

Predator-prey dynamics: Chasing by stochastic resetting

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We analyze predator-prey dynamics in one dimension in which a Brownian predator adopts a chasing strategy that consists in stochastically resetting its current position to locations previously visited by a diffusive prey. We study three different chasing strategies, namely, *active*, *uniform* and *passive* which lead to different diffusive behaviors of the predator in the absence of capture. When capture is considered, regardless of the chasing strategy, the mean first-encounter time is finite and decreases with the resetting rate. This model illustrates how the use of cues significantly improves the efficiency of random searches. We compare numerical simulations with analytical calculations and find excellent agreement.

Stochastic processes subject to resetting exhibit diffusive and first passage properties that markedly differ from ordinary diffusion [1–7]. When a Brownian particle is occasionally reset to a fixed position in space, the mean first passage time to a given target becomes finite and can be minimized with respect to the resetting rate [1]. Random searches based on resetting principles are advantageous in many contexts [4, 6], including situations where many targets or resetting points are distributed in space [2].

The statistics of first encounter times is key to understand reaction kinetics between freely diffusive molecules or prey/predators dynamics [8–12]. In the latter context, prey capture can involve relatively complex decisions by the predator depending on the position of the prey, or vice-versa [13, 14]. For instance, this is the case when the predator uses information about positions occupied by a prey, and decides to relocate to regions of space where it is more likely to be found [15]. There are other phenomena, such as olfaction in the case of olfaction-driven navigation in animals [15–17], backtrack recovery in RNA polymerases [18, 19] or the formation of physical contacts between distant segments of DNA by means of temporal and spatial motion scales [20], that can be modeled by a searcher influenced by cues whose spatial distribution is time dependent.

In this Letter we address a problem of two interacting Brownian particles for which the dynamics of one of them, called the *predator*, is subordinated to the dynamics of the other, called the *prey*, in one-dimensional space. In the following we will phrase the problem in terms of prey and predator for clarity. The chasing dynamics of the predator consist of frequent relocations to positions previously visited by the prey. In other words, this resetting dynamics correspond to a non-Markovian search process in which the predator stochastically visits previous prey positions. Prey motion is not influenced by the predator here. We focus on the effects of the predator search strategy on its own diffusion and on the statistics of first encounter times with the prey [21]. Our results may also be relevant in collective animal movement phenomena [22–25].

For this problem, we show that for a finite reset rate, the mean capture time is finite, contrary to the situation when the predator simply diffuses without resetting for which, as is well known, the mean capture-time diverges [12, 24].

We model the prey’s dynamics as an overdamped Brownian motion of a free particle diffusing in one dimensional space. The time evolution of the prey’s position, $y(t)$, is given by the stochastic differential equation

$$\frac{d}{dt}y(t) = \xi_y(t), \quad (1)$$

where $\xi_y(t)$ denotes a Gaussian-white noise, with mean $\langle \xi_y(t) \rangle = 0$, and autocorrelation function $\langle \xi_y(t)\xi_y(s) \rangle = 2D_y\delta(t-s)$, D_y being the prey’s diffusion coefficient and $\delta(t)$ the Dirac’s delta function.

The predator’s dynamics is modeled by the overdamped motion of a Brownian particle that randomly jumps from time to time, to a position previously visited by the prey, which makes the subordination process explicit. The time evolution of the predator’s position, $x(t)$, is determined by the following stochastic differential equation

$$\frac{d}{dt}x(t) = \xi_x(t)[1 - \sigma(t)] + \zeta[t, y(s); s \leq t]\sigma(t), \quad (2)$$

that describes the intermittent process of the predator dynamics. We consider the simplest case for the stochastic process $\xi_x(t)$, taken as an unbiased Gaussian-white noise, i.e. $\langle \xi_x(t) \rangle = 0$ and $\langle \xi_x(t)\xi_x(s) \rangle = 2D_x\delta(t-s)$, where D_x denotes the intrinsic diffusion coefficient of the predator. $\sigma(t)$ is a dichotomic stochastic process that takes the values 1 at a Poisson rate Q . $\zeta[t, y(s); s \leq t]$ denotes the stochastic discontinuous process that describes the predator chasing dynamics, namely, at a constant rate Q , the predator jumps from its current position $x(t)$, to a position $y(s)$ previously visited by the prey at the random time $s \leq t$ (as depicted in Fig. 1), the random variable s being distributed according to the probability density $\phi(s; t)$. This kernel entails the information that the predator has about past positions of the prey, which

we will refer henceforth, as the predator's memory. If the predator has unbiased complete memory, any previous time s is equally probable in the time interval $[0, t]$. Similar memory kernels have been considered in other models, such as the *elephant* random walk [26, 27] or the preferential visit model [28].

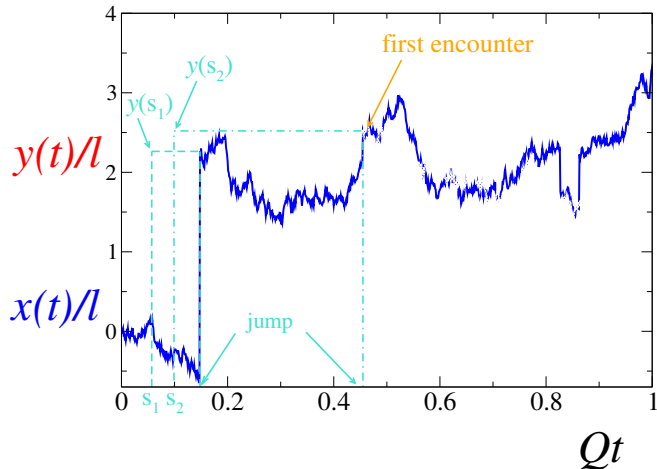


FIG. 1. Prey and predator dimensionless trajectories, $y(t)/l$ (red), $x(t)/l$ (blue) respectively, for the case when predators and prey diffusion constants are the same $D_x = D_y$. l denotes the length scale $\sqrt{D_y/Q}$. The first two jumps of the predator are marked with arrows at $Qt \approx 0.148$ and $Qt \approx 0.455$. In the first jump the predator chooses (from a uniform distribution) to jump to the previously position visited by the prey $y(s_1)$ where s_1 (≈ 0.057) is chosen from a uniform distribution in the interval $[0, 0.148]$. In this example the predator encounters for the first time the prey just right after the second jump (pointed with the orange arrow).

We first focus on the predator dynamics induced by the chasing when no capture of the prey is considered. In such a case, the stochastic processes defined by Eqs. (1) and (2) are equivalently formulated in terms of the conditional probability density functions $P(y, t|y_0)$, $\Pi(x, t|x_0)$. The prey's diffusion propagator at time t , $P(y, t|y_0)$, is given by $G_{D_y}(y, t|y_0) = \exp\{-(y - y_0)^2/4D_y t\}/\sqrt{4\pi D_y t}$, which is the Gaussian distribution, solution of the diffusion equation with diffusion coefficient D_y and the initial condition $G_{D_y}(y, t = 0|y_0) = \delta(y - y_0)$. The predator diffusion propagator, $\Pi(x, t|x_0)$, on the other hand, is given by the solution of the Fokker-Planck equation

$$\frac{\partial}{\partial t}\Pi(x, t|x_0) = D_x \frac{\partial^2}{\partial x^2}\Pi(x, t|x_0) - Q\Pi(x, t|x_0) + Q \int_0^t ds \phi(s; t) P(x, s|y_0), \quad (3)$$

with the initial distribution $\Pi(x, t = 0|x_0) = \delta(x - x_0)$. $\phi(s; t)$ gives the probability density of choosing the time instant s in the interval $[0, t]$. The first term in the right-

hand side of Eq. (3) corresponds to the predator diffusion process, while the second and third terms refer to the resetting process in which the predator jumps to a position previously visited by the prey, where $P(y, t)dy$ gives the probability of the prey being at $\{y, y + dy\}$ at time t . Equation (3) is akin to the continuous-space and continuous-time diffusion process under resetting with memory studied in Ref. [29]. In the present study, the subordination to the prey's dynamics leads to new qualitative features as is discussed afterwards.

The statistical properties of the predator diffusion process are derived from $\Pi(x, t|x_0)$. The solution of Eq. (3) for arbitrary resetting strategy $\phi(s; t)$ is given by

$$\Pi(x, t|x_0) = e^{-Qt}G_{D_x}(x, t|x_0) + Q \int_0^t ds e^{-Q(t-s)} \times \int_0^s ds' \phi(s'; s) G_{D_y}\left(x, \frac{D_x}{D_y}(t-s) + s' \middle| y_0\right), \quad (4)$$

As is expected, the Gaussian distribution $G_{D_x}(x, t|x_0)$ for the distribution of the predator positions is recovered from (4) by setting $Q = 0$. At finite Q and in the long-time regime, $Qt \gg 1$, Eq. (4) reads

$$\Pi(x, t) \sim \int_{-\infty}^{\infty} dx' L_{l_x}(x - x') \int_0^t ds \phi(s; t) G_{D_y}(x', s|y_0), \quad (5)$$

(see SM in Ref. [30]). $L_{l_x}(x)$ denotes the Laplace distribution that occurs in the related diffusion process of a Brownian particle that stochastically resets its position to the origin [1], given by $\exp\{-|x|/l_x\}/2l_x$, with $l_x = \sqrt{D_x/Q}$ the characteristic distance the predator travels between consecutive resetting. If this is vanishingly small, i.e., when either the resetting rate is large enough or the predator diffusion coefficient is small enough, $L_{l_x}(x - x')$ becomes sharply distributed around x , thus leading to $\Pi(x, t) \sim \int_0^t ds \phi(s; t) G_{D_y}(x, s|y_0)$.

From Eq. (4) the first two moments can be obtained for arbitrary strategy $\phi(s; t)$, these are given explicitly by

$$\langle x(t) \rangle = x_0 e^{-Qt} + y_0 (1 - e^{-Qt}), \quad (6a)$$

$$\langle x^2(t) \rangle = x_0^2 e^{-Qt} + \left(y_0^2 + \frac{2D_x}{Q}\right) (1 - e^{-Qt}) + 2D_y Q \int_0^t ds e^{-Q(t-s)} \bar{\tau}(s), \quad (6b)$$

where $\bar{\tau}(t)$ denotes the mean time of the distribution $\phi(\tau; t)$ given by the expression

$$\bar{\tau}(t) = \int_0^t d\tau \tau \phi(\tau; t). \quad (7)$$

From expression (6a) it can be deduced that: The average position of the predator is independent on the resetting strategy $\phi(s; t)$ and tends exponentially fast toward the

initial position of the prey, y_0 ; in the short-time regime it is given by $x_0 + (y_0 - x_0)Qt$, i.e., the predator travels on average ballistically with velocity $(y_0 - x_0)Q$.

We now specify these results for an illustrative case, namely, with exponential resetting strategies, where the probability density of picking an instant s in $[0, t]$ is given by

$$\phi(s; t) = \frac{\lambda e^{-\lambda s}}{1 - e^{-\lambda t}}, \quad (8)$$

with λ a real parameter in $(-\infty, \infty)$ that marks the range of the memory. For $\lambda < 0$, the chasing strategy is denoted as *active*, i.e., it is based on a short-term memory as the predator relocates with a large probability to the most recent positions visited by the prey. The $\lambda = 0$ case corresponds to a uniform memory, for which any instant s in the period of time $[0, t]$ is chosen with the same probability weight [26, 28]. The scenario given by $\lambda > 0$ corresponds to a *passive* chasing strategy, for which the predator relocates preferentially to the initial positions visited by the prey.

The predator's mean-squared displacement (6b), depends on the resetting strategy chosen through $\bar{\tau}(t)$. For the long-term memory strategy ($\lambda > 0$) and $Qt \gg 1$, we have $\bar{\tau}(t) \rightarrow \lambda^{-1}$, and thus the mean-squared displacement saturates $\langle x^2(t) \rangle - \left(y_0^2 + \frac{2D_x}{Q}\right) \approx 2D_y\lambda^{-1}$ (see Fig. 2), i.e., the predator gets trapped around the prey initial position, similarly to the process with stochastic resetting to the origin [1]. In the limit $\lambda \rightarrow \infty$, $\phi(s; t) \rightarrow \delta(s)$, thus, the predator stochastically resets to the prey's initial position, y_0 , and asymptotically we have $\Pi(x) = L_{l_x}(x - y_0)$, which corresponds to the stationary probability distribution found in Ref. [1].

For $\lambda = 0$, we have normal diffusion in the large-time limit, since $\langle x^2(t) \rangle \sim D_y t$, however, the kurtosis of $\Pi(x, t)$ approaches asymptotically to 4 indicating that it is not Gaussian. Therefore, this case belongs to a class of diffusion processes known as *Brownian yet non-Gaussian diffusion* [31], for which the probability distribution is not Gaussian in the long-time regime [see Eq. (5)]. Remarkably, the predator's diffuses with an effective diffusion coefficient that is half of the prey.

For the short-term strategy, $\lambda < 0$, the predator jumps to positions recently visited by the prey, which at large times yields linear-time dependence $\langle x^2(t) \rangle \sim 2D_y t$, which indicates that the predator diffuses with the same diffusivity as the prey. In the supplemental material (see Ref. [30]) we provide the explicit form of the mean squared displacement. In Fig. 2 we compare the time-dependence of the mean-squared displacement obtained from numerical simulations with Eq. (6b) for which we see an excellent agreement.

We continue our analysis in the scenario for which the predator captures the prey upon first encounter, and we study the statistics of these first-encounter times. In

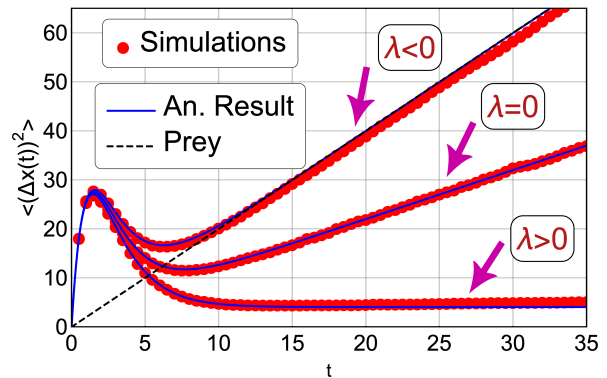


FIG. 2. Mean squared displacement of the predator as a function of time with $x_0 = 0$, $y_0 = 10$, $D_x = 1$, $D_y = 1$, $Q = 0.5$ and $\langle (\Delta x)^2 \rangle = \langle x^2(t) \rangle - \left(y_0^2 + \frac{2D_x}{Q}\right)$. The red dots were obtained by simulations, while the blue curves correspond to Eq. (6b). Notice that for large time, i.e., $t \gg 1/Q$, the mean square displacement (MSD) of the predator goes as $1/\lambda$, $D_y t$ and $2D_y t$ when $\lambda > 0$, $\lambda = 0$ and $\lambda < 0$, respectively, as shown in Eq. (6b). The MSD for the prey (dashed lines) is shown for reference.

the absence of the resetting process, the first-encounter time distribution reduces to the Lévy-Smirnov distribution $f(t; \mathcal{T}_0) = (\mathcal{T}_0/4\pi t^3)^{1/2} \exp\{-\mathcal{T}_0/4t\}$, where $\mathcal{T}_0 = z_0^2/(D_x + D_y)$ and z_0 is the initial relative distance between the prey and the predator. In the long-time regime, such distribution is characterized by the long tail $f_0(t; \mathcal{T}_0) \sim t^{-3/2}$, which implies the nonexistence of the mean first-encounter time [12]. The predator resetting process induces a *renewal* of the first-encounter time process, i.e., after the n -th resetting event the Lévy-Smirnov distribution turns into $f(t; \mathcal{T}_n)$, where \mathcal{T}_n is obtained by substituting z_0 by $z_n = |x_n - y_n|$, the relative distance between the predator and the prey just right after the stochastic relocation of the predator position. Additionally, this *renewal* process frustrates the long tail of the Levy distribution giving way to a finite mean-encounter time. We show numerical evidence of this in Fig. 3 for all values of λ and finite Q , where we have plotted the dimensionless mean-encounter time, $\langle t \rangle$. We further support this finding with arguments based on approximated analytical calculations.

The mean first-passage time can be computed from the survival probability $\mathcal{S}_Q(z_0, t)$, which can be written as a sum, over the number of resets, of the survival probability of a process with exactly n resets. We denote the latter as $\mathcal{S}^{(n)}(z_0, t)$ (see the SM in Ref. [30] for details on the derivation). For a given sequence of the predator position relocations, $\mathcal{S}^{(n)}(z_0, t)$ may be expressed as the convolution of the survival probabilities of the diffusive process between two successive reset events, $\mathcal{S}(z_i, t_i)$, multiplied by the probability that a reset event does not occur. Notice that the survival probability between any two consec-

utive resets is simply the survival probability at time t_i of a Brownian particle with initial position z_i and diffusivity $D = D_x + D_y$, *viz.* $\mathcal{S}(z_i, t_i) = \mathbf{Erf}(|z_i|/\sqrt{4Dt_i})$, where $\mathbf{Erf}(\bullet)$ is the error function. In Laplace domain we have

$$\tilde{\mathcal{S}}_Q(z_0, \{z_i\}, u) = \tilde{\mathcal{S}}(z_0, Q + u) \times \left(1 + \sum_{n=1}^{\infty} \prod_{i=1}^n [Q \tilde{\mathcal{S}}(z_i, Q + u)] \right). \quad (9)$$

In the above expression, we have fixed z_i , which are the relative distance once the i^{th} reset event occurs. The function $\tilde{\mathcal{S}}(z_0, u)$ is the Laplace transform of the survival probability of the process without reset, namely,

$$\tilde{\mathcal{S}}(z_0, u) = \frac{1}{u} \left(1 - e^{-\sqrt{\frac{u}{D}}|z_0|} \right), \quad (10)$$

Taking the limit $u \rightarrow 0$ in Eq. (9) yields the mean first-passage time. It is possible to show that when the resetting occurs such that $z_i = z_0$ for all i , then the summation in Eq. (9) is a geometrical summation and the mean first-passage time obtained coincides with the result obtained in Ref. [1] for the problem of a static prey. In our case, z_i is a random variable and the problem becomes analytically intractable, since averages must be performed over the z_i 's, of unknown distributions. Nevertheless, we can approximate the sum in Eq. (9) by replacing z_i by its typical value $\sqrt{2D_y i}/Q$ (which corresponds to $\lambda \rightarrow \infty$, since the predator relocates to the initial position of the prey) and by truncating the summation to $n = 1$ and $n = 2$ for $Q\mathcal{T}_0 < 1$ and $Q\mathcal{T}_0 > 1$, respectively. This choice is motivated by our simulations in Fig. 4, where we have plotted the mean number of resets before the first encounter *vs* the reset rate obtained from the simulations and an analytical approximation documented in the supplemental material [30]. Figure 3 displays the resulting mean first encounter times with solid lines, which show excellent agreement with the numerical simulation during seven orders of magnitude in the resetting rate Q .

Now notice that for $Q\mathcal{T}_0 < 1$ the two regimes depend on the predator chasing strategy (λ) whereas for $Q\mathcal{T}_0 > 1$ this dependence is lost as shown in Fig. 3. In addition, $\langle t \rangle$ diverges as $(Q\mathcal{T}_0)^{-1/2}$ for $Q\mathcal{T}_0 \rightarrow 0$, recovering the case at $Q = 0$. Around $Q\mathcal{T}_0 \sim 1$, a crossover to the scaling $(Q\mathcal{T}_0)^{-1}$ is observed for $Q\mathcal{T}_0 \gtrsim 1$. These two scaling regimes are also recovered from the exact analytical expression $\langle t \rangle = (1 - e^{-\sqrt{Q\mathcal{T}_0}})/Q$ for the case $\lambda \rightarrow -\infty$ (dashed line in Fig. 3) and from Eq. (9) by setting $z_i = 0$ for all i and taking the limit $u \rightarrow 0$.

Finally, as mentioned, from numerical simulations the average number of resets before the predator-prey encounter, increases from zero with Q and saturates to about 2.2 (for $\lambda \rightarrow -\infty$) and 1 (for $\lambda \rightarrow \infty$). We further derived an analytical approximation for the mean number of resets before the predator-prey's encounter

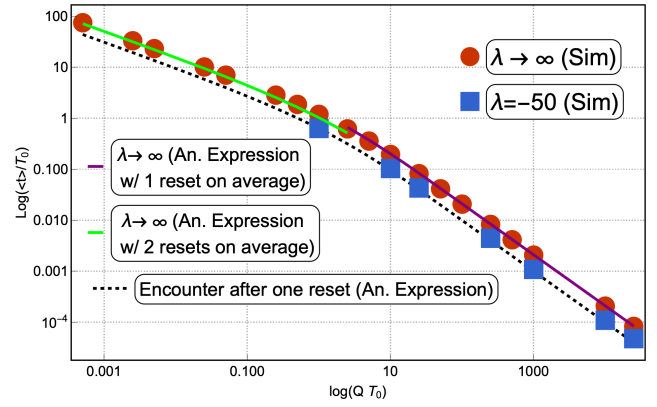


FIG. 3. Mean first-encounter time *vs* $Q\mathcal{T}_0$ for different values of λ (see legends). The dashed line corresponds to the short-term memory predator resetting strategy $\lambda \rightarrow -\infty$. The blue squares correspond to data obtained from numerical simulations with λ fixed at -50 and with time-step size ranging from 10^{-3} to 10^{-6} , depending on the value of Q . The red circles correspond to numerical simulations for which $\lambda \rightarrow \infty$. The continuous lines correspond to our approximate analytical result (see main text for discussion). Each data point corresponds to 10^7 simulations.

(see supplemental material in Ref. [30] for the analytical derivation). The solid lines in Fig. 4 corresponds to our analytical expression while the data points corresponds to simulations.

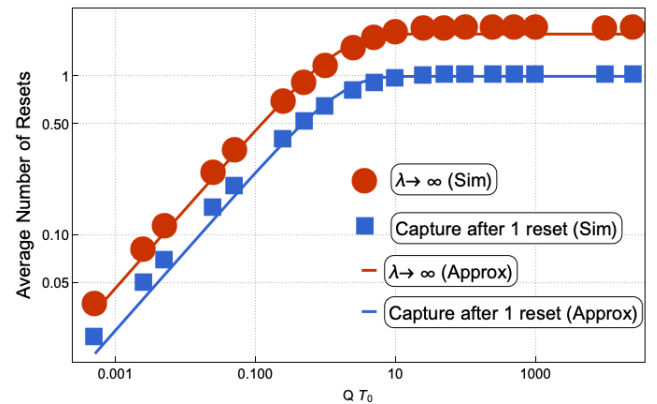


FIG. 4. Mean number of resets before the first encounter between the prey and predator *vs* Q for different values of λ (see legends). The data points were obtained from the simulations while the continuous lines correspond to our analytical results well documented in the SM in Ref. [30]. There is a threshold for the reset rate Q for which above that the mean number of resets before the first encounter saturate. Each point corresponds to 10^7 simulations.

In conclusion, we analyzed the distribution of a Brownian particle that resets to positions previously visited by another Brownian particle. This process depends on a memory function that accounts for the available infor-

mation of the previously visited locations of the prey. We have also studied the first-encounter times in this problem. We showed that both particles meet in a finite time, independently of the chasing behavior, and decreases as the resetting rate increases. Additionally, the long-time diffusion behavior of the predator is slaved to the diffusion of the prey. When only information about the recent locations of the prey is available to the predator, the latter tends to mimic the diffusion process of the prey, and ends up diffusing with the prey's diffusion coefficient. If only information of the initial positions visited by the prey is available to the predator, the latter becomes trapped around the initial position of the prey. In contrast, if the the whole information is equally available the predator ends up diffusing with half the diffusivity of the prey.

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