Mortality, Redundancy, and Diversity in Stochastic Search

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We investigate a stochastic search process in one dimension under the competing roles of mortality, redundancy, and diversity of the searchers. This picture represents a toy model for the fertilization of an oocyte by sperm. A population of N independent and mortal diffusing searchers all start at $x = L$ and attempt to reach the target at $x = 0$. When mortality is irrelevant, the search time scales as $\tau_D/\ln N$ for $\ln N \gg 1$, where $\tau_D \sim L^2/D$ is the diffusive time scale. Conversely, when the mortality rate μ of the searchers is sufficiently large, the search time scales as $\sqrt{\tau_D/\mu}$, independent of N. When searchers have distinct and high mortalities, a subpopulation with a non-trivial optimal diffusivity are most likely to reach the target. We also discuss the effect of chemotaxis on the search time and its fluctuations.

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Stochastic searching [1] underlies a wide variety of processes in biology [2–4], animal foraging [5–9], chemical reactions [10, 11], and search operations for missing persons or lost items [12–14]. A basic goal is to minimize the time needed to successfully find a desired target. Through evolution and algorithmic developments, Nature and man have developed clever strategies to optimize searches. Many of these processes involve a single searcher that continues the search for as long as necessary to reach the target. In this Letter, we investigate the role of fundamental influences on stochastic search that have not yet received sufficient attention: mortality, redundancy, and diversity. The notion that a searcher dies if it does not reach a target within a fixed time epitomizes unsuccessful foraging. While the properties of random walks that die at a fixed rate has been recently investigated [15–18], the general problem of how to best conduct a search with mortal searchers is barely explored [19].

When a searcher can die before reaching a target, a natural way to promote success is by launching many searchers. This redundancy embodies the fertilization of an oocyte, where (in humans) roughly 3×10^8 sperm cells initially attempt to reach the oocyte after copulation. Fertilization is an extremely complex and multifaceted process (see Refs. [20, 21] for reviews). We make no pretense of accounting for the many steps that a sperm undergoes to reach and ultimately fertilize the oocyte. However, sperm mortality, redundancy, and diversity all play roles in this fertilization process. Inspired by these basic facts, we investigate an idealized scenario of fertilization that are driven by the above attributes.

The geometry of the system is quite simple. An oocyte located at the origin, $x = 0$, is represented by an absorbing boundary condition. At time $t = 0$, N diffusing searchers, each of which represents a sperm cell, are launched from $x = L$. The basic questions that we address are: (i) What is the probability of fertilization—that at least one of the searchers reaches the origin? (ii) What is the average time to reach the origin as a function of N and the mortality rate of the sperm? If *immortal* searchers are uniformly distributed on the line, the survival probability of the target in one dimension is known to decay as $\exp(-\text{const.} \times \sqrt{t})$ [22–28]. However, the biologically relevant situation where the searchers all start at the same point has been less extensively investigated even when the searchers are immortal [29–33].

It is worth noting two important points: First, if the searchers are immortal, then a basic result of first-passage processes is that a single searcher will eventually reach the target, but the average time for this successful search is infinite [34]. The average search time is again infinite for $N = 2$ searchers, but is *finite* for $N \geq 3$ [29]. Second, for mortal searchers that die at a fixed rate, the average time for a successful search, even for a single searcher, is finite and approaches zero as the mortality rate increases. In this high-mortality limit, the only way for a searcher to reach the target is to do so very quickly.

We first determine how a single mortal diffusing searcher finds the target. Let $\rho(x, t)$ be the probability density that the searcher is located at $0 < x < \infty$ at time t. Its dynamics is determined by the diffusion-decay equation $\partial_t \rho = D\partial_x^2 \rho - \mu\rho$, where we assume a fixed diffusivity D and mortality rate μ. For a target at $x = 0$ and a searcher starting at $x = L$, the image method [34] gives the solution to this diffusion-decay equation as:

$$\rho(x,t) = \frac{e^{-\mu t}}{\sqrt{4\pi D t}} \left[e^{-(x-L)^2/4Dt} - e^{-(x+L)^2/4Dt} \right]. \quad (1)$$

The flux at $x = 0$ yields the probability density that the target is reached at time t:

$$f_1(t) = D\, \partial_x \rho(x,t)|_{x=0} = \frac{L}{\sqrt{4\pi D t^3}}\, e^{-\mu t - L^2/4Dt}, \quad (2)$$

while the probability $F_1(t) = \int_0^t dt'\, f_1(t')$ that the searcher reaches the target by time t is

$$F_1(t) = \tfrac{1}{2}\, e^{\sqrt{\frac{\mu}{D}}\, L} \text{erfc}\big(L/\sqrt{4Dt} + \sqrt{\mu t}\big) + \tfrac{1}{2}\, e^{-\sqrt{\frac{\mu}{D}}\, L}\, \text{erfc}\big(L/\sqrt{4Dt} - \sqrt{\mu t}\big), \quad (3)$$

where $\mathrm{erfc}(z) = 1 - \mathrm{erf}(z)$, and $\mathrm{erf}\, z = (2/\sqrt{\pi}) \int_0^z e^{-u^2} du$ is the error function. When the searcher is immortal (the case $\mu = 0$), Eq. (3) reduces to the more familiar expression $F_1(t) = \mathrm{erfc}\big(L/\sqrt{4Dt}\big)$ for the probability that a diffusing particle reaches the origin by time t. The probability $\mathcal{F}_1 \equiv F_1(t=\infty)$ that the target is *eventually* found is

$$\mathcal{F}_1 = \int_0^\infty dt\, f_1(t) = e^{-\sqrt{\mu/D}\, L}\,. \tag{4}$$

For an immortal searcher $\mathcal{F}_1 = 1$, whereas for high mortality rate $\mathcal{F}_1$ is exponentially small.

From the first-passage distribution (2), the average and the variance of the search time are

$$\langle T\rangle = \frac{\int_0^\infty dt\, t f_1(t)}{\int_0^\infty dt\, f_1(t)} = \frac{L}{\sqrt{4D\mu}} = \sqrt{\tau_D \tau_\mu}\,, \tag{5a}$$

$$\Sigma^2 = \langle T^2\rangle - \langle T\rangle^2 = \frac{2DL}{(4D\mu)^{3/2}} = \frac{1}{2}\sqrt{\tau_D \tau_\mu^3}\,, \tag{5b}$$

where $\tau_D \equiv L^2/4D$ is the diffusion time and $\tau_\mu \equiv 1/\mu$ is the lifetime of a mortal searcher. Notice that low-order moments of the search-time distribution involve non-trivial combinations of τ_D and τ_μ. Also notice that as $\mu \to 0$, corresponding to immortal searchers, both $\langle T\rangle$ and Σ^2 diverge.

We now turn to the case of N immortal searchers. The probability that one of them first reaches the target at time t is [32, 33]

$$\begin{aligned} f_N(t) &= N f_1(t)\big[1 - F_1(t)\big]^{N-1} \\ &= N\, \frac{L}{\sqrt{4\pi D t^3}}\; e^{-L^2/4Dt} \Big[\mathrm{erf}\big(L/\sqrt{4Dt}\big)\Big]^{N-1} \\ &\simeq N \frac{L}{\sqrt{4\pi D t^3}} \left(\frac{L}{\sqrt{\pi D t}}\right)^{N-1}, \qquad t \to \infty, \end{aligned} \tag{6}$$

where the third line follows from the $z \ll 1$ asymptotic of $\mathrm{erf}(z)$. An important feature of $f_N(t)$ is that it has the algebraic long-time tail $f_N(t) \sim t^{-(N+2)/2}$. Thus, as mentioned in the introduction, the average search time is divergent for $N \le 2$, but finite for $N \ge 3$ [29].

We now determine the average time for the first out of $N \ge 3$ immortal searchers to reach the target. By definition

$$\begin{aligned} \langle T_N\rangle &= \int_0^\infty dt\, t\, f_N(t) \\ &= \int_0^\infty dt\, t\, \frac{NL}{\sqrt{4\pi D t^3}}\; e^{-L^2/4Dt} \Big[\mathrm{erf}\big(L/\sqrt{4Dt}\big)\Big]^{N-1}. \end{aligned} \tag{7}$$

We integrate by parts and define the scaled variable $z = L/\sqrt{4Dt}$ to recast this expression as [32]

$$\langle T_N\rangle = \tau_D \Psi(N), \qquad \Psi(N) = 2\int_0^\infty \frac{dz}{z^3}\; \mathrm{erf}^N z. \tag{8}$$

For very large N, $\mathrm{erf}^N z$ effectively becomes the Heaviside step function $\theta(z - z_0)$, where $z_0 = z_0(N) \gg 1$. To determine $z_0(N)$, we use the large-z asymptotic $\mathrm{erf}\, z \simeq 1 - e^{-z^2}/(\sqrt{\pi}\, z)$, so that $\mathrm{erf}^N z \simeq \exp[-N e^{-z^2}/(\sqrt{\pi} z)]$. Now $z_0(N)$ is determined, with logarithmic accuracy, from the condition $N e^{-z^2}/z \sim 1$, or $z\, e^{z^2} \sim N$. This yields $z_0 \simeq [W(2N^2)]^{1/2}/\sqrt{2}$, where $W(\cdot)$ is the Lambert W-function—the inverse of $f(W) = We^W$ [35]. Thus

$$\Psi(N) \simeq 2\int_{z_0(N)}^\infty \frac{dz}{z^3} = \frac{1}{z_0^2(N)} \simeq \frac{2}{W(2N^2)}. \tag{9}$$

To leading order in $\ln N \gg 1$, this yields

$$\langle T_N\rangle \simeq \frac{L^2}{4D\, \ln N}\,. \tag{10}$$

This result coincides with the asymptotic that was quoted in Ref. [32]. The average search time (10) decays only logarithmically with N but still gives to a reduction by a factor of 20 compared with the characteristic diffusion time $\tau_D = L^2/4D$ for the typical number of human sperm ($N = 3\times 10^8$) that attempt to fertilize an oocyte.

For N identical and mortal searchers that all start from $x = L$, the probability that at least one of them eventually reaches the target is

$$p = \sum_{k=1}^N \binom{N}{k} \mathcal{F}_1^k (1-\mathcal{F}_1)^{N-k} = 1 - (1-\mathcal{F}_1)^N, \tag{11}$$

with $\mathcal{F}_1$ given by Eq. (4). It is convenient to introduce the dimensionless mortality rate $M = \sqrt{\mu\, \tau_D}$. For high mortality, $M \gg 1$, we approximate $p \simeq 1 - \exp(-N e^{-2M})$, which changes rapidly from being vanishingly small for $N < N_c(M)$ to being close to 1 for $N > N_c(M)$, with $N_c(M) \simeq e^{2M} \gg 1$. An important message from this simple argument is that a huge redundancy of searchers is needed to offset their high mortality for a search to be successful.

For mortal searchers, reaching the target is not guaranteed, and the average time of successful search is

$$\langle T_N\rangle = \frac{\int_0^\infty t\, f_N(t)\, dt}{\int_0^\infty f_N(t)\, dt} \equiv \tau_D\, \frac{\Psi_1(N,M)}{\Psi_0(N,M)}\,. \tag{12}$$

Here $\Psi_k(N,M) = \int_0^\infty dz\, z^{-2k}\, e^{-\Phi(N,M,z)}$ and, by using Eqs. (3) and (7), $z = L/\sqrt{4Dt}$, and also expressing all variables in scaled form, straightforward algebra gives

$$\begin{aligned} &\Phi(N,M,z) = z^2 + \frac{M^2}{z^2} \\ &-(N-1)\ln\left[1 - \frac{e^{2M}}{2}\mathrm{erfc}\Big(z + \frac{M}{z}\Big) - \frac{e^{-2M}}{2}\mathrm{erfc}\left(z - \frac{M}{z}\right)\right]. \end{aligned}$$

We are interested in the high-mortality regime, $M \gg 1$, where the probability that a single searcher eventually reaches the target, as given in Eq. (4), is exponentially small. The inequality $M \gg 1$ enables us to evaluate the integral in Ψ_k by the standard Laplace method [36]. The saddle point $z_*(N,M)$ is found by minimizing $\Phi(N,M,z)$ with respect to z:

$$\frac{d\Phi(N,M,z)}{dz} \simeq 2z - \frac{2M^2}{z^3} - \frac{2(N-1)}{\sqrt{\pi}}\, e^{-z^2-M^2/z^2}, \quad (13)$$

where we again use the $z \gg 1$ asymptotic of erfc(z). Since the functions Ψ_0 and Ψ_1 include the same exponent $e^{\Phi(N,M,z)}$, we obtain, after cancellations, $\Psi_1/\Psi_0 \simeq z_*^{-2}$.

There are two distinct limiting behaviors for the saddle point z_* that depend on the interplay between N and M. For $N \ll \sqrt{M}e^{2M}$, z_* is determined by balancing the first two terms in Eq. (13). This yields $z_* \simeq \sqrt{M}$. In this regime, we obtain

$$\langle T_N\rangle \simeq \sqrt{\tau_\mu \tau_D} = \frac{\tau_D}{M} = \frac{L}{\sqrt{4D\mu}}\,, \quad (14)$$

which coincides with Eq. (5a) for the average search time of a *single* searcher. In this high mortality regime, only the fastest searcher contributes to the average time, while the rest of the searchers (unless their number is huge, see below) are superfluous.

In the limit of $N \gg \sqrt{M}e^{2M}$, but with M also large, the saddle point is given by $2z - 2(N-1)e^{-z^2}/\sqrt{\pi} \simeq 0$, which yields $z_* \simeq z_0$, the same quantity that arises for immortal searchers, as given above Eq. (9). As a result, the final expression for $\langle T_N\rangle$ coincides with Eq. (10). Thus when the number of searchers is extremely large, their mortality (even when relatively high) is irrelevant in the determination of average search time.

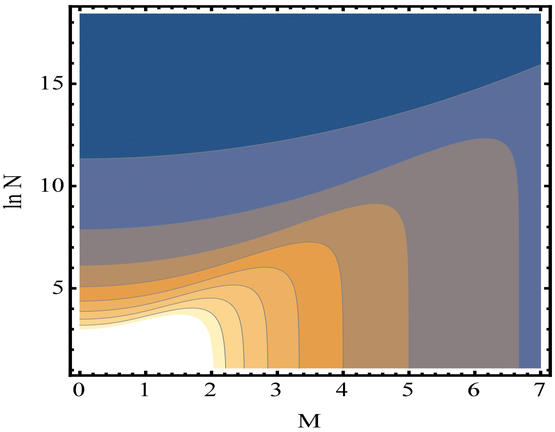

FIG. 1: (Color online) Contour plot of $\langle T_N\rangle/\tau_D$ from Eq. (12) vs. M and $\ln N$.

Figure 1 shows the dependence of $\langle T_N\rangle$ on M and $\ln N$. For not too large N, $\langle T_N\rangle$ in Eq. (12) exhibits a maximum as a function of the mortality rate, as evident from Fig. 1 and Fig. 2(a). This latter figure also shows that the $M \gg 1$ asymptotic $\langle T_N\rangle \simeq \tau_D/M$ is accurate already at $M \simeq 2$. Figure 2(b) shows $\langle T_N\rangle/\tau_D$ vs. $\ln N$ and the asymptotics (9) and (10).

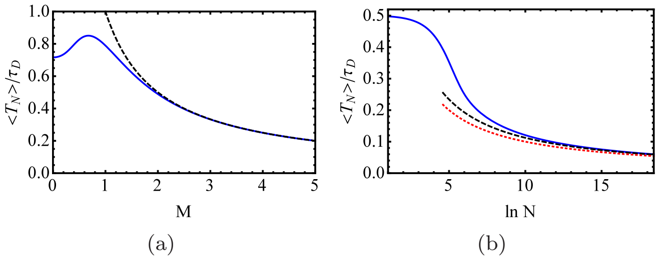

FIG. 2: (Color online) (a) Non-monotonic dependence of $\langle T_N\rangle$ from Eq. (12) on M for $N = 10$. The large-M asymptotic $\langle T_N\rangle/\tau_D \simeq 1/M$ (Eq. (14)) is shown dashed. (b) $\langle T_N\rangle/\tau_D$ vs. $\ln N$ for $M = 2$. The dashed and dotted lines are the respective asymptotics (9) and (10).

The biologically relevant situation where mortal searchers have distinct diffusivities D_k, $k = 1,\ldots,N$ [37] gives rise to a new optimization criterion for a successful search. Now the probability that a searcher with diffusivity D_k eventually reaches the target is

$$\mathcal{F}(D_k) = e^{-L\sqrt{\mu/D_k}} \ll 1. \quad (15)$$

When $N\mathcal{F}(D_k) \ll 1$ for typical diffusivity values, we may approximate the probability that a single searcher reaches the target as $p \simeq \sum_{k=1}^{N}\mathcal{F}(D_k)$. For $N \gg 1$, we may make the simplifying assumption that the diffusivity distribution is a Gaussian that is centered about a typical value D_0: $P(D) = \frac{1}{\sqrt{2\pi\sigma^2}}\, e^{-(D-D_0)^2/2\sigma^2}$, where $\sigma \ll D_0$. Then the summation for p may be replaced by the integral

$$\begin{aligned} p &\simeq \int_0^\infty dD\, \mathcal{F}(D)P(D) \\ &\simeq \frac{1}{\sqrt{2\pi\sigma^2}} \int_0^\infty dD\, e^{-L\sqrt{\mu/D}-(D-D_0)^2/2\sigma^2}. \end{aligned} \quad (16)$$

We again evaluate the integral by the Laplace method [36]. By straightforward rescaling, we redefine the above integral as

$$p = \frac{D_0}{\sqrt{2\pi\sigma^2}} \int_0^\infty dz\, e^{-L\sqrt{\frac{\mu}{D_0}}\,\Phi(z)}, \quad (17)$$

where $\Phi(z) = z^{-1/2} + A(z-1)^2$, with

$$A = \frac{D_0^2}{2\sigma^2} \times \frac{\sqrt{D_0}}{L\sqrt{\mu}} \quad \text{and} \quad z = \frac{D}{D_0}\,.$$

We find the saddle point z_* from the equation $\Phi'(z) = 2A(z-1) - (1/2)z^{-3/2} = 0$. The exact solution of this equation is cumbersome, and we confine ourselves to the asymptotics in the limits $A \gg 1$ and $A \ll 1$. In the low mortality limit where $A \gg 1$ (but still $L\sqrt{\mu/D_0} \gg 1$), z_* is very close to 1, and we find $z_* \simeq 1 + (4A)^{-1}$. Applying the Laplace method, the arrival probability is

$$p \simeq \exp\left(-\frac{L\sqrt{\mu}}{\sqrt{D_0}}\right), \qquad A \gg 1. \quad (18)$$

In this case, the dominant contribution to p comes from "typical" searchers—those whose diffusivity is close to D_0. This behavior is to be expected, as in the low-mortality limit the Gaussian in the integrand of Eq. (16) effectively acts as a delta-function peak centered at D_0.

The high-mortality limit, $A \ll 1$, is more interesting. Here $z_* \gg 1$, and we can replace $z-1$ with z in $\Phi(z)$ to arrive at $z_* \simeq (4A)^{-2/5}$. In this case, a small number of highly active searchers with $D \gg D_0$ give the dominant contribution to the probability that the target is found. Performing the Gaussian integral, we obtain

$$p \simeq \sqrt{\frac{2}{5}} \exp\left[-\left(2^{1/5}+2^{-9/5}\right)\left(\frac{\mu L^2}{\sigma}\right)^{2/5}\right], \qquad A \ll 1. \tag{19}$$

Surprisingly, this result for the arrival probability is *independent* of the average diffusivity D_0. Numerical integration of (17) shows that the arrival probability decays monotonically with the basic dimensionless parameter A, and the asymptotic forms (18) and (19) match the full solution in the respective limits of $A \ll 1$ and $A \gg 1$.

There are two additional attributes that naturally arise in the phenomenon of oocyte fertilization by sperm that can be accounted for within the present framework. One is the possibility of a diversity in searcher lifetimes. If the mortality rate μ is normally distributed, we find that the search dynamics is only trivially affected [38]. In this case, the main contribution to the probability that an ensemble of searchers reaches the target comes from typical searchers.

The role of chemotaxis, which is known to be a dominant effect as sperm approach the fertilization site [20], has more interesting consequences. A simplistic way to model chemotaxis is to include a constant drift velocity v in the diffusion-decay model. The probability evolution of a single searcher is now governed by the equation of motion $\partial_t \rho - v\partial_x \rho = -\mu\rho + D\partial_x^2 \rho$, where $v > 0$. When a single searcher starts at $x = L$ and seeks a target that is at the origin, the solution to this equation, subject to the boundary conditions $\rho(x=0,t) = \rho(x=\infty,t) = 0$ and the initial condition $\rho(x,t{=}0) = \delta(x-L)$, can again be found by the image method [34]. The result is

$$\rho(x,t) = \frac{1}{\sqrt{4\pi Dt}}\, e^{-\mu t}\left[e^{-(x+vt-L)^2/4Dt} - e^{vL/D} e^{-(x+vt+L)^2/4Dt}\right]. \tag{20}$$

From this expression, the probability density that the target is reached at time t is

$$f_1(t) = \frac{L}{\sqrt{4\pi Dt^3}}\, e^{-\mu t-(L-vt)^2/4Dt}. \tag{21}$$

Consequently, the probability that the target is eventually reached is

$$\mathcal{F}_1 = \int_0^\infty dt\, f_1(t) = e^{-\left(\sqrt{4D\mu+v^2}-v\right)L/2D}. \tag{22}$$

From Eq. (21), the average search time and its variance are

$$\langle T\rangle = \frac{L}{\sqrt{4D\mu+v^2}}, \qquad \Sigma^2 = \frac{2DL}{(4D\mu+v^2)^{3/2}}. \tag{23}$$

Interestingly, the variance is non-monotonic in D, and the largest fluctuations in the search time occur when $D = v^2/(2\mu)$. Using our general approach, we can extend this chemotactic search process to the case of many searchers and determine the behavior of the search time on the N, M, and the rescaled drift velocity, the Péclet number [34]. It is also possible to investigate this search process in higher dimensions and in more realistic geometries, with the goal of providing a realistic but still tractable model for fertilization.

To summarize, we elucidated the competing roles of mortality, redundancy, and diversity on a search process that represents a caricature for the fertilization of an oocyte by sperm. To optimize this search, one strategy is to have a sophisticated search algorithm. However, nature often seems to prefer the brute-force approach of dispatching many almost-identical searchers that follow a simple search algorithm. The effectiveness of this redundancy is counterbalanced by the mortality of the searchers, and it is miraculous that the correct (and a very small) number of sperm actually reach the oocyte in human fertilization. While we do not offer insight into why this miracle occurs, we quantified the dynamics of this search process as a function of the number of searchers and their mortality rate. We also found that searcher diversity can compete with mortality so that only the most active searchers are successful.

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