LÉVY FLIGHTS, OPTIMAL FORAGING STRATEGIES, 
AND FORAGERS WITH A FINITE LIFESPAN

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Abstract. In some recent work, we have introduced some efficiency functionals to account for optimal dispersal strategies of predators in search of food. The optimization parameter in this framework is given by the Lévy exponent of the dispersal of the predators. In this paper, we apply our model to the case of foragers with finite lifetime (i.e., foragers which need to eat a certain amount of food in a given time, otherwise they die). Specifically, we consider the case in which the initial distribution of the forager coincides with a stationary distribution of the targets and we determine the optimal Lévy exponent for the associated efficiency functional. Namely, we show that if the Fourier transform of the prey distribution is supported in a sufficiently small ball, then the optimizer is given by a Gaussian dispersal, and if instead the Fourier transform of the prey distribution is supported in the complement of a suitable ball, then the ballistic diffusion provides an optimizer (precise conditions for the uniqueness of these optimizers are also given).

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1. Introduction

Understanding animal foraging strategies is of great importance in biology and ethology, with applications in conservation biology and population dynamics (see [1, 2]). As a simplified model for this goal, one can consider a given distribution of targets and some predators which move according to some law in the space. The optimization problem is thus provided by some parameters that the predators can “tune” in order to maximize the success of their search.

Framed in this way, the problem goes even beyond the interest range of biology, since similar features can be shared by automatic searches of robots, internet engines, mine detection, human mobility, human cognition, and so on (see [3–9]).

In the last three decades, the investigation of animal search pattern has been deeply influenced by the so-called Lévy flight foraging hypothesis, as put forth in [10]. The working assumption of this setting is, roughly speaking, that the classical Brownian motion may be inadequate to capture the complexity of animal movements, even in the absence of chemotactical attractions or memory effects. Indeed, heavy-tailed distributions might provide advantageous searching patterns, especially for sparsely, randomly distributed, revisitable targets, since they potentially explore the environment faster and avoid long term confinement in regions with no available prey.

Keywords and phrases: Lévy flights, fractional Laplacian, optimal strategies, finite lifespan.

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The validity of the Lévy flight foraging hypothesis is subject to a very intense debate and a precise and rigorous approach appears to be essential for further progress (see in particular [11] and Sect. 2 in [12] for a list of major objections and scientific disagreements). One of the difficulties in the analysis of such a topic is that optimizers and pessimizers are often closely intertwined (see [13]): this is not a mere mathematical curiosity and indeed, especially in the presence of preys with high energy content, patterns of this type may lead to high-risk/high-reward hunting strategies of ambush type which have been observed in nature (see [14]).

Several quantifications of the hunting success are possible. In particular, in [15] we have introduced several efficiency functionals based on the random encounters between a predator, diffusing according to a fractional heat equation which accounts for heavy-tailed spatial relocations, and a given distribution of prey. The exponent of this Lévy-type tail is used as a free parameter that the predator can tune in order to maximize the amount of food found during the search (this efficiency functional can be also normalized to account for the length of the search, the energy spent, etc.).

In addition, recently (see [16]) the problem of animal foraging has also specifically considered the case of predators with a finite lifespan, subject to the success of the search for food: roughly speaking, in these models the forager is allowed to search for food during a finite time interval: then, on the one hand, if the search is successful, the forager is allowed for additional time, but, on the other hand, the forager dies if it does not find any prey within the given time frame.

In view of these recent trends, the goal of this paper is to determine the optimal Lévy exponent for the forager with finite lifetime in some specific conditions.

In particular, we establish that:

- if the Fourier transform of the distribution of a stationary prey is supported in a suitable volume, then the only optimal strategy for this forager is Gaussian, while
- if the Fourier transform of the distribution of a stationary prey is supported in the complement of a suitable volume, then the optimal strategy corresponds to the ballistic one.

Precise mathematical statements will be given in Theorem 2.4 and Corollary 2.5 below, which are the main results of this paper.

The above conditions about the support of the Fourier transform of the prey distribution may require a clarification. On the one hand, the assumption that the Fourier transform is supported in a suitable volume means that the stationary prey distribution is composed only of frequencies within a certain range and does not exhibit “too high” frequencies. This, roughly speaking, excludes “highly oscillatory” behaviors of this distribution and accordingly an assumption of this type can be considered as a “regularity” hypothesis.

On the other hand, the assumption that the Fourier transform of the distribution is supported in the complement of a suitable volume (in particular, zero is not in the support of the Fourier transform) indicates that the total mass of prey is equal to zero. It would be however too simplistic to dismiss this situation as biologically inessential, for at least two reasons.

The first reason is conceptual: whenever one has a result under an assumption on the support of the Fourier transform, it is of fundamental importance to understand whether this assumption is required. Our dichotomy above makes it clear that this is the case: in particular, it highlights that the detection of the optimal strategy cannot overlook the support of the Fourier transform, i.e. the oscillatory patterns, of the prey distribution.

As an explicit example of distribution with Fourier transform supported away from an interval, one can consider a smooth and even function \( \tau \in C_0^\infty(\mathbb{R}) \) with \( \tau = 1 \) in \([-\rho, \rho]\) and take

\[
\hat{\rho}(\xi) := (1 - \tau(\xi)) e^{-|\xi|^2}.
\]

The corresponding distribution reads

\[
p(x) := \int_{-\infty}^{\infty} \hat{\rho}(\xi) e^{2\pi i x \xi} d\xi = \int_{-\infty}^{\infty} \left(1 - \tau(\xi)\right) e^{-|\xi|^2} \cos(2\pi x \xi) d\xi.
\]
The second reason is in terms of modelization: in this paper, the calculations do not actually require that the prey distribution is nonnegative. As stated by Paul Dirac [17], these negative values (in the setting of negative probabilities, or quasiprobabilities) "should not be considered as nonsense. They are well-defined concepts mathematically, like a negative of money" (similar observations were also pointed out by Richard Feynman [18]). Not only these notions are commonly used in quantum physics (e.g., for antiparticles) and finance (e.g., for risk neutral probabilities), but they have a natural counterpart in animal foraging: for example, negative values of the prey can model traps or potential hazard sites for the predator (such as a predator of the predator). In this sense, the case of Fourier transforms supported away from zero appears to be ideal to describe complex, and biologically relevant situations in which the predator is also at some risk of being attacked or framed (though in different settings, ballistic optimizers were also detected in [14, 19] as a result of a high-risk/high-gain foraging pattern; differently than in the existing literature, the risk here is embodied by the negative values of the prey distribution).

The rest of this paper is devoted to the rigorous statements and proofs of these results. While on the subject, we will also provide additional results in Theorems 2.1 and 2.3 to relate the efficiency functional with the success or failure of the search.

More specifically, the main results will be stated in Section 2 and their proofs will be presented in Section 3. The conclusions of this paper will be summarized in Section 4.

2. Mathematical framework and main results

In this section, we state precisely our main results, in view of a quantitative mathematical formulation. We specifically address here the case of foragers that can only search for food during a finite time interval and die if they do not find any prey within such a time frame. In our setting, the “discrete” notion of finding a prey is replaced by a given threshold on the efficiency functional. Specifically, in our model, the forager dies if the corresponding efficiency functional after a certain time is below this threshold.

To focus on an elementary case, we consider a closed interval $I \subseteq [0, 1]$, time spans $T_1 > 0$ and $T_2 > T_1$, and a threshold $c_1 > 0$. We take into account a forager diffusing as in

$$\partial_t u(t, x) = -(-\Delta)^s u(t, x) \quad \text{for all} \quad (t, x) \in (0, +\infty) \times \mathbb{R}^n,$$

with $s \in I$, and looking for prey in the time interval $[0, T_2]$ (unless it dies before). Here above, the initial condition for $u$ is that at time $t = 0$ it coincides with the prey distribution.

As customary, the fractional Laplace operator $(-\Delta)^s$ can be defined in the Fourier space as the operator for which, given any smooth and rapidly decaying function $\phi$, the Fourier transform of $(-\Delta)^s \phi$ equals $(2\pi |\xi|)^{2s} \hat{\phi}(\xi)$, where $\hat{\phi}$ is the Fourier transform of $\phi$, namely

$$\hat{\phi}(\xi) := \int_{\mathbb{R}^n} \phi(x) e^{-2\pi i x \cdot \xi} \, dx.$$

We consider a distribution of prey $p = p(x)$ and, for all $s \in I$, we let

$$E(s, T) := \int_0^T \int_{\mathbb{R}^n} u(t, x) p(x) \, dx \, dt.$$

This efficiency functional can be conveniently expressed in the Fourier space as

$$E(s, T) = \int_0^T \int_{\mathbb{R}^n} e^{-(2\pi |\xi|)^{2s} t} |\hat{p}(\xi)|^2 \, d\xi \, dt = \int_{\mathbb{R}^n} \frac{1 - e^{-T(2\pi |\xi|)^{2s}}}{(2\pi |\xi|)^{2s}} |\hat{p}(\xi)|^2 \, d\xi,$$

see Theorem 3.5 and equation (4.6) in [12].
We suppose that the forager dies at time $T_1$ if $E(s, T_1) < c_1$, while if $E(s, T_1) \geq c_1$ then the forager can keep looking for food till time $T_2$. In this way, the efficiency functional for this finite lifespan forager can be written in the form

\[
I \ni s \mapsto \mathcal{E}(s) := \begin{cases} 
E(s, T_1) & \text{if } E(s, T_1) < c_1, \\
E(s, T_2) & \text{if } E(s, T_1) \geq c_1.
\end{cases}
\] (2.2)

For this simple case, unless the forager always dies at time $T_1$, the optimal Lévy exponent is given by the optimizer of $E(s, T_2)$ among all $s$ guaranteeing the survival after time $T_1$:

**Theorem 2.1.** We have the following dichotomy:

- either $E(s, T_1) < c_1$ for all $s \in I$, and in this case
  \[
  \sup_{s \in I} \mathcal{E}(s) = \sup_{s \in I} E(s, T_1),
  \]

- or there exists $s \in I$ such that $E(s, T_1) \geq c_1$, and in this case
  \[
  \sup_{s \in I} \mathcal{E}(s) = \sup_{s \in I} E(s, T_2),
  \]

where

\[
I_\ast := \{ s \in I \text{ s.t. } E(s, T_1) \geq c_1 \}.
\]

The construction above can be iterated in order to comprise more than two and possibly infinitely many lifespans. To do so, it is convenient to introduce the extended natural numbers $\mathbb{N} := \mathbb{N} \cup \{ \infty \}$, where $\infty$ denotes a maximum element for the naturals. In particular, we have that $j + \infty = \infty + j = \infty$ for every $j \in \mathbb{N}$ and $\infty - j = \infty$ for every $j \in \mathbb{N}$. In this way, we can present the case of finite and infinite (but countable) lifespans in a unified framework.

For this, we consider $k \in \mathbb{N} \cap \{ 2, 3, 4, \ldots, \infty \}$, an ordered set of lifespans $\{ T_i \}_{i \in \{ 1, \ldots, k \}}$ such that $0 < T_i < T_{i+1}$ and $\{ c_i \}_{i \in \{ 1, \ldots, k-1 \}}$ with $c_i > 0$ for every $i \in \mathbb{N} \cap \{ 1, \ldots, k-1 \}$. Also, if $k = \infty$, we make the assumption that

\[
\lim_{i \to \infty} T_i = T_\infty = +\infty.
\]

We suppose that the forager dies at time $T_j$ for some $j \in \mathbb{N} \cap \{ 1, \ldots, k-1 \}$ if $E(s, T_j) < c_j$, while if $E(s, T_j) \geq c_j$ the forager survives and can look for food till time $T_{k+1}$.

In this situation, the efficiency functional for this forager can be written in the form

\[
I \ni s \mapsto \mathcal{E}(s) := \begin{cases} 
E(s, T_j) & \text{if } E(s, T_i) \geq c_i \text{ for all } i \in \{ 1, \ldots, j-1 \} \text{ and } E(s, T_j) < c_j, \\
E(s, T_k) & \text{if } E(s, T_i) \geq c_i \text{ for all } i \in \mathbb{N} \cap \{ 1, \ldots, k-1 \}.
\end{cases}
\] (2.3)

Note that in this setting the forager cannot modify the Lévy exponent $s$ for all the duration of its life (in the future, we plan to consider also the case in which this exponent can be adjusted at each time step, but for the moment we stick to the simpler scenario).

Without loss of generality, we can suppose from now on that the surviving thresholds are monotone, consistently with the biological idea that the total food threshold at a subsequent foraging time is higher than the ones at previous times. Namely, without loss of generality, we will assume that

\[
c_{j+1} \geq c_j,
\] (2.4)

thanks to the following observation:
Lemma 2.2. Let $k \in \mathbb{N} \cap \{2, 3, 4, \ldots, \infty\}$ and $\tilde{c}_j := \max\{c_1, \ldots, c_j\}$ with $j \in \mathbb{N} \cap \{1, \ldots, k - 1\}$ and

$$I \ni s \mapsto \tilde{E}(s) := \begin{cases} E(s, T_j) & \text{if } E(s, T_i) \geq \tilde{c}_i \text{ for all } i \in \{1, \ldots, j - 1\} \text{ and } E(s, T_j) < \tilde{c}_j, \\ E(s, T_k) & \text{if } E(s, T_i) \geq \tilde{c}_i \text{ for all } i \in \mathbb{N} \cap \{1, \ldots, k - 1\}. \end{cases}$$

Then, $\tilde{E} = E$.

The generalization of Theorem 2.1 in the setting of (2.3) goes as follows:

Theorem 2.3. Let $k \in \mathbb{N} \cap \{2, 3, 4, \ldots, \infty\}$. We have the following dichotomy:

- either there exists $s_* \in I$ such that $E(s_*, T_i) \geq c_i$ for all $i \in \mathbb{N} \cap \{1, \ldots, k - 1\}$, in which case
  $$\sup_{s \in I} E(s) = \sup_{s \in I_{k-1}} E(s, T_k), \quad (2.5)$$
  where
  $$I_{k-1} := \{s \in I \text{ s.t. } E(s, T_i) \geq c_i \text{ for all } i \in \mathbb{N} \cap \{1, \ldots, k - 1\}\},$$

- or there exists $j_* \in \mathbb{N} \cap \{1, \ldots, k - 1\}$ such that\footnote{As customary, we use the notation $[1, j_* - 1] = \emptyset$ when $j_* = 1$, and in this case the requirement on $i$ becomes void. For instance, if $j_* = 1$, then $I_{j_*} = I$.} if $s \in I$ and $E(s, T_i) \geq c_i$ for all $i \in \{1, \ldots, k - 1\} \cap [1, j_* - 1]$, then necessarily $E(s, T_{j_*}) < c_{j_*}$, and the set
  $$I_{j_*} := \{s \in I \text{ s.t. } E(s, T_i) \geq c_i \text{ for all } i \in \{1, 2, 3, \ldots, k - 1\} \cap [1, j_* - 1]\}$$
  is nonempty.
  In this case,
  $$\sup_{s \in I} E(s) = \sup_{s \in I_{j_*}} E(s, T_{j_*}). \quad (2.6)$$

In Figure 1, we present a simulation of the energy in (2.3) for $k = 3$ and for three different choices of energy thresholds. These have been selected to showcase the content of Theorem 2.3.

Specifically, the first set of thresholds is taken such that $E(s, T_1) < c_1$ for all $s \in (0, 1)$, and in this way the supremum of $\mathcal{E}(s)$ coincides with the supremum of $E(s, T_1)$ over $I_1 = (0, 1)$.
Figure 2. Plot of the function \((0, 1) \times (0, 6) \ni (s, T) \rightarrow E(s, T)\) with \(\hat{p} = \chi_{(-0.3, 0.3)}\) (in red) compared to the graph of the step functions \((0, 1) \times (0, 6) \ni (s, T) \rightarrow L^i(s, T) = \sum_{j=1}^{2} c_j^i \chi(T_j, T_{j+1})(T)\) (in blue) for \(i \in \{1, 2, 3\}\), \((T_1, T_2, T_3) = (2, 4, 6)\) and \(((c_1^1, c_2^1), (c_1^2, c_2^2), (c_1^3, c_2^3)) = ((1, 2), (0.6, 1), (0.6, 0.8))\).

Figure 3. Plot of the function \((0, 6) \ni T \rightarrow E(0.5, T)\) (in red) with \(\hat{p} = \chi_{(-0.3, 0.3)}\) compared to the graph of the step functions \((0, 6) \ni T \rightarrow L^i(T) = \sum_{j=1}^{2} c_j^i \chi(T_j, T_{j+1})(T)\) (in blue) for \(i \in \{1, 2, 3\}\), \((T_1, T_2, T_3) = (2, 4, 6)\) and \(((c_1^1, c_2^1), (c_1^2, c_2^2), (c_1^3, c_2^3)) = ((1, 2), (0.6, 1), (0.6, 0.8))\).

In the second plot, \((c_1^2, c_2^3)\) are taken so that there are some values of \(s \in (0, 1)\) such that \(E(s, T_1) \geq c_1^2\) and \(E(s, T_2) < c_2^3\) for all \(s \in (0, 1)\). Thus, in this case, we obtain that the supremum of \(E\) coincides with the supremum of \(E(s, T_2)\).

In the last simulation in Figure 1, the thresholds have been chosen in such a way that there exist some values of \(s \in (0, 1)\) such that \(E(s, T_1) > c_1^2\) and \(E(s, T_2) > c_2^3\). In this case, we have that the supremum of \(E\) coincides with the supremum of \(E(s, T_3)\).

In Figure 2, we compare the energy \(E(s, T)\) with the step function \(L(s, T) = \sum_{j=1}^{2} c_j^i \chi(T_j, T_{j+1})(T)\) with \(c_j^i\) as in the plots of Figure 1. More precisely, the three-dimensional plots in Figure 2 are built with the same data of Figure 1 with the purpose of detecting the change between \(E(s, T_j)\) and \(E(s, T_{j+1})\), which in turn is visible as a discontinuity of the graphs in Figure 1, with respect to the thresholds \(c_j^i\).

The three graphs in Figure 3 are given by the intersection of the graphs in Figure 2 with the plane passing through \(s = \frac{1}{2}\) and parallel to the one spanned by the time and vertical axes. In this case we can visualize, at a given \(s\) (in this case \(s = 1/2\)), how different choices of energy thresholds lead to different energy levels.

More specifically, we can compare Figure 3 with Figure 1 as follows: in the first simulation starting from the left in Figure 3 we see that \(E(1/2, T_1) < c_1^2\) and therefore in Figure 1 we have that \(E(1/2) = E(1/2, T_1)\). On the other hand, in the second picture in Figure 3 we have that \(E(1/2, T_1) > c_1^3\) and \(E(1/2, T_2) < c_2^3\). As a consequence of this, in Figure 1 we have that \(E(1/2) = E(1/2, T_2)\).

Then, in the third plot from the left in Figure 3, we observe that \(E(1/2, T_j) > c_1^3\) for every \(j \in \{1, 2\}\). As a consequence of (2.3) and as plotted in the third picture in Figure 1, we obtain that \(E(1/2) = E(1/2, T_3)\).
In general, for many thresholds and time spans, the explicit analysis of the maximizers of Theorem 2.3 could be quite involved. There are however special cases in which explicit maximizers can be obtained. For instance, one can rely on Theorem 3.5 in [12] and obtain the following result:

**Theorem 2.4.** Let  \( n \geq 1 \) and  \( k \in \mathbb{N} \cap \{2, 3, 4, \ldots, \infty\} \). Consider a forager diffusing as

\[
\begin{align*}
\partial_t u(t, x) &= -(-\Delta)^{s} u(t, x) \quad \text{for all} \quad (t, x) \in (0, +\infty) \times \mathbb{R}^n, \\
u(0, x) &= p(x).
\end{align*}
\]

for a prey distribution  \( p \) not identically zero.

Suppose that this forager has a finite lifespan, as in (2.3), with  \( I := [0, 1] \).

Then,

(i) if the Fourier transform of the prey  \( p \) is supported in the ball of radius \( \frac{1}{2\pi} \), then the Gaussian dispersal  \( s = 1 \) is a maximizer for  \( \mathcal{E} \). Also, if either  \( n \geq 2 \) or  \( k \in \mathbb{N} \) the maximizer is unique.

(ii) if instead the Fourier transform of  \( p \) is supported in the complement of the ball of radius \( \frac{1}{2\pi} \), then  \( s = 0 \) is the unique maximizer for  \( \mathcal{E} \).

The condition that  \( n \geq 2 \) in Theorem 2.4(i) can be relaxed. In fact, this condition was used only to guarantee the finite energy condition in (3.20) in the proof. In particular, it was used to establish uniqueness of the maximizer in the case  \( k = \infty \).

In dimension  \( n = 1 \) and for  \( k = \infty \) a result similar to Theorem 2.4(i) holds true as well, with the only caveat that the counterpart of Theorem 2.4(i) cannot exclude that there are more maximizers for which the efficiency functional attains infinite value. Thus, for completeness, we state and prove the version of Theorem 2.4(i) for dimension  \( n = 1 \):

**Corollary 2.5.** Let  \( n = 1 \) and  \( k = \infty \). Consider a forager diffusing as in (2.7), for a prey distribution  \( p \) not identically zero.

Suppose that this forager has a finite lifespan, as in (2.3), with  \( I := [0, 1] \).

Then, if the Fourier transform of the prey  \( p \) is supported in \( -\frac{1}{2\pi}, \frac{1}{2\pi} \), then the Gaussian dispersal  \( s = 1 \) is a maximizer for  \( \mathcal{E} \); moreover, if either for every  \( s_0 \in [0, 1) \) there exists  \( j \in \{2, 3, 4, \ldots\} \) such that

\[
E(s_0, T_i) \geq c_i \quad \text{for all} \quad i \in \{1, \ldots, j - 1\}, \quad E(s_0, T_j) < c_j \quad \text{and} \quad E(s_0) = E(s_0, T_j)
\]

or

\[
\int_{(-\frac{1}{2\pi}, \frac{1}{2\pi})} \frac{|\hat{p}(\xi)|^2}{|\xi|^2} \, d\xi < +\infty,
\]

then  \( s = 1 \) is the unique maximizer.

As a final remark, we point out that, for the sake of concreteness, we focused here on “discrete lifespans”. It is possible, however, to treat as well the case of continuous lifespans, in which the efficiency functional is compared, for every time  \( T \geq 0 \), to a given threshold, and the forager dies as soon as this threshold is not met. For this, it suffices to consider a continuous threshold  \( c = c(T) \), define

\[
T_* := \sup \{ \tau \geq 0 \text{ s.t. } E(s, T) \geq c(T) \text{ for all } T \in [0, \tau]\}
\]

and introduce, as a continuous analogue of (2.3), the functional

\[
I \ni s \mapsto \mathcal{E}_*(s) := E(s, T_*).
\]
Actually, the discrete setting can be considered as a particular case of the continuous one, in the special situation of piecewise constant thresholds, as pointed out in the next result. To this end, we use the notation $c_0 := 0$ and $T_0 := 0$.

**Theorem 2.6.** Let $k \in \mathbb{N} \cap \{1, 2, 3, \ldots \}$ and suppose that $C(T) = c_{j-1}$ for all $T \in [T_{j-1}, T_j)$ and all $j \in \mathbb{N} \cap \{1, 2, 3, \ldots , k\}$.

Then, either $T_* = T_k$ or there exists $j \in \mathbb{N} \cap \{1, 2, 3, \ldots , k-1\}$ such that $T_* = T_j$.

In the first case, we have that $E_*(s) = E(s, T_k)$. In the second case, we have that $E_*(s) = E(s, T_j)$.

In any case, $E_*(s) = E(s, T_*) = E(s)$.

### 3. Proofs of the main results

Below are the detailed proofs of the main results presented in Section 2.

**Proof of Theorem 2.1.** If $E(s, T_1) < c_1$ for all $s \in I$, then, for all possible choices of $s \in I$, the forager always dies at time $T_1$. In this situation, for all $s \in I$ we have that $E(s) = E(s, T_1)$. This says that we are in the first case showcased in the statement of Theorem 2.1.

We can therefore now suppose that $I_* \neq \emptyset$. We observe that

$$\sup_{s \in I} E(s) = \sup_{s \in I_*} E(s). \tag{3.1}$$

Indeed, if not, then necessarily

$$\sup_{s \in I} E(s) > \sup_{s \in I_*} E(s).$$

and accordingly

$$\sup_{s \in I \setminus I_*} E(s) > \sup_{s \in I} E(s).$$

But when $s \in I \setminus I_*$ it holds that $E(s) = E(s, T_1) \leq c_1$ while when $s \in I_*$ we have that $E(s) = E(s, T_2) \geq E(s, T_1) \geq c_1$. From this, a contradiction plainly follows and the proof of (3.1) is complete.

The claim stated in the second case of Theorem 2.1 now follows from (3.1), since if $s \in I_*$ then $E(s) = E(s, T_2)$.

**Proof of Lemma 2.2.** The desired result is a consequence of these two claims:

$$E(s, T_i) \geq \tilde{c}_i \text{ for all } i \in \{1, \ldots , j-1\}$$

if and only if $E(s, T_i) \geq c_i$ for all $i \in \{1, \ldots , j-1\}$ \tag{3.2}

and, if either of the above holds,

$$E(s, T_j) < \tilde{c}_j \text{ if and only if } E(s, T_j) < c_j. \tag{3.3}$$

To prove (3.2), we first point out that $\tilde{c}_i \geq c_i$, whence the first condition in (3.2) implies the second one.

Conversely, if the second condition in (3.2) is fulfilled, then, for all $i \leq l \leq j-1$, we have that $E(s, T_l) \geq E(s, T_l) \geq c_i$, yielding that $E(s, T_l) \geq \max\{c_1, \ldots , c_l\} = \tilde{c}_l$ for all $l \in \{1, \ldots , j-1\}$, which is the first condition in (3.2). This establishes (3.2).

Concerning (3.3), the fact that $\tilde{c}_j \geq c_j$ gives that the second condition in (3.3) implies the first one.
Besides, if the first condition in (3.3) holds true, together with either of the equivalent conditions in (3.2), suppose by contradiction that $E(s, T_j) \geq c_j$. Hence, we see that, for each $i \leq j$, $E(s, T_j) \geq E(s, T_i) \geq c_i$, giving that $E(s, T_j) \geq \max\{c_1, \ldots, c_j\} = \tilde{c}_j$, which is absurd, and the proof of (3.3) is thereby complete.

Proof of Theorem 2.3. Let us first suppose that there exists $s_\star$ as mentioned in the first claim of Theorem 2.3. Then, we have that $s_\star \in I_{k-1} \neq \emptyset$.

Moreover,

$$\text{if } s \in I_{k-1} \text{ then } \mathcal{E}(s) = E(s, T_k). \quad (3.4)$$

We claim that

$$\sup_{s \in I} E(s) = \sup_{s \in I_{k-1}} E(s). \quad (3.5)$$

Indeed, if not, then necessarily

$$\sup_{s \in I} E(s) > \sup_{s \in I_{k-1}} E(s)$$

and accordingly

$$\sup_{s \in I \setminus I_{k-1}} E(s) > \sup_{s \in I_{k-1}} E(s). \quad (3.6)$$

However, if $s \in I \setminus I_{k-1}$, then there exists $k_s \in \mathbb{N} \cap \{1, 2, 3, \ldots, k - 1\}$ for which $E(s, T_{k_s}) < c_{k_s}$, and thus

$$\mathcal{E}(s) \leq E(s, T_{k_s}) < c_{k_s} \leq E(s_\star, T_{k_s}) \leq E(s_\star, T_k) = \mathcal{E}(s_\star) \leq \sup_{s \in I_{k-1}} \mathcal{E}(s),$$

leading to

$$\sup_{s \in I \setminus I_{k-1}} \mathcal{E}(s) \leq \sup_{s \in I_{k-1}} \mathcal{E}(s).$$

This is in contradiction with (3.6) and it thereby proves (3.5).

The claim in (2.5) now follows from (3.4) and (3.5).

Having established the first claim in Theorem 2.3, we can now suppose that

there exists no $s_\star \in I$ such that $E(s_\star, T_j) \geq c_j$ for all $j \in \mathbb{N} \cap \{1, 2, 3, \ldots, k - 1\}. \quad (3.7)$

The first step of this argument focuses on proving that (3.7) implies that the setting in the second part of Theorem 2.3 is in place, namely that

there exists $j_\star \in \mathbb{N} \cap \{1, 2, 3, \ldots, k - 1\}$, such that if $s \in I$ and $E(s, T_{j_\star}) \geq c_{j_\star}$

for all $j \in \{1, 2, 3, \ldots\} \cap [1, j_\star - 1]$, then necessarily $E(s, T_{j_\star}) < c_{j_\star}. \quad (3.8)$

and that

$$I_{j_\star} \neq \emptyset. \quad (3.9)$$

To this end, let us first remark that, for all $S \in I$ and all $T > 0$,

$$\lim_{s \to S} E(s, T) = E(S, T), \quad (3.10)$$

thanks to (2.1) and the Dominated Convergence Theorem.
Then, to prove (3.8) and (3.9), we define $J_0 := I$ and recursively, for all $j \in \mathbb{N} \cap \{1, 2, 3, \ldots, k-1\}$,

$$J_j := \{ s \in J_{j-1} \text{ s.t. } E(s, T_j) \geq c_j \}$$

and we claim that there exists $j^* \in \mathbb{N} \cap \{1, 2, 3, \ldots, k-1\}$ for which

$$J_{j^*} = \emptyset. \quad (3.11)$$

Indeed, if not, for every $j \in \mathbb{N} \cap \{1, 2, 3, \ldots, k-1\}$ there would exist $s_j \in J_j \subseteq I$ for all $i \leq j$. This would give that $E(s_j, T_i) \geq c_i$ for all $i \leq j$. If $k \in \mathbb{N} \cap \{2, 3, 4, \ldots\}$, then this implies that

$$E(s_{k-1}, T_i) \geq c_i$$

for all $i \in \{1, \ldots, k-1\}$, which is in contradiction with (3.7) and the proof of (3.11) for the case $k \in \mathbb{N} \cap \{2, 3, 4, \ldots\}$ is complete. On the other hand, if $k = \infty$, since $I$ is compact, up to a subsequence we may suppose that $s_j$ converges to some $s_\infty \in I$ as $j \to \infty$. Accordingly, by (3.10), given any $i \in \mathbb{N}$ we see that

$$E(s_\infty, T_i) = \lim_{j \to +\infty} E(s_j, T_i) \geq c_i,$$

But this is in contradiction with (3.7) and the proof of (3.11) is complete also for the case $k = \infty$.

Moreover, in (3.11), by taking $j^*$ as small as possible, we can also suppose that $J_{j^*} \neq \emptyset$ for all $j \leq j^* - 1$. In this way, we see that $I_{j^*} = J_{j^* - 1} \neq \emptyset$ and we obtain (3.8) and (3.9), as desired.

From this, in order to complete the proof of Theorem 2.3, we only need to check (2.6). To this end, we claim that, in this case,

$$\sup_{s \in I} \mathcal{E}(s) = \sup_{s \in I_{j^*}} \mathcal{E}(s). \quad (3.12)$$

Indeed, if not, then necessarily

$$\sup_{s \in I} \mathcal{E}(s) > \sup_{s \in I_{j^*}} \mathcal{E}(s)$$

and accordingly

$$\sup_{s \in I \setminus I_{j^*}} \mathcal{E}(s) > \sup_{s \in I_{j^*}} \mathcal{E}(s). \quad (3.13)$$

Now, if $s \in I \setminus I_{j^*}$, then there exists $j_s \in \{1, 2, 3, \ldots, k-1\} \cap [1, j^* - 1]$ for which $E(s, T_{j_s}) < c_{j_s}$ and consequently $\mathcal{E}(s) \leq \mathcal{E}(s, T_{j_s}) < c_{j_s}$. In view of our monotonicity assumption in (2.4), as motivated by Lemma 2.2, this gives that $\mathcal{E}(s) \leq c_{j_s - 1}$. As a result,

$$\sup_{s \in I \setminus I_{j^*}} \mathcal{E}(s) \leq c_{j_s - 1}. \quad (3.14)$$

Instead, if $s \in I_{j^*}$, we have that $E(s, T_{j_s - 1}) \geq c_{j_s - 1}$, yielding that

$$\sup_{s \in I_{j^*}} \mathcal{E}(s) \geq c_{j_s - 1}.$$

From this, (3.13) and (3.14) a contradiction follows and the proof of (3.12) is thereby complete.
Now we observe that, by construction, if \( s \in I_j \), then \( \mathcal{E}(s) = E(s, T_{j^*}) \). From this and (3.12) we obtain (2.6), as desired.

**Proof of Theorem 2.4.** Notice that we do not aim here at determining the lifespan of the forager, but only its optimal strategy. This will be possible thanks to a monotonicity trick. Indeed, by Theorem 3.5 in [12] we know that, in this setting, for every \( T > 0 \), each efficiency functional \([0, 1] \ni s \mapsto E(s, T)\) is monotone in \( s \), and specifically strictly increasing in case (i) and strictly decreasing in case (ii).

Therefore, in case (i) we have that \( E(s, T) < E(1, T) \) for all \( s \in [0, 1) \), and in case (ii) that \( E(s, T) < E(0, T) \) for all \( s \in (0, 1] \).

Now, suppose that we are in case (i) (the argument for case (ii) being analogous) and pick any \( s_0 \in [0, 1) \).

Then, by (2.3), two situations arise: either for some \( j \in \mathbb{N} \cap \{1, \ldots, k-1\} \)

\[
E(s_0, T_i) \geq c_i \text{ for all } i \in \{1, \ldots, j-1\}, \quad E(s_0, T_j) < c_j \quad \text{and} \quad \mathcal{E}(s_0) = E(s_0, T_j)
\]  

(3.15)
or

\[
E(s_0, T_i) \geq c_i \text{ for all } i \in \mathbb{N} \cap \{1, \ldots, k-1\} \quad \text{and} \quad \mathcal{E}(s_0) = E(s_0, T_k).
\]  

(3.16)

If (3.15) arises, then \( E(1, T_i) > E(s_0, T_i) \geq c_i \) for all \( i \in \{1, \ldots, j-1\} \) and accordingly

\[
\mathcal{E}(1) \geq E(1, T_j) > E(s_0, T_j) = \mathcal{E}(s_0).
\]  

(3.17)

If instead (3.16) occurs, then \( E(1, T_i) > E(s_0, T_i) \geq c_i \) for all \( i \in \mathbb{N} \cap \{1, \ldots, k-1\} \). Therefore, if \( k \in \mathbb{N} \), we have that

\[
\mathcal{E}(1) = E(1, T_k) > E(s_0, T_k) = \mathcal{E}(s_0).
\]  

(3.18)

From this and (3.17) we deduce that \( s = 1 \) is the unique maximizer for \( \mathcal{E} \) in \((0, 1)\) if \( k \in \mathbb{N} \), concluding the proof of (i) for \( k \in \mathbb{N} \).

On the other hand, if \( k = \infty \), we have that

\[
\mathcal{E}(1) = E(1, +\infty) = \lim_{T \to +\infty} E(1, T) \geq \lim_{T \to +\infty} E(s_0, T) = E(s_0, +\infty) = \mathcal{E}(s_0).
\]  

(3.19)

Combining this and (3.17), we infer that the Gaussian exponent is a maximizer also if \( k = \infty \). Some more work is needed to check that the Gaussian exponent is the unique maximizer, the technical issue is that the strict inequality is lost in the above limit procedure. To this end, we pick \( s_0 \in (0, 1) \). If (3.15) holds true, then \( \mathcal{E}(1) > \mathcal{E}(s_0) \), in light of (3.17), therefore we can focus on the case in which (3.16) is satisfied. Thus, we deduce from (2.1) that, for all \( s \in [0, 1) \),

\[
E(s, +\infty) = \int_0^{+\infty} \int_{\mathbb{R}^n} e^{-(2\pi|\xi|^2)t}[\hat{p}(\xi)]^2 \, d\xi \, dt = \int_0^{+\infty} \int_{\mathbb{R}^n} e^{-t} \frac{|\hat{p}(\xi)|^2}{(2\pi|\xi|)^{2s}} \, d\xi \, dt.
\]

Since \( n \geq 2 > 2s \), we conclude that

\[
E(s, +\infty) < +\infty \text{ for all } s \in [0, 1).
\]  

(3.20)
We recall the expression in (2.1) and differentiate under the integral sign (see Eq. (4.12) in [12] for a justification of this) and we see that

$$\partial_s \int_{\mathbb{R}^n} \frac{1 - e^{-T(2\pi|\xi|)^{2s}}}{(2\pi|\xi|)^{2s}} |\hat{p}(\xi)|^2 \, d\xi = \int_{\mathbb{R}^n} T^2 k(\xi, s) \sigma'(T(2\pi|\xi|)^{2s}) |\hat{p}(\xi)|^2 \, d\xi. \quad (3.21)$$

Here above and in what follows, we use the notation

$$\sigma(x) := \frac{1 - e^{-x}}{x}$$

and

$$k(\xi, s) := 2 \ln(2\pi|\xi|)(2\pi|\xi|)^{2s}. \quad (3.22)$$

Accordingly, we use (2.1), (3.20) and (3.21), we use the Fundamental Theorem of Calculus and we see that

$$E(1) - E(s_0) = \lim_{T \to +\infty} \left( E(1, T) - E(s_0, T) \right) = \lim_{T \to +\infty} \int_{s_0}^1 \int_{\mathbb{R}^n} T^2 k(\xi, s) \sigma'(T(2\pi|\xi|)^{2s}) |\hat{p}(\xi)|^2 \, d\xi \, ds. \quad (3.23)$$

We recall (see Eq. (4.10) in [12]) that

$$\sigma'(x) \leq 0 \quad \text{for each} \quad x \in (0, +\infty) \quad \text{and} \quad \sigma' \in L^\infty((0, +\infty)). \quad (3.24)$$

We also notice that $k \leq 0$ in the support of $\hat{p}$. This and the sign of $\sigma'$ detected in (3.24) give that the integrand in (3.23) is nonnegative.

As a consequence, by Fatou’s Lemma,

$$E(1) - E(s_0) \geq \int_{s_0}^1 \int_{\mathbb{R}^n} \lim_{T \to +\infty} T^2 k(\xi, s) \sigma'(T(2\pi|\xi|)^{2s}) |\hat{p}(\xi)|^2 \, d\xi \, ds. \quad (3.25)$$

We observe that

$$\sigma'(x) = \frac{e^{-x}(x + 1) - 1}{x^2}$$

and therefore

$$T^2 \sigma'(T(2\pi|\xi|)^{2s}) = \frac{e^{-T(2\pi|\xi|)^{2s}}(T(2\pi|\xi|)^{2s} + 1) - 1}{(2\pi|\xi|)^{4s}}.$$. 
We plug this information and (3.22) into (3.25) and we find that
\[
\mathcal{E}(1) - \mathcal{E}(s_0) = \frac{1}{2} \int_{s_0}^{1} \left[ \int_{\mathbb{R}^n} \lim_{T \to +\infty} \frac{\ln(2\pi|\xi|)}{(2\pi|\xi|)^{2s}} e^{-T(2\pi|\xi|)^{2s}} \left( T(2\pi|\xi|)^{2s} + 1 \right) - 1 \right] \hat{p}(\xi)^2 \, d\xi \right] \, ds
\]
(3.26)
which is strictly positive, thus confirming that \( s = 1 \) is the unique maximizer.

**Proof of Corollary 2.5.** We begin by observing that \( s = 1 \) is a maximizer, since this part of the proof of Theorem 2.4(i) is not affected by dimensionality.

Now, if (2.8) holds true, then we deduce from (3.17) that \( \mathcal{E}(1) > \mathcal{E}(s_0) \) for all \( s_0 \in [0,1) \) and we are done. Therefore, we can reduce ourselves to (2.9), under the condition that (2.8) is violated.

In this situation, since (2.8) does not hold true, we infer from the monotonicity result in Theorem 3.5 in [12] that there exists \( s_0 \in [0,1) \) such that, for all \( j \in \{1,2,3,\ldots\} \),
\[
E(1,T_j) \geq E(s_0,T_j) \geq c_j
\]
and accordingly \( \mathcal{E}(1) = E(1, +\infty) \) and \( \mathcal{E}(s_0) = E(s_0, +\infty) \).

Besides, in view of (2.9), for every \( s_0 \in [0,1) \),
\[
\int_{(-\frac{1}{2\pi}, \frac{1}{2\pi})} \frac{\hat{p}(\xi)^2}{|\xi|^{2s_0}} \, d\xi \leq \int_{(-\frac{1}{2\pi}, \frac{1}{2\pi})} \frac{\hat{p}(\xi)^2}{|\xi|^2} \, d\xi < +\infty
\]
and therefore both \( E(1, +\infty) \) and \( E(s_0, +\infty) \) are finite (recall (2.1)).

Consequently, we can apply Fatou's Lemma as in (3.25) and (3.26) to conclude that
\[
\mathcal{E}(1) - \mathcal{E}(s_0) = E(1, +\infty) - E(s_0, +\infty) > 0,
\]
as desired. \( \square \)

**Proof of Theorem 2.6.** Assume first that \( T_\ast = T_k \). In this case, we have that \( E(s,T) \geq c(T) \) for all \( T \in [0,T_k) \), and accordingly \( E(s,T_j) \geq c(T_j) = c_j \) for all \( j \in \{1,\ldots,k-1\} \), giving that both \( E_\ast(s) \) and \( \mathcal{E}(s) \) are equal to \( E(s,T_k) \), as claimed.

We now suppose that \( T_\ast < T_k \). Since, for every \( T \in [0,T_1) \) it holds that \( E(s,T) \geq 0 = c_0 \), it follows that \( T_\ast \geq T_1 \). Thus, we take \( j \in \mathbb{N} \cap \{1,2,3,\ldots,k-1\} \) such that \( T_j \in [T_j,T_{j+1}) \).

Given \( T \in [0,T_\ast) \), we know that \( E(s,T) \geq c(T) \) and in particular, for each \( i \leq j \), we have that \( E(s,T_i) \geq c(T_i) = c_i \).

Also, by construction, \( E(s,T_{j+1}) < c_{j+1} \). Accordingly, \( \mathcal{E}(s) = E(s,T_j) = E_\ast(s) \), as desired. \( \square \)

4. Conclusions

In this paper, the foraging model of a predator with finite lifetime was considered and the optimal search strategy was determined as an optimal Lévy exponent for an efficiency functional.

We determined that the optimal exponent varies depending on the Fourier transform of the prey distribution. When this distribution is supported in a sufficiently small ball, then the optimizer is given by a Gaussian
dispersal. If instead the support lies in the complement of a suitable ball, then the ballistic diffusion provides an optimizer.

Both these situations have biological relevance: that of Fourier transforms with small support corresponding to distributions of preys with low oscillations and those supported away from the origin being related to hunts in the presence of risks or traps for the predator.

The process of decomposing a function into its elementary oscillatory components is the core of Fourier analysis, which is abundantly employed in mathematical biology and ecology, see e.g. [20–22]. In the framework of this paper, this methodology is useful to decompose “low frequency” patterns (roughly speaking, the ones in which the oscillations take place only at a large scale) and “high frequency” ones (the ones in which wilder oscillations take place at a small scale), relating the latter to an “unpredictable” behavior similar to that of a hunt by ambush.

For a visual representation of how high-frequency components in the Fourier transform are used to represent the “irregular” or “rapidly changing” parts of a function, see e.g. Figure 9.4 in [23].

Uniqueness conditions for the optimizing strategies were also given. We remark that uniqueness conditions for the optimizing strategies are important from an ecological perspective, since they suggest that evolution may select this unique optimizer through the process of natural selection (instead, in the process of more optimizers, different foraging patterns could in principle be selected). For more details about how unique optimal foraging strategies may emerge as a result of the evolutionary pressures of natural selection, see e.g. [24].

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References


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