

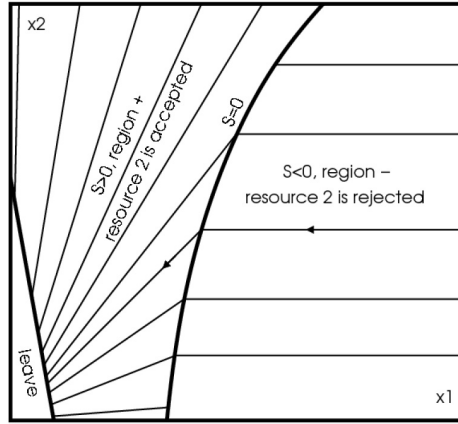


FIG. 3.1. *The Nash-optimal fields of trajectories in the state-space  $(x_1, x_2)$ .*

*Proof.* Let  $s$  be such that  $dt =: qD(u)ds$ . Let  $\dot{x} := dx/ds$  and  $f(x, u) := \dot{x}$ . The dynamics become:

$$\begin{cases} \dot{x}_1 = -x_1(1 + (n-1)D(u)/D(v)), & x_1(0) = x_1^0 \\ \dot{x}_2 = -x_2(u + v(n-1)D(u)/D(v)), & x_2(0) = x_2^0 \end{cases}.$$

Our criterion can now be expressed as follows: let

$$\mathcal{J} := J/q = \int_0^{s^*} \mathcal{L}(x, u) ds \quad \text{with} \quad \mathcal{L}(x, u) = e_1 x_1 + u e_2 x_2 - \gamma^* D(u).$$

Clearly,  $\partial \mathcal{J} / \partial s^* = \mathcal{L}(x(s^*), u(s^*)) = 0$ . It directly yields that the optimal end time is such that  $\mathcal{L}$ —which does not depend on  $s$ —be zero on the optimal trajectories; this corresponds to Charnov's patch leaving rule. The oblique line sloping to the left in figure 3.1 represents this terminal manifold.

Let  $\lambda$  be the adjoint vector, associated with the focal forager. It yields the Hamiltonian:

$$\mathcal{H} = e_1 x_1 + u e_2 x_2 - \gamma^* D(u) - \lambda_1 x_1 (1 + (n-1)D(u)/D(v)) - \lambda_2 x_2 (u + v(n-1)D(u)/D(v)).$$

According to Pontryagin's maximum principle<sup>5</sup>, the optimal policy is thus bang-bang, according to the switch-function

$$\sigma = [\delta_2 - \lambda_1(n-1)h_2x_1/D(v) - \lambda_2(1+v(n-1)h_2x_2/D(v))]x_2.$$

We have:

$$\begin{aligned}\dot{\lambda}_1 &= \lambda_1[(1+(n-1)D(u)/D(v)) + (n-1)h_1x_1(1/D(v) - D(u)/D(v)^2)] + \\ &\quad \lambda_2v(n-1)h_1x_2(1/D(v) - D(u)/D(v)^2) - \delta_1, \quad \lambda_1(s^*) = 0. \\ \dot{\lambda}_2 &= \lambda_2[(u+v(n-1)D(u)/D(v)) + v(n-1)h_2x_2(u/D(v) - vD(u)/D(v)^2)] + \\ &\quad \lambda_1(n-1)h_2x_1(u/D(v) - vD(u)/D(v)^2) - u\delta_2, \quad \lambda_2(s^*) = 0.\end{aligned}$$

Clearly,  $u^*(s^*) = 1$  as  $\sigma(s^*) = \delta_2x_2 \geq 0$  by hypothesis.

Proceeding as in to [26], we first assume that the opponents are opportunists. The optimal strategy is then given via integrating backward the above differential equations, with  $v = 1$ . As long —from the end time— as  $\sigma$  remains positive, being opportunistic is optimal. Thus if it remains so backwards up to time zero, being opportunistic the whole time spent on the patch is the evolutionarily stable strategy. Otherwise, i.e. if the sign of  $\sigma$  changes in backward time, being selective is, at least locally, optimal before the switch-point. Thanks to the assumed symmetry among foragers, if such a switch-point appears, then it prevails for any competitor on the patch. Therefore, we shall assume in a second time that  $v = 0$  from this possible switch-point down to  $s = 0$ . However, a prerequisite to reiterate a similar process backward in time is that being selective be optimal against selective opponents.

Let  $(\hat{s}, \hat{x})$  be either the first —in backward time— switch-point, if there is one, or  $(0, x(0))$  otherwise; i.e. beyond this point, being opportunistic remains optimal up to the end time. Let the superscript  $+$  denote the region of the state space beyond the last switch-point; thus we postulate that in region  $+$  the Nash-optimal strategies are  $u = v = 1$ . For instance, let  $D^+ := D(1) = \alpha + h_1x_1 + h_2x_2$ . We have  $\forall s \in (\hat{s}, s^*)$ ,  $\forall i \in \{1, 2\}$ ,

$$\dot{x}_i = -nx_i, \quad x_i(s^*) =: x_i^* \quad \text{and} \quad \dot{\lambda}_i^+ = n\lambda_i^+ - \delta_i, \quad \lambda_i^+(s^*) = 0.$$

We also have

$$(3.3) \quad \sigma^+ = [\delta_2 - \lambda_1^+(n-1)h_2x_1/D^+ - \lambda_2^+(1+(n-1)h_2x_2/D^+)]x_2$$

and  $\mathcal{H}^+ = e_1x_1 + e_2x_2 - \gamma^*D^+ - \lambda_1^+x_1n - \lambda_2^+x_2n$ . It yields  $\forall s \in (\hat{s}, s^*)$ ,  $\forall i \in \{1, 2\}$ ,

$$(3.4) \quad x_i(s) = x_i^*e^{n(s^*-s)} \quad \text{and} \quad \lambda_i^+(s) = \delta_i \left(1 - e^{-n(s^*-s)}\right) / n.$$

As a consequence

$$(3.5) \quad \lambda_1^+(s) = \delta_1(1 - x_1^*/x_1)/n \geq 0.$$

Moreover, one can notice from equation (3.4) that  $\forall s \in (\hat{s}, s^*)$ ,  $x_1^*/x_1 = x_2^*/x_2$  or equivalently that  $x_1/x_2$  is invariant over  $[\hat{s}, s^*]$  —this results from our assumption of homogeneous probing on the patch and that is why in figure 3.1, the field of optimal trajectories is a radial one. Furthermore, as the Hamiltonian remains constant all

<sup>5</sup>as long as the opponent use a Lipschitz continuous, here constant, strategy —w.r.t.  $x$ .

along the optimal trajectory, it remains equal to zero here and this yields  $\forall s \in (\hat{s}, s^*)$ ,  $\forall i \in \{1, 2\}$ ,

$$(3.6) \quad x_i^*/x_i = \frac{\gamma^* \alpha}{x_1 \delta_1 + x_2 \delta_2}.$$

Hence the claim of the theorem.

The switch-function can also be rewritten as follows:

$$\sigma^+ = [(e_2 - \lambda_2^+)(\alpha + h_1 x_1) - (e_1 - \lambda_1^+)h_2 x_1] x_2 / D^+.$$

Let us now assume that there is a switch-point by definition such that  $\sigma^+(\hat{s}) = 0$ . Our aim is now to verify that switching —in backward time—  $u$  to zero remains optimal if  $v$  switches to zero simultaneously at time  $\hat{s}$ . Let the superscript  $-$  denote the region of the state space where we conjecture that the Nash-optimal strategies are  $u = v = 0$ . For instance, let  $D^- := D(0) = \alpha + h_1 x_1$ . We have

$$\sigma^-(\hat{s}) = [\delta_2 - \lambda_1^-(\hat{s})(n-1)h_2 \hat{x}_1 / D^-(\hat{s}) - \lambda_2^-(\hat{s})] \hat{x}_2.$$

One also has  $\mathcal{H}^-(\hat{s}) = e_1 \hat{x}_1 - \gamma^* D^-(\hat{s}) - \lambda_1^-(\hat{s}) \hat{x}_1 n$ .

Notice that the time instant  $\hat{s}$  depends on the trajectory considered, and thus  $x(\hat{s})$  describes a switch manifold  $S(x) = 0$  —the curve in figure 3.1. Therefore,  $\lambda_1^-(\hat{s})$  and  $\lambda_2^-(\hat{s})$  must satisfy the system of equations below —the difference of the adjoint vectors is a normal to the manifold, see, e.g., [1]:

$$(3.7) \quad \begin{pmatrix} \lambda_1^-(\hat{s}) \\ \lambda_2^-(\hat{s}) \\ -\mathcal{H}^-(\hat{s}) \end{pmatrix} = \begin{pmatrix} \lambda_1^+(\hat{s}) \\ \lambda_2^+(\hat{s}) \\ -\mathcal{H}^+(\hat{s}) \end{pmatrix} + \kappa \begin{pmatrix} \partial S(\hat{s}) / \partial x_1 \\ \partial S(\hat{s}) / \partial x_2 \\ \partial S(\hat{s}) / \partial s \end{pmatrix},$$

where  $\kappa$  is a scalar that remains to be determined and  $S$  is any function that characterizes the manifold  $\sigma^+ = 0$  in the plane  $(x_1, x_2)$ . Indeed, equation (3.5) and (3.6) clearly show that  $\sigma^+$  can be expressed as a function of  $x_1$  and  $x_2$  alone, and not  $s$ . Hence  $\partial S / \partial s = 0$ . Therefore,  $\mathcal{H}^-(\hat{s}) = \mathcal{H}^+(\hat{s}) = 0$  and it yields  $\lambda_1^-(\hat{s}) = [e_1 \hat{x}_1 - \gamma^* D^-] / \hat{x}_1 n$ ; thus  $\lambda_1^-(\hat{s}) - \lambda_1^+(\hat{s}) = (\delta_1 x_1^* - \gamma^* \alpha) / (\hat{x}_1 n) \leq 0$  as  $\mathcal{L}(s^*) = \delta_1 x_1^* + \delta_2 x_2^* - \gamma^* \alpha = 0$ .

Moreover, using  $\mathcal{H}^-(\hat{s}) = 0$ ,  $\sigma^-(\hat{s})$  can be rewritten as follows:

$$\sigma^-(\hat{s}) = [(e_2 - \lambda_2^-(\hat{s}))(\alpha + h_1 \hat{x}_1) - (e_1 - \lambda_1^-(\hat{s}))h_2 \hat{x}_1] x_2 / D^-(\hat{s}).$$

Using the fact that  $\sigma^+(\hat{s}) = 0$  yields

$$\sigma^-(\hat{s}) = \kappa \left( \frac{\partial S(\hat{s})}{\partial x_1} h_2 \hat{x}_1 - \frac{\partial S(\hat{s})}{\partial x_2} (\alpha + h_1 \hat{x}_1) \right) \hat{x}_2 / D^-(\hat{s})$$

and we have

$$(3.8) \quad \sigma^-(\hat{s}) = [\lambda_1^-(\hat{s}) - \lambda_1^+(\hat{s})] \left( h_2 \hat{x}_1 - (\alpha + h_1 \hat{x}_1) \frac{\partial S(\hat{s})}{\partial x_2} \Big/ \frac{\partial S(\hat{s})}{\partial x_1} \right) \hat{x}_2 / D^-(\hat{s}).$$

Describing the switch manifold via an implicit function  $\hat{x}_1 = \xi(\hat{x}_2)$ , equation (3.8) also reads

$$\sigma^-(\hat{s}) = [\lambda_1^-(\hat{s}) - \lambda_1^+(\hat{s})] \left( h_2 \hat{x}_1 + (\alpha + h_1 \hat{x}_1) \frac{d\xi(\hat{x}_2)}{dx_2} \right) x_2 / D^-(\hat{s}).$$

Choose  $S(x_1, x_2) := n(x_1\delta_1 + x_2\delta_2)D^+\sigma^+/x_2$  and  $S$  can be expressed as follows:

$$(3.9) \quad \left\{ \begin{array}{l} S(x_1, x_2) = a(x_2)x_1^2 + b(x_2)x_1 + c(x_2) \text{ or } S(x_1, x_2) = d(x_1)x_2 + e(x_1), \text{ where} \\ \left. \begin{array}{l} a := -(n-1)\delta_1\zeta \leq 0 \\ c := x_2\delta_2h/\delta_1 + \delta_2\gamma^*\alpha^2 \geq 0 \\ d := -fx_1 + \delta_2h/\delta_1 = \delta_2(ax_1 + h)/\delta_1 \\ e := -ax_1^2 + (g+h)x_1 + \delta_2\gamma\alpha^2 \end{array} \right\} \quad \left. \begin{array}{l} b := -fx_2 - g + h \text{ with:} \\ f := -\delta_2a/\delta_1 \geq 0 \\ g := \zeta\gamma^*\alpha \geq 0 \\ h := \alpha\delta_1(e_2n - \delta_2) \geq 0 \end{array} \right\} .$$

Hence  $\xi(x_2) = (-b - \sqrt{b^2 - 4ac})/2a$  and one has

$$\frac{d\xi(x_2)}{dx_2} = -\frac{d}{2a\xi(x_2) + b} = \frac{\delta_2}{\delta_1} \frac{a\xi(x_2) + h}{2a\xi(x_2) + b} = -\frac{\delta_2}{2\delta_1} \left( 1 + \frac{b-2h}{\sqrt{b^2-4ac}} \right).$$

As  $b - 2h \leq 0$ , it yields

$$\frac{d\xi(x_2)}{dx_2} = -\frac{\delta_2}{2\delta_1} \left( 1 - \sqrt{\frac{(b-2h)^2}{b^2-4ac}} \right) = -\frac{\delta_2}{2\delta_1} \left( 1 - \sqrt{1 + \frac{\iota}{b^2-4ac}} \right) \geq 0$$

as  $\iota = 4[ac - h(b-h)] = 4n\zeta\gamma^{*2}\alpha^2\delta_1h_2 \geq 0$ . Hence  $\forall x_2$ ,  $d\xi(x_2)/dx_2 \geq 0$ —it justifies the orientation of the curve in figure 3.1. As a consequence,  $\sigma^-(\hat{s}) \leq 0$ .

As long as  $u$  remains equal to zero while going backward in time from  $\hat{s}$ , one has

$$\begin{cases} \dot{\hat{x}}_1 = -n\hat{x}_1, & x_1(\hat{s}) =: \hat{x}_1 \\ \dot{\hat{x}}_2 = 0, & x_2(\hat{s}) =: \hat{x}_2 \end{cases} ,$$

and  $\sigma^- = [(e_2 - \lambda_2^-)(\alpha + h_1x_1) - (e_1 - \lambda_1^-)h_2x_1]x_2/D^-$ , with

$$\begin{cases} \overset{\circ}{\lambda}_1^- = n\lambda_1^- - \delta_1, & \lambda_1^-(\hat{s}) = [e_1\hat{x}_1 - \gamma^*D^-(\hat{s})]/\hat{x}_1n \\ \overset{\circ}{\lambda}_2^- = 0, & \lambda_2^-(\hat{s}) = \cdot \end{cases} .$$

Thus, still going backward in time from  $\hat{s}$  with  $u = v = 0$ , one has

$$\begin{cases} x_1(s) = \hat{x}_1 e^{n(\hat{s}-s)} \\ x_2(s) = \hat{x}_2 \end{cases} \quad \text{and} \quad \begin{cases} \lambda_1^-(s) = (e_1x_1 - \gamma^*D^-)/x_1n \\ \lambda_2^-(s) = \lambda_2^-(\hat{s}) \end{cases} .$$

Introducing  $y(x_1) := e_1h_2(n-1)x_1/[n(\alpha + h_1x_1)]$  yields  $\sigma^- - \sigma^-(\hat{s}) = y(\hat{x}_1) - y(x_1)$ . It is easy to see that  $y(x_1)$  is increasing. Thus  $\forall s \in [0, \hat{s}]$ ,  $\sigma^- \leq 0$ . Hence there is at most one switch-point.

Finally, it is also necessary to check that if the focal forager does not switch to the generalist strategy upon reaching the switch manifold, the state nevertheless crosses the said manifold, and enters the region where the optimal behavior for all players is to be opportunistic. The so-called “*permeability condition*” [1]<sup>6</sup>.

To that aim, let  $\nu = (-1, d\xi/dx_2)$  be a normal vector to the switch-manifold pointing in the same direction as the outgoing trajectories. Thus

$$\langle \nu, f(x, 1, 1) \rangle = \left( x_1 - x_2 \frac{d\xi}{dx_2} \right) > 0.$$

<sup>6</sup>Yet, this is a non-zero sum game, and one cannot conclude as in [1] that the adjoint variables are continuous.



We calculate

$$\langle \nu, f(x, 0, 1) \rangle = x_1 + (n - 1) \frac{\alpha + h_1 x_1}{\alpha + h_1 x_1 + h_2 x_2} \left( x_1 - x_2 \frac{d\xi}{dx_2} \right),$$

which, taking the previous inequality into account, is clearly positive. Hence the permeability condition is satisfied.

Therefore, the evolutionarily stable strategy is indeed either to be opportunistic the whole time spent on the patch, or it consists of being selective first and, after a while, being opportunistic.  $\square$

Our aim is now to characterize this possible switch-point. Clearly,  $\hat{x}_2 = 1 - x_1^0$  thus  $\hat{x}_1 = \xi(1 - x_1^0)$ .

Figure 3.2 shows the switch-manifolds associated to several values of  $e_2$  in the state space  $(x_1, x_2)$ . Interestingly, we see that the threshold  $\hat{x}_1$  is almost independent from  $x_2$ . In other words, the curve in figure 3.1 seems to be qualitatively very close to a straight line of constant  $x_1$ .

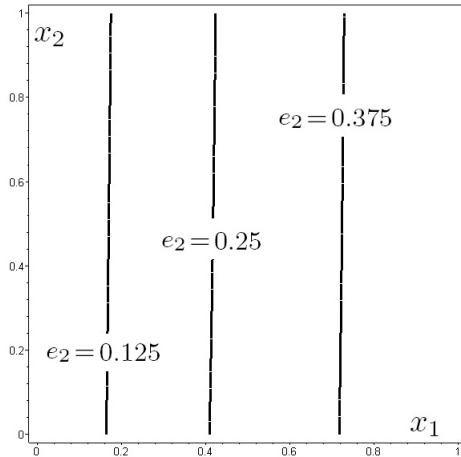


FIG. 3.2. *The switch-manifolds associated to several values of  $e_2$  in the state space  $(x_1, x_2)$ . We took  $n = 2$ ,  $e_1 = 1$ ,  $\alpha = 1$ ,  $h_1 = h_2 = 1$ ,  $\gamma^* = 0.1$  and from the left to the right,  $e_2 = \{0.125, 0.25, 0.375\}$ .*

Figure 3.3 shows the mapping  $n \mapsto \hat{x}_1$ . Interestingly, the greater the number of foragers on the patch, the closer becomes the evolutionarily stable strategy to intake-rate maximization.

**3.1. Partial conclusion.** Our results are in agreement with those of [26], obtained via a similar approach —although this author ignored the discontinuities on the adjoint variables, see equation (3.7). Our innovation lies in the fact that we do not consider any arbitrarily predetermined residence time or final patch state. It allows us to analyze the sensitivity of the switch-point to the initial conditions and our model reveals<sup>7</sup> that it seems almost independent from them. Qualitatively, the evolutionarily stable strategy is then close to intake-rate maximization, a policy that consists in being selective until the best resource is depleted down to an optimal threshold

<sup>7</sup>compared to [26], as the author of [35] also observed that the switch-point is “*nearly independent of [...] the ratio of the prey types [...] initially present on the patch.*”

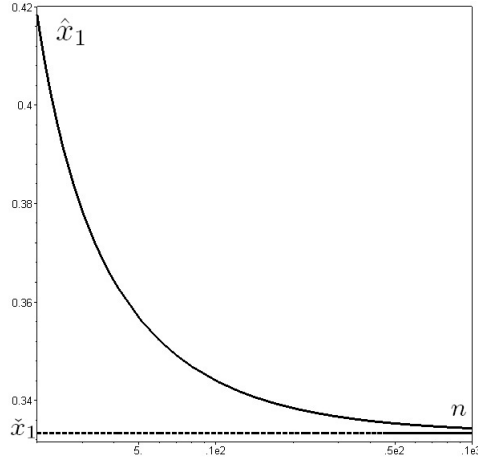


FIG. 3.3. The mapping  $n \mapsto \hat{x}_1$ . We took  $e_2 = 0.25$ ,  $x_1^0 = 0.5$ ,  $n \in [2, 100]$  and let the others parameters unchanged. The horizontal axis has a logarithmic scale. The dashed line represent the threshold  $\tilde{x}_1$  that corresponds to intake-rate maximization; indeed, intake-rate maximization consists of being selective while  $x_1$  remains larger than a given threshold  $\tilde{x}_1 := e_2\alpha/\zeta$ , independent of  $x_2$ .

—whatever the abundance of the less profitable resource. However, the intake-rate maximization threshold remains a lower bound; for instance, the larger the number of foragers on the patch, the closer the evolutionarily stable strategy to intake-rate maximization. Moreover, these results are also in agreement with those of [15, 35] obtained by quite different approaches.

As the diet selection policy of an isolated —not subject to competition— forager is really different from the evolutionarily stable strategy relevant in a situation of actual competition, the question that arises then is “what should a lone forager entering a patch do if the probability of facing a situation of competition is non-zero ?”.

**4. An asynchronous but deterministic foraging game.** As a preliminary approach, this section focuses on an asynchronous two forager game, where the arrival time  $t_a$  of the second one is assumed deterministic —this might be relevant in a case of group foraging with “information sharing” [7], assuming that the first forager on a patch has some time to take advantage of its discovery.

Once the second forager arrives, the evolutionarily stable policy only depends on the current patch-state  $x$  and is detailed in Section 3. It thus remains to determine the optimal strategy before the intruder’s arrival.

We claim the following result —see figure 4.1:

**THEOREM 4.1.** *In the deterministic arrival time problem, the optimal strategy of the first forager before the arrival of the second one is:*

- Any admissible policy that leads to  $S(x) = 0$  at  $t = t_a$ , provided that it is feasible —if so, there exists an infinite number of optimal trajectories.
- Otherwise, take  $u = 0$ , respectively  $u = 1$ , all along the trajectory if this leads to  $S(x) < 0$ , respectively  $S(x) > 0$ , at time  $t = t_a$ .

*Proof.* As we now need to consider the variable  $t$  explicitly, we let it be a state

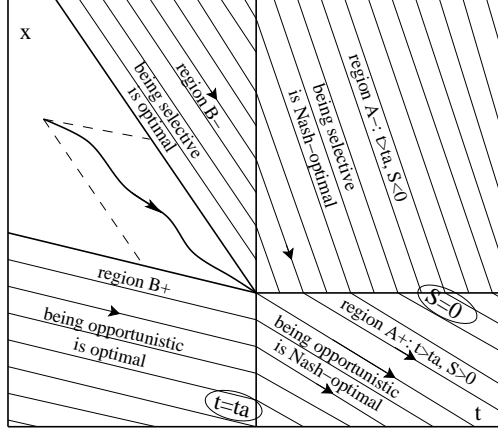


FIG. 4.1. This graph represents the optimal fields of trajectories in the state-space  $(t, x)$ . The regions  $B$  —before the opponent’s arrival— and  $A$  —after— correspond respectively to  $t < t_a$  and  $t \geq t_a$  —or equivalently to  $n = 1$  and  $n = 2$ . The signs  $-$  and  $+$  denote respectively that being strictly selective or strictly opportunistic is the —Nash— optimal policy in the region considered. In the latter case, optimal trajectories are, symbolically, linearly plotted. The vertical line represents the manifold  $t = t_a$ . The horizontal one in region  $A$  represents the switch-manifold given by  $S(x) = 0$ . The curvilinear trajectory starting in the white —non cross-hatched by “linear” trajectories— region reflects the fact that any trajectory that remains in this region is optimal.

variable; thus the dynamics are extended as follows:

$$\begin{cases} \dot{x}_1 = -x_1[1 + (n-1)D(u)/D(v)], & x_1(0) = x_1^0 \\ \dot{x}_2 = -x_2[u + v(n-1)D(u)/D(v)], & x_2(0) = x_2^0 = 1 - x_1^0 \\ \dot{t} = D(u), & t(0) = 0 \end{cases} .$$

From now on, we shall refer to figure 4.1 to support our reasoning; we stress that this is just a rough sketch that only pretends to a symbolic value. In region  $A$ , the Nash-optimal fields of trajectories are perfectly known, thanks to Section 3; i.e. the evolutionarily stable strategy only depends on the sign of  $S(x)$ .

It remains to determine the optimal fields of trajectories in region  $B$ .

For ease of notations, we let  $\mu$  and  $H$  be respectively the adjoint vector and the Hamiltonian associated to the trajectories evolving in region  $B$  —the part of the game during which the forager is still alone. Connecting  $\mu$  to  $\lambda$  is a matter of transversality conditions relative to the manifold  $t = t_a$  —or possibly only to its intersection with the switch-manifold given by  $S(x) = 0$ . The plane  $t = t_a$ , parallel to the  $x$  subspace, is consequently transparent for this patch-state variable. Thus the only possible discontinuity concerning the adjoint vector is on the co-state variables associated to  $t$ , say  $\mu_3$  and  $\lambda_3$  —except on the intersection of the two manifolds. Thus, apart from this particular 1-D curve, we have the following relation:

$$\begin{pmatrix} \mu_1(s_a) \\ \mu_2(s_a) \\ \mu_3(s_a) \\ -H(s_a) \end{pmatrix} = \begin{pmatrix} \lambda_1(s_a) \\ \lambda_2(s_a) \\ \lambda_3(s_a) = 0 \\ -\mathcal{H}(s_a) = 0 \end{pmatrix} + \nu \begin{pmatrix} 0 \\ 0 \\ 1 \\ 0 \end{pmatrix},$$

where  $\nu$  is a scalar that remains to be determined and  $s_a$  is such that  $t(s_a) = t_a$ . To be exhaustive, the transversality condition associated to the curve given by the

intersection of the two manifolds is the following, but we shall not need it:

$$\begin{pmatrix} \mu_1(s_a) \\ \mu_2(s_a) \\ \mu_3(s_a) \\ -\mathbf{H}(s_a) \end{pmatrix} = \begin{pmatrix} \lambda_1(s_a) \\ \lambda_2(s_a) \\ \lambda_3(s_a) \\ -\mathcal{H}(s_a) \end{pmatrix} + \tilde{\kappa} \begin{pmatrix} \partial S(s_a)/\partial x_1 \\ \partial S(s_a)/\partial x_2 \\ \partial S(s_a)/\partial t = 0 \\ \partial S(s_a)/\partial s = 0 \end{pmatrix} + \tilde{\nu} \begin{pmatrix} 0 \\ 0 \\ 1 \\ 0 \end{pmatrix}.$$

As, in region  $B$ ,  $n = 1$ , one has  $\mathbf{H} = \mathcal{L} - \mu_1 x_1 - \mu_2 u x_2 + \mu_3 D(u)$ .

Let  $\varsigma = \partial \mathbf{H}/\partial u = (\delta_2 - \mu_2 + h_2 \mu_3) x_2$ . The fact that  $\mathbf{H}(s_a) = \mathcal{H}(s_a) = 0$  yields

$$\mu_3(s_a) = \nu = -\frac{\mu_1 x_1(s_a) + \mu_2 u x_2(s_a)}{\alpha + h_1 x_1(s_a) + h_2 x_2(s_a)}.$$

Thus  $\varsigma(s_a) = \sigma(s_a)$ : the discontinuity on the co-state variable associated to  $t$  precisely maintains the switch-function continuous. Moreover, one has

$$\begin{cases} \dot{\mu}_1 = -\partial \mathbf{H}/\partial x_1 = \delta_1 - \mu_1 + h_1 \mu_3, & \mu_1(s_a) = \lambda_1(s_a) \\ \dot{\mu}_2 = -\partial \mathbf{H}/\partial x_2 = -u(\delta_2 - \mu_2 + h_2 \mu_3), & \mu_2(s_a) = \lambda_2(s_a) \\ \dot{\mu}_3 = -\partial \mathbf{H}/\partial t = 0, & \mu_3(s_a) = \nu \end{cases},$$

and it yields  $\dot{\varsigma} = 0$ . We now investigate the possible geometry of the trajectory fields referring the reader to the four sketches of figure A.2. As it is clear that being opportunistic does not deplete the best resource as much as being selective during the same time, the fourth quadrant represents an impossible scenario. If being selective until the intruder's arrival yields  $S(x(s_a)) < 0$ —second quadrant—, this is optimal. In a similar fashion, if being opportunistic yields  $S(x(s_a)) > 0$ —first quadrant—, this is optimal. Otherwise—third quadrant—, the optimal policy is such that  $S(x(s_a)) = 0$ . Moreover, as  $d\xi/dx_2 \geq 0$ , the scenario of the third quadrant, now considering the dashed line as the switch-manifold, cannot happen. Hence there is no state prior to  $t_a$  through which trajectories of the two extremal fields would pass. On the contrary, there is indeed a gap—a region uncovered by our extremal fields— between regions  $+$  and  $-$  in region B of figure 4.1.

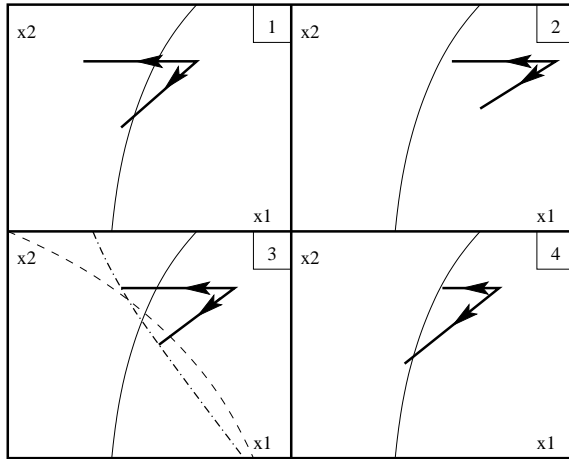


FIG. 4.2. Each quadrant represents a state-space  $(x_1, x_2)$ . The thick arrows are possible trajectories. The solid curves represent the switch-manifold  $S(x) = 0$ . The time horizon is the same for both trajectories plotted: ‘being selective’ and ‘being opportunistic’.

Appendix A provides a relation giving the time spent to move from a point of the state-space  $(x_1, x_2)$  to another —as it does not depend on the trajectory followed—, via the same dynamics if taken with  $n = 1$ . It thus yields the locus of all points attainable in a time  $t_a$  from a given point  $(x_1^0, x_2^0)$  —the manifold represented by the dot-dashed line in the third quadrant of figure 4.2 contains the said locus. More precisely, this manifold corresponds to the application

$$x_1 \mapsto x_2^0 - [t_a - \alpha \ln(x_1^0/x_1) - (x_1^0 - x_1)h_1]/h_2,$$

clearly monotonously decreasing. Hence for each initial condition, there is a unique point  $(\hat{x}_1, \hat{x}_2)$  such that  $S(\hat{x}_1, \hat{x}_2) = 0$  at time  $t_a$  —this is the intersection of the two manifolds. Therefore, any trajectory that remains in the gap has to reach this unique point and therefore yields the same overall payoff. Further, since optimal trajectories cannot penetrate any of the two extremal fields, any trajectory remaining in the gap and reaching the switch manifold at  $t = t_a$  is optimal.  $\square$

**5. An asynchronous stochastic foraging game.** It remains to be known how to forage optimally under the risk of competition, i.e. if the intruder's arrival is no more deterministic.

As in the last section, once the possible intruder arrives, the optimal policy only depends on the current patch-state  $x$  and is detailed in Section 3. Therefore, the optimal total future reward  $V_2(x)$  is known. It thus remains to determine the optimal strategy before a possible intruder's arrival.

Notice that taking  $V_2 = 0$  addresses the question of the optimal diet selection when the end time is random —for instance, the sudden arrival of a predator could oblige the forager to flee from the patch.

Let this possible perturbation be a Poisson variable of intensity  $\pi$ .

Yet, we still let the time have a cost —in terms of missed opportunities— of  $\gamma^*$  per unit, thus the forager is nevertheless incited to leave the patch in order to avoid wasting its time.

Let  $t^*$  be the time the forager would remain on the patch if not interrupted before and  $\epsilon$  be the random event time, exponentially distributed with mean  $1/\pi$ .

Our dynamics are:

$$(5.1) \quad \begin{cases} q\dot{x}_1 = -x_1/D(u), & x_1(0) = x_1^0 \\ q\dot{x}_2 = -ux_2/D(u), & x_2(0) = x_2^0 \end{cases}.$$

Let our criterion be:

$$(5.2) \quad G = \mathbb{E} J \quad \text{with} \quad J = \int_0^{\epsilon \wedge t^*} L(x, u) dt + \begin{cases} V_2(x(\epsilon \wedge t^*)) & \text{if } \epsilon < t^* \\ 0 & \text{otherwise} \end{cases}$$

and  $L(x, u) = e_1 x_1/D(u) + u e_2 x_2/D(u) - \gamma^*$ .

We claim the following result:

**THEOREM 5.1.** *The optimal policy in the stochastic arrival time problem stated by equations (5.1) and (5.2) is a bang-bang one with a single switch from  $u = 0$  to  $u = 1$ , occurring before reaching the manifold  $S(x) = 0$ . The leaving policy is unchanged from theorem 3.1.*

*Proof.* Using the fact that  $P(\epsilon > t^*) = e^{-\pi t^*}$ , we have

$$G = \mathbb{E}_{\epsilon < t^*} \left[ \int_0^\epsilon L(x, u) dt + V_2(x) \right] + e^{-\pi t^*} \int_0^{t^*} L(x, u) dt$$

$$\begin{aligned}
&= \int_0^{t^*} \left[ \left( \int_0^\epsilon L(x, u) dt \right) + V_2(x) \right] \pi e^{-\pi\epsilon} d\epsilon + e^{-\pi t^*} \int_0^{t^*} L(x, u) dt, \\
&= \int_0^{t^*} L(x, u) \left( \int_t^{t^*} \pi e^{-\pi\epsilon} d\epsilon \right) dt + \int_0^{t^*} V_2(x) \pi e^{-\pi\epsilon} d\epsilon + e^{-\pi t^*} \int_0^{t^*} L(x, u) dt, \\
&= \int_0^{t^*} [L(x, u) + \pi V_2(x)] e^{-\pi t} dt.
\end{aligned}$$

Having in mind these equivalent dynamics  $f(x, u)$ ,

$$\begin{cases} \hat{x}_1 = -x_1, & x_1(0) = x_1^0 \\ \hat{x}_2 = -u x_2, & x_2(0) = x_2^0 \end{cases},$$

our criterion can also be expressed as follows:

$$G = q \int_0^{s^*} \mathcal{L}(x, u) e^{-\pi t(s)} ds, \quad \mathcal{L}(x, u) = \delta_1 x_1 + u \delta_2 x_2 - \gamma^* \alpha + \pi V_2(x) D(u),$$

with  $t(s) := \alpha s + h_1(x_1^0 - x_1) + h_2(x_2^0 - x_2)$  —see appendix A— and  $t(s^*) := t^*$ .

However, let us consider an equivalent criterion:

$$\mathcal{G} = e^{\pi(h_1 x_1^0 + h_2 x_2^0)} G/q = \int_0^{s^*} \mathcal{L}(x, u) e^{-\pi(\alpha s - h_1 x_1 - h_2 x_2)} ds.$$

Our stochastic end-time optimization problem is thus equivalent to the above deterministic one. Formulated in such a fashion, it directly yields that the end time is such that  $\mathcal{L}$  is zero. As  $V_2$  is zero beyond the manifold  $\delta_1 x_1 + \delta_2 x_2 - \gamma^* \alpha = 0$ , the latter is the terminal manifold corresponding to this problem. Therefore, we introduce the *value function*  $V$ , or the optimal total future reward, the solution of the following Hamilton-Jacobi-Bellman equation:

$$\begin{cases} \forall x, V(x, s^*) = 0 & \text{and} & \forall(x, s < s^*), \\ -\partial V(x, s)/\partial s = \max_u [\langle \nabla_x V(x, s), f(x, u) \rangle + \mathcal{L}(x, u) e^{-\pi(\alpha s - h_1 x_1 - h_2 x_2)}] \end{cases}.$$

Let  $V(x, s) := e^{-\pi(\alpha s - h_1 x_1 - h_2 x_2)} \mathcal{V}(x)$ ,  $\forall i \in \{1, 2\}$ ,  $\mu_i := \partial \mathcal{V}/\partial x_i$  and  $\mathbb{V}(x) := \mathcal{V}(x) - V_2(x)$ ;  $\mathbb{V}$  is thus solution of the following stationary Hamilton-Jacobi-Bellman equation:

$$\begin{cases} \forall(x|\mathcal{L} \leq 0), \mathbb{V}(x) = 0 & \text{and} & \forall(x|\mathcal{L} > 0), \\ \alpha \pi \mathbb{V}(x) = \max_u [x_1(\delta_1 - \pi h_1 \mathbb{V}(x) - \mu_1) + u x_2(\delta_2 - \pi h_2 \mathbb{V}(x) - \mu_2) - \gamma^* \alpha] \end{cases}.$$

Let us notice that  $\mathcal{V}(x)$  is indeed the optimal value of our payoff  $\mathcal{G}$ . Hence  $\mathbb{V}(x)$  is non-negative.

As it is clear that the optimal control is bang-bang, let us introduce the switch-function  $\sigma = \delta_2 - \pi h_2 \mathbb{V}(x) - \mu_2$ . We conjecture that there is at most one switch. Let the superscript  $+$  denote the region of the state space beyond the switch-point, where we postulate that the optimal strategy is  $u = 1$ . For instance, let  $D^+ := D(1) = \alpha + h_1 x_1 + h_2 x_2$ .

We have  $\forall i \in \{1, 2\}$ ,  $\mu_i^+(s^*) = 0$ . It yields  $\sigma^+(s^*) = \delta_2 \geq 0$  by hypothesis. Thus at the end time, the optimal policy is to be opportunistic, i.e. to take both resources.

The Hamilton-Jacobi-Bellman equation states that  $\forall(x|\mathcal{L} > 0)$  in region  $+$ ,

$$\pi D^+ \mathbb{V}^+(x) = x_1(\delta_1 - \mu_1^+) + x_2(\delta_2 - \mu_2^+) - \gamma^* \alpha.$$

Let  $\forall i \in \{1, 2\}$ ,  $\nu_i := \partial V / \partial x_i = \mu_i - \lambda_i$ , as  $\lambda_i = \partial V_2 / \partial x_i$ .

According to the classical theory of characteristics [4],  $\forall i \in \{1, 2\}$ ,

$$\dot{\mu}_i^+ = \pi D^+ \nu_i^+ - (\delta_i - \pi h_i V^+(x) - \mu_i^+), \quad \mu_i^+(\hat{s}) = \hat{\mu}_i.$$

It thus comes  $\dot{\sigma}^+ = \pi h_2(x_1 \nu_1^+ + x_2 \nu_2^+) - \dot{\mu}_2^+ = \pi h_2 x_1 \nu_1^+ - \pi D^- \nu_2^+ + \sigma^+$ .

Our aim is now to show that, if  $\sigma^+$  becomes zero while going backward in time, switching  $u$  to zero remains optimal down to the initial time. Let the superscript  $-$  denote the region of the state space where we conjecture that the optimal strategy is  $u = 0$ . For instance, let  $D^- := D(0) = \alpha + h_1 x_1$ .

In the latter region, the Hamilton-Jacobi-Bellman equation states that  $\forall x$ ,

$$(5.3) \quad \pi D^- V^-(x) = x_1(\delta_1 - \mu_1^-) - \gamma^* \alpha.$$

Via a similar calculation of the characteristics:

$$\begin{cases} \dot{\mu}_1^- = \pi D^- \nu_1^- - (\delta_1 - \pi h_1 V^-(x) - \mu_1^-), & \mu_1^-(\hat{s}) = \hat{\mu}_1 \\ \dot{\mu}_2^- = \pi D^- \nu_2^-, & \mu_2^-(\hat{s}) = \hat{\mu}_2 \end{cases},$$

where  $\hat{s}$  is the time at which the switch-manifold is reached.

It thus comes  $\dot{\sigma}^- := \pi h_2 x_1 \nu_1^- - \dot{\mu}_2^- = \pi h_2 x_1 \nu_1^- - \pi D^- \nu_2^-$ . Hence on the switch-manifold,  $\dot{\sigma}^-(\hat{s}) = \dot{\sigma}^+(\hat{s}) \geq 0$ .

Using equation (5.3), we have

$$\begin{aligned} \dot{\mu}_1^- &= \pi D^- \nu_1^- - (\alpha \pi V^-(x) + \gamma^* \alpha) / x_1 \\ &= \pi D^- \mu_1^- - [(\alpha \pi V^-(x) + \gamma^* \alpha) / x_1 + \pi D^- \lambda_1]. \end{aligned}$$

Let  $\Theta(x) := [(\alpha \pi V^-(x) + \gamma^* \alpha) / x_1 + \pi D^- \lambda_1] \geq 0$ ,

$$\chi(s, \hat{s}) := \exp\left(\pi \int_s^{\hat{s}} D^- dl\right) = e^{\pi[t(s) - t(\hat{s})]},$$

and

$$\phi(s, \hat{s}) := \alpha \pi \int_s^{\hat{s}} \Theta(x) \chi(s, \ell) dl \geq 0,$$

as it is clear from Section 3 that  $\forall x$ ,  $\lambda_1(x) \geq 0$ .

We have  $\forall s \in [0, \hat{s}]$ ,

$$\begin{cases} \mu_1^-(s) = \hat{\mu}_1 \chi(s, \hat{s}) + \phi(s, \hat{s}) \\ \mu_2^-(s) = \hat{\mu}_2 \chi(s, \hat{s}) \end{cases}.$$

Let  $\psi(x_1) := \pi h_2 x_1 \hat{\mu}_1^- - \pi D^- \hat{\mu}_2^- = \pi(h_2 \hat{\mu}_1 - h_1 \hat{\mu}_2) x_1 - \pi \alpha \hat{\mu}_2$  and it yields

$$\dot{\sigma}^- = \psi(x_1) \chi(s, \hat{s}) + \phi(s, \hat{s}) \pi h_2 x_1.$$

As  $\psi(\hat{x}_1) = \dot{\sigma}^-(\hat{s}) \geq 0$ ,  $(h_2 \hat{\mu}_1 - h_1 \hat{\mu}_2)$  is clearly positive. Thus  $\psi(x_1)$  is increasing in  $x_1$ . Therefore  $\dot{\sigma}^-$  remains positive in region  $-$ . As an expected consequence, the trajectory generated by taking  $u = 0$  backwards from the switch-manifold implies that  $\sigma^-$  remains negative down to the initial time. Hence the optimal strategy is indeed an at most one-switch bang-bang one.  $\square$

**5.1. A digression on the random end time problem.** In this subsection, our aim is to numerically characterize the switch-manifold for a random end time problem, i.e. taking  $\forall x, V_2(x) = 0$ .

Integrating forward the trajectory field where  $u = 1$  yields

$$\mathcal{V}^+(x) = \Delta B_1(\beta) - \gamma^* \alpha B_0(\beta),$$

with  $\Delta := \delta_1 x_1 + \delta_2 x_2$ ,  $\beta := \pi(h_1 x_1 + h_2 x_2)$  and the function  $B_n$  is defined as follows,  $n \in \mathbb{N}$ :

$$B_n(\beta) := \int_0^{s^*} e^{-(n+\pi\alpha)s - \beta(1-e^{-s})} ds.$$

Integrating by parts easily yields:

$$\begin{cases} B_1(\beta) = (1 - z_0(\beta) - \pi\alpha B_0(\beta))/b \\ B_2(\beta) = (1 - z_1(\beta) - (1 + \pi\alpha)B_1(\beta))/\beta \end{cases},$$

with  $z_n(\beta) := e^{-(n+\pi\alpha)s^* - \beta(1-e^{-s^*})}$ .

Using either the explicit form of  $s^*$ <sup>8</sup> or the remark that it maximizes  $\mathcal{G}$  and the envelope lemma, it yields

$$\forall i \in \{1, 2\}, \quad \mu_i^+ = \delta_i B_1(\beta) - \Delta \pi h_i (B_1(\beta) - B_2(\beta)) + \gamma^* \alpha \pi h_i (B_0(\beta) - B_1(\beta)).$$

As  $\sigma^+ := \delta_2 - \pi h_2 \mathcal{V}^+ - \mu_2^+$ , it yields

$$\begin{aligned} \sigma^+ &= \delta_2 - \delta_2 B_1(\beta) - \Delta \pi h_2 B_2(\beta) + \gamma^* \alpha \pi h_2 B_1(\beta) \\ &= (\delta_2 - \Delta \pi h_2 (1 - z_1(\beta))/\beta) - (\delta_2 - (1 + \pi\alpha) \Delta \pi h_2 / \beta - \gamma^* \alpha \pi h_2) B_1(\beta). \end{aligned}$$

The switch-manifold is thus given by  $\sigma^+(x) = 0$ . Figure 5.1 shows the switch-manifolds associated to various values of  $\pi$ .

**5.2. Implications for the original problem.** It is clear that the switch-manifold corresponding to the original problem is bounded by that of the synchronous foraging game characterized in Section 3, as it corresponds to being disturbed by a conspecific with a probability one. Besides the latter point, it is likely that qualitatively, the optimal policy remains equivalent to the random end time problem, i.e. switching at a given  $x_1$ , depending on the intensity of the Poisson process.

**6. Conclusion.** Our aim was to determine the evolutionarily stable strategy [20] that foragers competing for a plural and depleting resource should adopt, both in terms of diet-selection and patch-leaving decision [3, 33].

First, we reformulated the optimal diet selection policy [23] for a lone forager, in a similar fashion to [26] except that we allow for a free patch-leaving time. On our way, we solved the optimal diet selection problem for a single forager with an end time either fixed or possibly random.

Next, we investigated the foraging game involving several foragers arrived simultaneously on a patch containing two distinct types of resources. The resulting differential game involves discontinuous state feedback strategies constructed via a classical synthesis technique, and hence requires for its solution a careful analysis of

<sup>8</sup>As  $s^*$  is the time to leave the patch as a function of the current state, we have  $s^* = -\ln(\gamma^* \alpha / \Delta)$ , see equation (3.6) and the dynamics taken with  $u = 1$ .



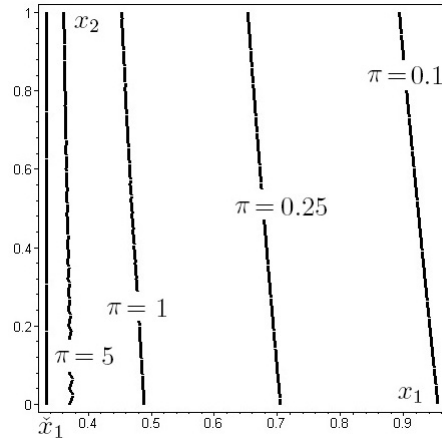


FIG. 5.1. *The switch-manifolds in the state space  $(x_1, x_2)$  associated to several value of  $\pi$ ; from right to left,  $\pi = \{0.1, 0.25, 1, 5\}$ , with  $\alpha = 1$ ,  $h_1 = 1$ ,  $h_2 = 1$ ,  $e_1 = 1$ ,  $e_2 = 0.25$  and  $\gamma^* = 0.1$ . The left bound corresponds to the intake rate maximization switch-manifold, i.e.  $\hat{x}_1 = e_2\alpha/\zeta$ .*

the induced discontinuities of the adjoint variables. The end result is a one-switch bang-bang evolutionarily stable strategy. This is in agreement with [15, 26, 35] and more precise in several respects.

As there is a qualitative gap between the optimal behavior of an isolated forager and that of competing foragers, the question that thus arose was that of the optimal strategy of a single forager, subject to a potentially imminent competition.

As a preliminary approach, we solved an asynchronous two forager game, where the inter-arrival time was assumed deterministic. Partial preferences arose in several fashions.

Finally, we no longer considered a deterministic inter-arrival time but let the probability that an opponent enters the game follow a Poisson distribution. We showed that the optimal policy belongs to a qualitative continuum that fills<sup>9</sup> the gap that separates the two extremal policies found previously.

Thus, although the classical diet selection policy states that a lone forager should take both resources indifferently during the whole time spent on the patch—see Section 2—, we showed that it suffices to add some stochasticity in the model to predict a qualitatively different behaviour. Indeed, under the risk of viewing a predator—resp. a conspecific— shorten the time spent—resp. alone— on the patch, a lone forager should be selective for a while, at least if the probability of being disturbed is non-negligible.

**7. Discussion and prospects.** Our results are based on the assumption that foragers are identical in terms of their ability to find and consume resources and of the relative values they attribute to resources with respect to both other resources and their environment. The game is symmetric in this sense. In recent years, however, foraging theory has looked more at the effect of foragers' state, see [16]. Thus arises the question of the robustness of our results to relevant differences in forager state such as, for instance,

- competitive ability, which may be correlated to the size of the animal [25, 24],

<sup>9</sup>By playing on the intensity of the Poisson variable.

- level of satiation or body reserves, acting on the relative values of food resources compared to other resources or opportunities in the environment, such as finding a mate,
- as well as the time away from nest, acting on the “cost of the time”,
- or simply the life expectancy of the animal [36], i.e. a time horizon,

as the game would no longer be symmetric. Moreover, the question of the information on the opponent state would also arise. Yet, we conjecture that, of course, the foragers would probably not switch nor leave simultaneously, but a qualitatively similar behavior would persist; i.e. switching from being selective to opportunistic and leaving according to —their own, this time— Charnov’s rule.

Also, in our model, foragers’ ability to gather resources is not affected by the presence of conspecifics; the present paper ignores interference (i.e. contacts or fights) that could occur among them. As in the single resource case, as long as there is no interference, the evolutionarily stable strategy is pure, in particular in terms of patch-leaving policy. We conjecture that including interference in the model would result in a war of attrition, or random patch-leaving times, but would not qualitatively affect the resource acceptance policy. More accurately, we conjecture that a war of attrition occurs after foragers have switched from a selective diet to an opportunistic one. Yet, this makes sense to us as long as interference intensity does not depend on the resource-acceptance policy. If it does, i.e. if interference is greater when both players focus on the best quality resource, the question is open (see [25, 24] for experimental evidence of a competition avoidance behavior).

Last, but not least, the question arises of the relevance of this model with respect to the real life. A field study in the Negev Desert, Israel, [12] was realized on Nubian ibex *Capra nubiana*, wild social goats that actually compete for resources. Interestingly, an indirect observation based on ‘giving-up densities’ [2] tends to show that Nubian ibex “*forage selectively on plants of higher quality until a certain threshold density, switching later to a more opportunistic foraging*”. Also, such an interpretation may hold with respect to similar observations made on kangaroo rats *Dipodomys merriami* foraging on the same patch, in Arizona [3]. As pointed out by [11], diet selection dynamics are rarely directly observed<sup>10</sup>. Nevertheless, the authors of [27] observed, through laboratory experiments with the cichlid fish *Haplochromis piceatus* (a predator accustomed to forage in group) a switch in their resource acceptance policy, whether they were alone or by pair. However, the switch-point occurred at a higher density of the preferred resource when foraging by pair than when foraging alone [35]. In the light of the present model, an inverse ranking of the switch points would have been expected; i.e. if uncertainty with respect to the time available to exploit resources —possibly before the expected arrival of a competitor— makes a single forager focus on the best resources first, such a selectivity is expected to be exacerbated, or at least unaffected, under competition. Our simple model is therefore falsifiable and seems to be so in this species. Moreover, white king pigeons, which also forage in group under natural conditions, have been shown [29, 28] to be more “choosy” alone than in presence of a competitor. More accurately, the authors actually observed that pigeons switch “earlier” under competition. It may be that interference occurring when focusing on the preferred resource qualitatively changes the resource acceptance policy. Further theoretical investigations are thus needed to better understand how competition affects the dynamics of diet selection.

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<sup>10</sup>yet, this article refers to other (of a physiological nature) dynamics, ignoring resource depletion and competition.

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## Appendix A. Optimal diet selection with a fixed end time.

In the body of the paper, we allow the forager for a free patch-leaving time, given that the time itself has a cost  $\gamma^*$  per unit. This section is a digression on the optimal diet selection problem under a fixed residence time constraint, as already addressed by some authors [26, 19] —the example of an intertidal forager is mentioned. Our patch dynamics are closer to that of [26]<sup>11</sup>, whose author argues that there is a partial preference region in the state space; our aim is to prove this statement.

Although the question addressed be other, our basic model remains that detailed in the body of the paper. As we consider a lone forager in an environment that offers two types of resources, the notations we shall use are those introduced from Section 3. For instance, we assume that resource 1 is more profitable than resource 2, i.e.  $e_1/h_1 \geq e_2/h_2$ .

We claim the following result, see figure A.1:

**THEOREM A.1.** *In the fixed end time problem, the optimal strategy is as follows: let  $\hat{x}_1 = e_2\alpha/\zeta$ ,*

- *Any admissible strategy that leads to  $x_1(T) = \hat{x}_1$ , provided that it is feasible. If so, there exists an infinite number of optimal trajectories, all of them reaching the same point  $(\hat{x}_1, \hat{x}_2)$ ;  $\hat{x}_2$  being given by equation (A.1).*
- *Otherwise, take  $u = 0$ , respectively  $u = 1$ , all along the trajectory if this leads to  $x_1(T) > e_2\alpha/\zeta$ , respectively  $x_1(T) < e_2\alpha/\zeta$ .*

<sup>11</sup>The dynamics of [19] are, then, really stochastic, as they allow for “a run of back luck” that leads the forager to “become more selective as the time left in the patch runs out”.

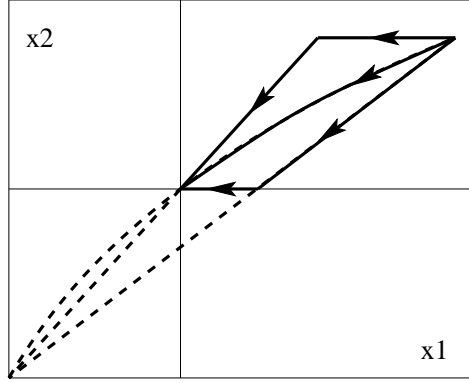


FIG. A.1. Three of the optimal trajectories in the state-space  $(x_1, x_2)$ : “accepting the less profitable resource with a constant optimal acceptance rate”, “switching from selective to opportunistic” and vice versa. The intersection of the vertical and horizontal lines represents the point  $(\hat{x}_1, \hat{x}_2)$ .

*Proof.* As we need to consider the variable  $t$  explicitly, we let it be a state variable. We thus have the following dynamics  $f(x, u)$ :

$$\begin{cases} \dot{x}_1 = -x_1, & x_1(0) = x_1^0 \\ \dot{x}_2 = -ux_2, & x_2(0) = x_2^0 = 1 - x_1^0 \\ \dot{t} = D(u), & t(0) = 0 \end{cases} .$$

Our criterion is:

$$\mathcal{J} = \mathcal{K}(x(T)) \quad \text{where} \quad \mathcal{K}(x) := e_1(x_1^0 - x_1) + e_2(x_2^0 - x_2)$$

and  $T$  is a fixed final time.

Let  $S$  be the final  $s$ , i.e.  $t(S) = T$ . Let  $\lambda$  be the adjoint vector. It yields the Hamiltonian:

$$\mathcal{H} = \langle \lambda, f(x, u) \rangle = -\lambda_1 x_1 - \lambda_2 u x_2 + \lambda_3 D(u) .$$

According to Pontryagin’s maximum principle if a policy  $u^*(s)$  generating a trajectory  $x^*(s)$  is optimal, then there exists an adjoint trajectory  $\lambda(s)$  such that

$$\begin{cases} \dot{\lambda} = -\nabla_x \mathcal{H}(\lambda, u^*, x^*) \\ \lambda(s^*) = \nabla_x \mathcal{K}(x^*) + \mathbf{v} \\ \mathcal{H}(s^*) = 0 \\ \left| \begin{array}{l} \forall s \in [0, s^*] \text{ where } u^*(\cdot) \text{ is continuous,} \\ \mathcal{H}(\lambda(s), u^*(s), x^*(s)) = \max_{u \in [0,1]} \mathcal{H}(\lambda(s), u, x^*(s)) \end{array} \right. \end{cases} ,$$

where  $\mathbf{v}$  is a normal vector to the target manifold. As the latter is the plane  $t = T$ , the only non-zero component of  $\mathbf{v}$  is that in  $t$ , say  $\nu$ . We have

$$\begin{cases} \dot{\lambda}_1 = -\partial \mathcal{H} / \partial x_1 = \lambda_1 - \lambda_3 h_1, & \lambda_1(S) = \partial \mathcal{K} / \partial x_1 = -e_1 \\ \dot{\lambda}_2 = -\partial \mathcal{H} / \partial x_2 = u(\lambda_2 - \lambda_3 h_2), & \lambda_2(S) = \partial \mathcal{K} / \partial x_2 = -e_2 \\ \dot{\lambda}_3 = -\partial \mathcal{H} / \partial t = 0, & \lambda_3(S) = \partial \mathcal{K} / \partial t + \nu = \nu \end{cases} .$$

The last condition above translates into the switch-function

$$\sigma = \partial \mathcal{H} / \partial u = x_2(\lambda_3 h_2 - \lambda_2) .$$

As  $S$  is free, the final value of the Hamiltonian is zero. It yields

$$\forall s, \lambda_3(s) = \nu = -\frac{e_1 x_1(S) + u e_2 x_2(S)}{\alpha + h_1 x_1(S) + h_2 x_2(S)}.$$

Thus

$$\sigma(S) = x_2(S) \left( \frac{e_2 \alpha + x_1(S)(e_2 h_1 - e_1 h_2)}{\alpha + h_1 x_1(S) + h_2 x_2(S)} \right).$$

It is easy to show that  $\forall s, \dot{\sigma} = 0$ . Let  $\hat{x}_1 = e_2 \alpha / \zeta$ . Hence

$$\begin{cases} \text{if } x_1(S) > \hat{x}_1 \text{ then } \forall s, \sigma < 0 \Rightarrow u^* = 0 \\ \text{if } x_1(S) = \hat{x}_1 \text{ then } \forall s, \sigma = 0 \Rightarrow u^* \in [0, 1] \\ \text{if } x_1(S) < \hat{x}_1 \text{ then } \forall s, \sigma > 0 \Rightarrow u^* = 1 \end{cases}.$$

We now investigate the possible geometry of the trajectory fields refering the reader to the four sketches of figure A.2. Therefore, if being opportunistic yields a ratio of the best resource that remains lower than  $\hat{x}_1$  —first quadrant—, this is optimal. In a similar fashion, if being selective yields a ratio of the best resource that remains greater than  $\hat{x}_1$  —second quadrant—, this is optimal. Otherwise —third quadrant—, the optimal policy is such that the ratio of best resource equals  $\hat{x}_1$  at the end time. As it is clear that being opportunistic does not deplete the best resource as much as being selective during the same time, the fourth quadrant represents an impossible scenario.

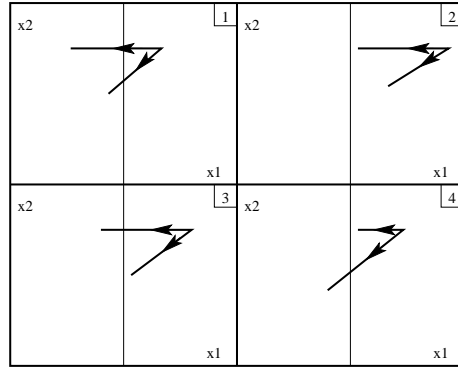


FIG. A.2. Each quadrant represents a state-space  $(x_1, x_2)$ , the vertical lines the manifold  $x_1 = \hat{x}_1$ . The temporal horizon is the same for both trajectories plotted: ‘being selective’ and ‘being opportunistic’.

However, Pontryagin’s maximum principle provides only necessary conditions; it does not prove that *any* policy that leads to  $x_1(S) = \hat{x}_1$  is optimal.

It is easy to see that

$$\forall u, s, t(s) = \alpha s + [x_1^0 - x_1(s)]h_1 + [x_2^0 - x_2(s)]h_2,$$

and that  $S = \ln(x_1^0 / \hat{x}_1)$ . Hence there is a unique  $x_2(S)$  such that  $x_1(S) = \hat{x}_1$ ; i.e.  $x_2(S) =: \hat{x}_2$  is such that

$$(A.1) \quad T = \alpha \ln(x_1^0 / \hat{x}_1) + [x_1^0 - \hat{x}_1]h_1 + [x_2^0 - \hat{x}_2]h_2.$$

However, it does not mean that the optimal trajectory is unique as the time needed to move from a point  $(x_1, x_2)$  to another does not depend on the path followed. Therefore, any strategy that leads to  $x_1(S) = \hat{x}_1$  is indeed optimal. For instance, figure A.1 represents some possible optimal trajectories in the state space  $(x_2, x_1)$ .  $\square$

Figure A.3 shows the differing regions in the parameter space  $(x_1^0, T)$  that correspond to each policy: being selective, opportunistic and having ‘‘partial preferences’’. The manifold separating the ‘selective’ region and the ‘partial preferences’ one is given by the application

$$x_1^0 \mapsto \alpha \ln(x_1^0/\hat{x}_1) + [x_1^0 - \hat{x}_1]h_1,$$

as  $x_2^0 = \hat{x}_2$  on this boundary, and the other one is given by

$$x_1^0 \mapsto \alpha \ln(x_1^0/\hat{x}_1) + (x_1^0 - \hat{x}_1)[h_1 + h_2 x_2^0/x_1^0],$$

as on this boundary,  $x_1^0/x_2^0 = \hat{x}_1/\hat{x}_2$ .

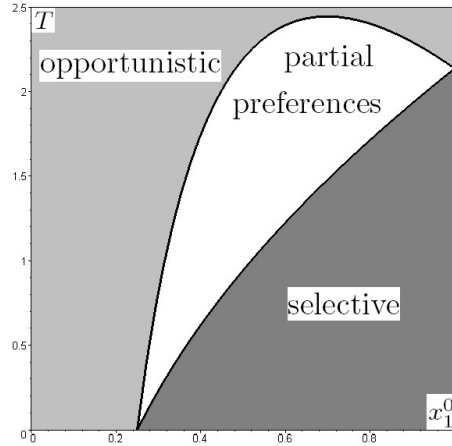


FIG. A.3. The differing regions in the parameter space  $(x_1^0, T)$ . We took  $\alpha = 1$ ,  $e_1 = 1$ ,  $e_2 = 1$ ,  $h_1 = 1$  and  $h_2 = 5$ .