Lotka–Volterra systems with stochastic resetting

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Abstract
We study the dynamics of predator–prey systems where prey are confined to a single region of space and where predators move randomly according to a power-law (Lévy) dispersal kernel. Site fidelity, an important feature of animal behavior, is incorporated in the model through stochastic resetting dynamics of the predators to the prey patch. We solve in the long time limit the Lotka–Volterra rate equations that describe the evolution of the two species’ densities. Fixing the demographic parameters and the Lévy exponent, the total population of predators can be maximized for a certain value of the resetting rate. This optimal value achieves a compromise between the overexploitation and underutilization of the habitat. Similarly, at a fixed resetting rate, there exists a Lévy exponent that is optimal regarding predator abundance. These findings are supported by 2D stochastic simulations and show that the combined effects of diffusion and resetting can broadly extend the region of species coexistence in ecosystems facing resource scarcity.

Keywords: Lévy flights, stochastic resetting, population dynamics, predator–prey models

(Some figures may appear in colour only in the online journal)

1. Introduction
In situations of rapid population growth, species that exploit limited resources can face scarcity and risks of extinction. An essential question in ecology and population dynamics is to identify the strategies that individuals may adopt in unfavorable conditions for their own survival, as well as for the persistence of large populations. Among these strategies, mobility plays an important role. In recent years, it has been recognized that population dynamics is strongly affected by the spatial structure of the environment [1] and by the way living organisms move through it [2, 3]. For instance, species abundances depend on the spatial distribution of prey
patches and how predators commute between these patches [4, 5]. In experiments of bacterial predator–prey systems, species may coexist thanks to diffusion and a nonuniform spatial distribution of individuals [6, 7].

Fragile ecosystems, i.e. systems close to extinction thresholds, are often spatially fragmented or composed of small populations well separated in space [4]. For this reason, single patch systems where resources or prey are restricted to a limited area have attracted particular interest from both practical and theoretical point of views [8]. The one-patch configuration, a limiting case of a fragile system, allows us to study in detail the effects of predator mobility on species survival within and outside the patch [4, 9].

In spatially explicit population models, animal movements are usually modeled by Brownian diffusion, a mode of transport that reflects the dispersion of individuals performing Markovian random walks [10, 11]. In situations of low prey density, however, predator species often forage under conditions of high uncertainty and move across many landscape scales to search for resources [12]. When foragers have located profitable areas, they often exhibit site fidelity [13]. The random walk description obviously ignores these two important features of animal mobility, namely, multiscale movements and memory effects.

In recent years, technological advances in individual tracking have revealed that animal foraging movements are often better described by Lévy flights or Lévy walks than ordinary random walks [14–23]. Lévy flights are random walks composed of independent displacement steps, whose lengths \( l_i \) are broadly distributed, following a power-law distribution with infinite variance, or \( p(l) \sim l^{-\beta} \) at large \( l \), with \( 1 < \beta < 3 \) [24]. Under environmental uncertainty, multiscale movement represents a mechanism by which exploratory behavior and information gathering can be improved: Lévy flights allow an increase in the number of visited sites, without preventing returns to previous sites [12]. In this context, the anomalous diffusion generated by Lévy motion can represent an efficient random search strategy for finding prey items in unpredictable environments, i.e. when prey are scarce and distributed in patches [14, 15].

Although the Lévy flight model has been extensively applied to animal movement in recent years, other paradigms exist. We mention for instance that the long-range migration of individuals on a lattice is sometimes modeled by small-world Watts–Strogatz networks, where quenched shortcuts connect distant lattice sites. The lengths of these shortcuts can be chosen to follow a power-law distribution, in analogy with Lévy diffusion [25, 26]. Such a network model exhibits diffusive behaviors similar to Lévy flights for \( \beta > 2 \), as long as the probability of presence at the origin or the number of distinct visited sites is considered. Nevertheless, differences with Lévy flights are noticeable in one-dimension (1D) when the exponent parameter \( \beta \) is smaller than two, where the processes are transient.

Long-range displacements can have a drastic impact on ecosystems dynamics. In cyclic Lotka–Volterra models, such as the rock–scissors–paper game, the addition of long-range links to a regular lattice can give rise to a transition to global oscillations [27, 28]. In such systems without strict competitive hierarchy, local mobility is nevertheless advantageous for biodiversity: extinctions can occur if the density of long-range links is too high [27]. Similarly, diversity can be lost in similar models if the mobility of individuals is too large [29, 30].

Many animal species also rely on spatial memory during foraging [31], and individuals often exhibit a tendency to regularly revisit places that are associated with successful foraging experiences [32, 33]. This behavior can occur for instance during traplaining, which consists of visiting several known resource sites before returning to a shelter, or by cropping, which is when foragers exploit a particular area for some time and then temporarily abandon it to give the resources time to regenerate [34]. A simple way to model fidelity to a profitable patch consists of interrupting diffusion stochastically (say, at some rate \( r \)) and to reset the forager position to the resource patch. From this site, a new diffusing path is then generated until the
next resetting event. This model, of interest in the present work, is motivated by the fact that
the properties of ordinary diffusing particles subjected to stochastic resetting are mathemati-
cally tractable, as shown by a body of recent studies [35–38], including extensions to the case
of Lévy flights [39, 40]. An important effect of resetting to a single site on diffusion is the gen-
eration of a stationary probability density profile around the resetting point after a long time,
which is similar to the home range behavior of animals [41] and in contrast with the vanishing
densities of unbounded diffusing processes. For a particle that diffuses and is subject to reset-
ting, the mean square displacement reaches a finite asymptotic value. This type of motion was
shown to represent an efficient search strategy to find hidden targets by a single searcher, but
has not yet been investigated in population models.

Throughout this paper, we define optimal strategies as those that maximize the abundance
of a predator population (although other related quantities can be considered). This point of
view differs from the usual definitions of efficiency in random search problems with a single
forager, which typically focus on the individual’s foraging efficiency through the mean first
hitting time to a target. In principle, there is an important distinction between the reproductive
interest of an individual and the survival of a species, as noticed by Williams [42] some time
ago. At the population scale, because of interactions and demographic constraints, individu-
ally efficient foragers do not necessarily have a positive impact on abundances. For instance,
efficient predators may overexploit resources, leading to low abundance and even extinctions.
Conversely, less-efficient foragers may give resources time to regenerate, allowing that same
forager species to survive over many generations.

In a recent work, we studied a Lotka–Volterra model, where a colony of mortal predators
performing ordinary random walks or Lévy flights fed on many small prey patches separated
in space [43]. The predators had a fixed death rate, could diffuse freely outside the patches, and
could only reproduce within a patch. It was shown that the use of Lévy strategies could maxi-
mize forager abundances and avoid extinctions, which were likely in the Brownian regime.
Here, we continue with the methodology used in [43] and consider the case of prey that are
confined to a single patch and predators that are subjected to stochastic resetting to this patch,
which models memory effects. The purpose of modifying the previous model is to investigate
how (anomalous) diffusion and site fidelity combined impact species coexistence. When the
predator reproductive rate is low, we expect that in the absence of resetting the fluxes of dif-
fusing foragers, leaving the patch will not be compensated by the birth of new foragers from
individuals that are still in the patch. In those cases, low abundances or even extinctions are
likely. In the same conditions, a large resetting rate will sharply localize the foragers around
the patch, increasing their density as well as competition for prey, which may negatively affect
the overall abundance. One hence expects that the predator population reaches a maximum at
some finite resetting rate. Similarly, for a fixed resetting rate, the predator abundance may be
maximized by tuning the Lévy exponent \( \beta \) to a certain value. We investigate more generally
how the movement parameters \( r \) and \( \beta \), which maximize predator abundances, depend on the
reproduction and death rates.

2. Analytical Lotka–Volterra model with patchy prey and mobile predators

We retake here the setup of the model presented in [43]. Let us consider a regular \( D \)-dimensional
lattice of square cells with length \( R \), where the positions of the center of each cell are repre-
sented by a vector \( \mathbf{n} \) with integer components. Predators occupy the cells and perform inde-
pendent random motion (the resetting part will be introduced below). The lengths of these
displacements are in principle continuous and we set the unit length as the smallest possible
displacement performed by a predator ($1 < R$). We denote the probability distribution of the dispersal of a predator between cells as follows:

$$p (l) = p_0 \delta_{l0} + (1 - p_0) f(l),$$

(1)

where $l$ is a vector with integer components. The quantity $p_0$ represents the probability that the predator remains in the same cell after moving. This is possible because each cell has a spatial extent $R$ and a predator may not exit the cell ($l = 0$) if its actual displacement is too small (see equation (16) below). The function $f(l)$ is a normalized dispersal distribution between non-identical cells, and will take the form of an inverse power-law with exponent $\beta$ in the following. More detail is given in section 2.2. It satisfies $f(0) = 0$ and the normalization condition

$$\sum_{l | l \neq 0} f(l) = 1.$$

(2)

In this model, only the origin cell $n = (0,0)$ can contain prey, and it is also the only place where predators reproduce. Assuming that the number of individuals per cell is large, we neglect fluctuations and write two deterministic rate equations of the Lotka–Volterra type that are inspired by the model studied in [11]. One equation describes the time evolution of the density of predators in cell $n$ at time $t$, denoted as $a(n,t)$; the other equation describes the time evolution of the density of prey $b(t)$ at the origin cell (the prey patch). As mentioned earlier, the predators can also relocate (reset) stochastically to the origin cell, independent of their current position in the system. This process happens at rate $r$. Once the predator has reset to the origin, it continues its dynamics from there until the next resetting event (and in a way analogous to the problem studied in [35]). The equation for the predator density reads

$$\frac{\partial a(n,t)}{\partial t} = - \alpha(1 - p_0)a(n,t) + \alpha \sum_{l | l \neq 0} p(l)a(n - l,t) - \lambda a_0(t)b(t)\delta_{n,0} - \mu a(n,t) + ra(n,t) + \left[ r \sum_m a(m,t) \right] \delta_{n,0}.$$

(3)

The first term in the right-hand side represents the rate at which predators leave the cell $n$, and $\alpha$ is the movement rate. The second term describes the rate at which predators arrive at the cell from another one through a random step, the third term accounts for reproduction at rate $\lambda$ (which only occurs at the origin cell, where prey are present), and the fourth term represents predator mortality, where $\mu$ is the mortality rate. The last two terms describe the resetting process and depart from the model of [43]: the fifth term indicates that predators are removed from their current location at rate $r$, while the last term represents the increase in density at the origin due to predators resetting from everywhere in the system. It is clear that new predators are not created at the origin; they are just brought from elsewhere at rate $r$.

The prey density $b(t)$ in the prey patch obeys the ordinary differential equation:

$$\frac{db}{dt} = \sigma b \left( 1 - \frac{b + a_0}{K} \right) - \lambda' a_0 b$$

(4)

where we have denoted $a_0(t) = a(0,t)$ as the predator density at the prey patch, $\sigma$ as the prey reproductive rate, and $\lambda'$ as the predation rate. $K$ represents the prey carrying capacity, which, as usual in biology population modelling [8, 11], enforces the fact that prey cannot grow indefinitely but are limited by finite resources instead. Note that this realistic assumption was
not present in the original Lotka–Volterra model [44, 45]. Hence, in the absence of predators, the prey density asymptotically reaches its maximum value $K$.

In the absence of movement ($\alpha = 0$, $r = 0$), populations vanish everywhere at a large time except at the prey patch, where equations (3)–(4) reduce to two ordinary differential equations (which have been studied in detail [11]). Two simple stationary fixed points, $\left( a_0^{(o)}, b_0^{(o)} \right) = (0, 0)$ and $\left( a_0^{(u)}, b_0^{(u)} \right) = (0, K)$, correspond to total extinction (the overexploitation point) and predator extinction (the underexploitation point), respectively. A third, globally stable coexistence fixed point exists for $\mu/\lambda < K$, and is given by

$$a_{\text{coex}}^0 = \frac{K - \mu/\lambda}{1 + \lambda K'/\sigma}$$

and

$$b_{\text{coex}}^0 = \frac{\mu}{\lambda}.$$

(If $K < K_c = \mu/\lambda$, predators go extinct and $b_{\text{coex}}^0 = K$.)

Oscillatory solutions do not exist in this problem [11], and this feature probably holds in the space-dependent problem as well. See [46] for an extended discussion on this latter aspect.

2.1. Stationary solution

In the following we focus our analysis on steady state solutions. Expressions for the stationary prey and predator densities, denoted by $a_n$ and $b$, respectively, can be derived by setting the time derivatives to zero. For the prey, one obtains the trivial solution $b = 0$ and

$$a = K - a_0 (1 + K\lambda'/\sigma),$$

where $a_0$ is the stationary predator density at the prey patch, a constant yet to be determined. We introduce the discrete Fourier transforms

$$\hat{a}(k) \equiv \sum_n a_n e^{-i k \cdot n}, \hat{f}(k) \equiv \sum_l f(l) e^{-i k \cdot l},$$

and take the Fourier transform of equation (3) with the steady state condition. One obtains

$$\hat{a}(k) = \frac{\lambda a_0 [K - a_0 (1 + K\lambda'/\sigma)] + rA}{\alpha (1 - p_0)} \left[ 1 - \hat{f}(k) \right] + \mu + r,$$

where $A = \sum_m a_m = \hat{a}(k = 0)$. This solution differs from the predator density calculated in [43] due to the presence of resetting and the single patch geometry. By setting $k = 0$ in equation (7) we can solve for $A$ (note that $\hat{f}(k = 0) = 1$ by normalization):

$$A = \frac{\lambda a_0}{\mu} \left[ K - a_0 (1 + K\lambda'/\sigma) \right].$$

(8)

A quantity of primary interest here is the total population of predators ($N_p$). It is simply given by

$$N_p = R \sum_n a_n = R \hat{a}(k = 0).$$

(9)

Replacing into equation (9) the quantity $a(k = 0)$ given by equation (8) gives

$$N_p = R \frac{\lambda a_0}{\mu} \left[ K - a_0 (1 + K\lambda'/\sigma) \right].$$

(10)

The predator density in the prey patch $a_0$ can be obtained self-consistently from the inverse Fourier transform of $a(k)$ evaluated at the origin $n = 0$. We use equation (7) and the inverse relation
where $B$ means that we are integrating over the Brillouin zone, which in one dimension ($D = 1$) is the interval $-\pi < k < \pi$, and in two dimensions ($D = 2$) the domain $-\pi < k_x, k_y < \pi$. Setting $n = 0$ in equation (11) we obtain an equation for $a_0$, which admits the trivial solution $a_0 = 0$ and a non-trivial one:

$$a_0 = \frac{1}{1 + K \lambda / \sigma} \left\{ K - \left\lfloor \frac{\lambda}{\mu (2\pi)^D} \int_B \alpha (1 - p_0) [1 - f(k)] + r \right\rfloor \right\}^{-1}. \tag{12}$$

If the above solution happens to be negative, then only the solution $a_0 = 0$ is acceptable.

Equations (10) and (12) fully determine the total number of predators in the system as a function of the different parameters. The number of prey is deduced from equation (5). We notice from (10) that $N_p$ obeys a logistic relation with respect to $a_0$, the predator density at the origin patch. Therefore, the total number of predators is maximal when $a_0 = a_0^{\text{max}} = K/[2(1 + K \lambda / \sigma)]$ whereas $N_p$ vanishes at $a_0 = 0$ and at $a_0 = K/(1 + K \lambda / \sigma) = 2a_0^{\text{max}}$.

Equation (9) shows that in the low-density regime, i.e. $0 < a_0 < a_0^{\text{max}}$, an increase in $a_0$ produces an increase in $N_p$: this is the underexploitation regime. Meanwhile, for $a_0^{\text{max}} < a_0 < 2a_0^{\text{max}}$, i.e. the high-density regime, any increase in $a_0$ decreases the total population (overexploitation regime). When $a_0 > 2a_0^{\text{max}}$, the solution is no longer valid and the only non-negative steady state solution of equation (4) is $b = 0$, implying $a_0 = 0$ and $N_p = 0$. This point corresponds to the global extinction of prey and predators.

Using equation (12) and solving the equation $a_0 = a_0^{\text{max}}$, we obtain a relation (which may not always admit solutions) between the movement parameters $r$ and $\beta$ and the demographic parameters, and such that the predator abundance in the whole system is maximal. This relation reads as follows:

$$\frac{1}{(2\pi)^D} \int_B \frac{dk}{(1 - p_0)[1 - f(k)] + \mu^* + r^*} = \frac{2\mu^*}{(r^* + \mu^*) \lambda^* K}. \tag{13}$$

where the reduced parameters are defined as $\mu^* = \mu / \alpha$, $r^* = r / \alpha$, and $\lambda^* = \lambda / \alpha$. To simplify the notation, from now on we will set the movement rate $\alpha$ to 1 and write the reduced parameters without an asterisk. Thus, by fixing the ecological parameters $\mu$, $\lambda$, and $K$, there exists in principle a set of pairs $(\beta, r)$ that satisfy equation (13). We recall that the dependence in $\beta$ is contained in $f(k)$.

To gain insight into the stationary states calculated above, we will consider the simpler 1D case in the numerical applications (results in 2D are qualitatively similar, as will be shown further below). The jump probability distribution in equation (1) becomes

$$p(l) = p_0 \delta_{l,0} + (1 - p_0) f(l) \tag{14}$$

where $l = 0, \pm 1, \pm 2$, etc.

### 2.2. Predator movements

We now calculate the probability $p_0$ for an agent to leave a cell of length $R$ in the 1D case. The same calculation can be found in the supplemental information of [43]. We assume that predators perform continuous steps of length $x$, which are independent and identically distributed. We choose a symmetric, normalized power-law distribution:
\[ \psi(x) = \frac{\beta - 1}{2} |x|^{-\beta} \quad \text{for} \quad |x| > 1. \] (15)

The exponent \( \beta \) characterizes the forager displacements; they have a minimal length of 1, which means that \( \psi(x) = 0 \) for \( |x| < 1 \). The three important movement scenarios are as follows: (1) when \( \beta \geq 3 \), the predators diffuse normally, similarly to Brownian motion; (2) if \( 1 < \beta < 3 \), the movements correspond to Lévy flights; and (3) in the highly superdiffusive regime \( \beta \approx 1 \), the foragers take extremely long steps.

We assume that the walkers occupying the patch can be anywhere inside with a uniform probability. The average probability that a step does not bring the walker out of the cell is

\[ p_0 = 2 \int_0^R dr \int_0^r dx \psi(x). \] (16)

Factor 2 takes into account the right and left moves. One then obtains

\[ p_0 = 1 - \frac{1}{R} + \frac{1 - R^{2-\beta}}{(2 - \beta)R} \quad \text{for} \quad \beta \neq 2 \] (17)

and \( p_0 = 1 - \frac{1}{R} - \frac{\ln(R)}{R} \) for \( \beta = 2 \). When \( \beta \) is large (Brownian diffusion), \( p_0 \approx 1 - 2/R \rightarrow 1 \) at large \( R \); only the predators located close to the boundary of the cell can exit the cell in one step. Conversely, \( p_0 \rightarrow 0 \) as \( \beta \rightarrow 1 \), as is expected if the walkers take very long steps. Following the same arguments, one may calculate the probability that the walker jumps over \( l \) cells in one step, with \( l \) being a nonzero integer. For simplicity, we assume for this quantity a normalized power-law distribution with the same exponent \( \beta \) as in equation (15):

\[ f(l) = \frac{|l|^{-\beta}}{2 \sum_{m=1}^{\infty} m^{-\beta}} \quad \text{for} \quad l = \pm 1, \pm 2, \ldots \] (18)

### 3. Results in 1D

Without lack of generality, we fix \( K = 1 \) and \( \sigma = 1 \) in the following, since these parameters appear only as prefactors of the predator abundance \( N_p \) (see equations (10) and (12)). The size of the prey patch is set to \( R = 10 \).

#### 3.1. Predator populations

We first focus on the variations of the total number of predators with respect to the mortality rate \( \mu \) and the exponent \( \beta \), for various values of the resetting rate and of the reproduction rate \( \lambda \). The expressions are calculated using Mathematica.

Figure 1 represents the case of a system with \( \lambda = 0.5 \). At \( r = 0 \) (no resetting, or free diffusion) and at fixed \( \mu \), predators become extinct below a certain value of \( \beta \), which increases as \( \mu \) increases (see figure 1(a)). This means that predators that are too superdiffusive escape from the patch and do not return to it for predation and reproduction, thus leading to extinction. At high mortality rates, even Brownian predators \((\beta > 3)\) cannot avoid extinction. However, at low mortality rates, \( N_p \) takes a maximum value in the Lévy regime when \( \beta \approx 2 \).

If \( r > 0 \) (figures 1(b) and (c)), the predators regularly return to the prey patch due to resetting independently of their Lévy exponent. At low \( \mu \), predators tend to overexploit the patch and \( N_p \) is larger when \( \beta \) tends to one, corresponding to the highly superdiffusive regime. However, when \( \mu \) takes large values, we can find a behavior similar to that found for the case
of \( r = 0 \): for a fixed \( \mu \), \( N_p \) vanishes below a certain value of \( \beta \). In all cases, above a critical \( \mu \), predators go extinct due to the mortality of predators. The critical value of \( \mu \) increases as \( r \) increases (see figure 1(c)).

In figure 2, the reproduction rate is lower than in figure 1. As shown by figures 2(a) and (b), where \( \mu \) is relatively large (meaning that the conditions are unfavorable for predators), \( N_p \) can become nonzero for \( r > 0 \). At fixed \( \beta \), \( N_p \) increases with \( r \), which indicates the positive effect of resetting on predator abundance. At fixed \( r \), Brownian foragers (larger \( \beta \)) have larger populations.

When \( \mu \) is smaller (figure 2(c)), the behavior is quite different: (1) the region with the nonzero predator population is much larger, and (2) at fixed \( \beta \), a maximal population abundance is reached for a finite optimal value of \( r \). If \( r \) is too small, resources are underexploited and the predator may go extinct like in the \( r = 0 \) case; meanwhile, larger values lead to resource overexploitation, which limits predator reproduction. Note that with a fixed \( r \) and varying \( \beta \), the variations are much softer. The resetting process has stronger effects here on the populations than the type of movement between resetting events.

In figure 3, \( \mu \) is set to 0.01 (like in figure 2(c)) whereas in figure 4 it is set to 0.0001. These figures display the total predator population as a function of \( r \) for different choices of the Lévy exponent \( \beta \) and reproductive rate \( \lambda \). For convenience, the rescaled variable \( r/\lambda \) is used in the figures. We observe a nonmonotonic behavior with a maximum at a particular \( r_{\text{opt}} \), whose value depends on \( \beta \) and \( \lambda \), as expected from equation (13). As \( \lambda \) increases, \( r_{\text{opt}} \) decreases (figure 3(a)). Fast-reproducing predators need to revisit the prey patch less often; otherwise, they would overexploit it. When \( \beta \) is larger, namely, the diffusion is slower (figures 3(b) and (c)), \( r_{\text{opt}} \) tends to decrease. This can be due to the fact that resetting is less needed because predators can often return to the origin by random movement.

Figures 5 (\( \mu = 0.01 \)) and 6 (\( \mu = 0.0001 \)) display \( N_p \) as a function of \( \beta \) for different combinations of \( r \) and \( \lambda \). The predator abundance is sometimes nonmonotonic in the Lévy range and exhibits a maximum at a particular value \( \beta_{\text{opt}} \). In general, the value of \( \beta_{\text{opt}} \) maximizing the predator abundance can be in the Lévy interval \((1, 3)\), be \( \geq 3 \), or take the minimal value 1. This exponent represents the optimal random movement strategy for the predator population as a whole. The three aforementioned regimes for the optimal value of \( \beta \) were also observed in the model studied in [43], which considered \( r = 0 \) and a finite patch density, i.e. a finite separation distance between neighboring patches.

In the absence of resetting (figures 5(a) and 6(a)), \( \beta_{\text{opt}} \) is in the Brownian regime \((\beta_{\text{opt}} > 3)\) in the present single patch configuration. Too much superdiffusion causes predators to not return to the patch often enough, thus implying a population decline, and even extinctions at small \( \beta \). When the reproduction rate \( \lambda \) increases, so does \( N_p \) and the range of \( \beta \) allowing
Figure 2. Total population of predators in the \((\beta, r)\)-plane for three values of \(\mu\) and \(\lambda = 0.1\). (a) \(\mu = 0.08\). (b) \(\mu = 0.05\). (c) \(\mu = 0.01\).

Figure 3. Total population of predators as a function of the resetting rate, for several values of \(\beta\) and high reproductive rates \(\lambda\). (In all cases, \(\mu = 0.01\).) (a) \(\beta = 1.1\). (b) \(\beta = 2.0\). (c) \(\beta = 3.0\).

Figure 4. Total population of predators as a function of the resetting rate, for several values of \(\beta\) and low reproductive rates \(\lambda\). (In all cases, \(\mu = 0.0001\).) (a) \(\beta = 1.1\). (b) \(\beta = 2.0\). (c) \(\beta = 3.0\).

Figure 5. Total population of predators as a function of \(\beta\), for several values of \(r\) and reproductive rates \(\lambda\). In all cases, \(\mu = 0.01\) (high mortality.) (a) \(r = 0.0\). (b) \(r = 0.01\). (c) \(r = 0.15\).
survival. In the many-patch model of [43], $\beta_{\text{opt}}$ could be found in the Lévy range for some intermediate values of the mortality and reproduction rates.

When the resetting rate is switched on, the range of values of $\beta$ allowing survival is significantly wider since predators always return to the prey patch sooner or later to feed and reproduce. For this reason, at fixed $\lambda$ and for low values of $\beta$, increasing $r$ from zero has a positive effect on $N_p$ (figures 5(b) and (c)). At fixed $\mu$, the predation pressure can be increased by making $\lambda$ larger and the diffusion slower (i.e. $\beta$ larger): in this case, increasing $r$ implies a decrease in $N_p$ (compare the top curve of figures 5(b) and (c) for $\beta \sim 3$). At low mortality, this effect is more drastic, as can be noticed by the difference in the vertical scales between figure 6(a) ($r = 0$) and (c) ($r = 0.15$). Meanwhile, $\beta_{\text{opt}}$ decreases when $\lambda$ increases: the overexploitation of resources is avoided by an optimal movement mode that becomes more superdiffusive. We thus conclude that resetting has a greater impact on the survival of highly superdiffusive Lévy populations than on Brownian populations.

A comparison of figures 5(b), (c) and 6(b), (c) also reveals that $\beta_{\text{opt}}$ decreases as $r$ increases.

The bell shape can even disappear and be replaced by a monotonic decay from $\beta_{\text{opt}} = 1$.

3.2. Parameters maximizing predator populations

It follows from the above results that the predator abundance reaches a maximum when the movement parameter $\beta$ is set to some value $\beta_{\text{opt}}$, which can be in the Lévy range $1 < \beta_{\text{opt}} < 3$. We proceed below to better locate the region of optimal Lévy flights in parameter space.

We wish to find the movement parameters $\beta$ and $r$ that maximize the forager abundance at given $\mu$ and $\lambda$. Due to the difficulty of representing this domain in a three-dimensional frame, we fix $\lambda$ and vary the other three parameters in two different ways. In the first case, we fix $\mu$ and $\beta$ in the Lévy range $(1, 3)$, find the $r_{\text{opt}}$ that maximizes $N_p$, and repeat the operation for many pairs $(\mu, \beta)$, as shown in figure 7. In the second case, we fix $(\mu, r)$ and determine $\beta_{\text{opt}}$, as shown in figure 8. In the latter case $\beta_{\text{opt}}$ is not necessarily in the Lévy range, and thus we can address the question of whether Lévy strategies are often optimal or require some particular conditions.

Figure 7 exhibits in color-scale the optimal $r_{\text{opt}}$ as a function of $\mu$ and $\beta$ ($\lambda$ being set to four different values). When using the rescaled variable $\mu/\lambda$, all graphs are very similar. As previously noticed, nonzero values of $r$ are advantageous for superdiffusive predators in the whole range of $\mu$. When the mortality is very high ($\mu > \lambda/4$), the maximum population is even reached with $r^* \geq 1$, irrespective of the value of $\beta$, meaning that the foragers reset so often that they practically remain localized on the prey patch. Long lived ($\mu \ll \lambda$) and not-so-super-diffusive foragers ($\beta > 2$) require a small resetting rate to maximize their population.
In figure 8, the optimal $\beta$ is classified into the three regimes $\beta_{\text{opt}} > 3$ (Brownian), Lévy, and $1 < \beta_{\text{opt}} < 1.1$ (highly superdiffusive). Brownian strategies are advantageous for values of $\mu/\lambda$ above a certain threshold and below the extinction threshold ($N_p = 0$ in the white region). When $r$ is small, the former threshold is fairly small (see figures 8(a), (c), and (d)). At a lower mortality rate, Lévy flights become advantageous since they avoid overpopulation on the patch. Interestingly, Lévy strategies become optimal when both $r$ and $\mu/\lambda$ become very small. The highly superdiffusive regime is never favored at low $r$, but becomes vastly optimal at larger $r$ and small $\mu/\lambda$ (see figure 6(c) for an example).

3.3. Stochastic 2D simulations

To illustrate the usefulness of the 1D cases considered so far to infer properties of 2D systems, we perform Monte Carlo simulations of a 2D stochastic population model that is the stochastic analogue of equations (3) and (4) for the species densities. At high densities, the stochastic and deterministic descriptions become equivalent [11], but when the number of individuals is small, fluctuations can play an important role. We implement an algorithm (see caption of figure 9(a)) that is exposed with more detail in [11] and [43].
The curves of predator abundance in 2D, displayed in figures 9(b)–(d), are similar to those shown in figures 2(a)–(c) for the 1D case and the same parameter values. The only difference is the value of $R$, which is the length of a cell in 1D and the radius of a circular patch in 2D. In figure 9(b), where $\mu/\lambda \sim 1$, the total number of predators is small and subject to large fluctuations due to stochasticity. At smaller $\mu/\lambda$ (figure 9(c)), the monotonic behavior with $r$ and $\beta$ becomes noticeable, whereas $N_p$ remains zero at small $\beta$ and $r$. These results are qualitatively similar to those of the deterministic model (figures 2(a) and (b)). In figure 9(d), where $\mu/\lambda = 0.1$, one also recovers the most salient features of the analytical model in this regime (figure 2(c)), namely, the nonmonotonic behavior with $r$, the decrease of $r_{\text{opt}}$ with $\beta$, and the persistence of extinct states at small $\beta$ and $r$.

4. Discussion and conclusions

In this work, we analyzed the properties of diffusing elements, with stochastic resetting to the origin, that interact through a population dynamics model. More specifically, we considered a predator–prey system where prey are scarce, i.e. confined to the origin cell (patch). Predators reproduce on the prey patch and randomly migrate from cell to cell on the lattice according to a power-law dispersal kernel with exponent $\beta$. The fact that predators stochastically relocate
(reset) from time to time to the origin is motivated by site fidelity, an important aspect of foraging ecology [47–50]. Our model admits asymptotic stationary distributions for the species densities, and we obtained analytical expressions for the species abundances. Fixing the demographic parameters, chiefly, the predator mortality and reproduction rates, there exists in general many pairs of movement parameters ($\beta$ and the resetting rate $r$) for which the predator population is maximal. Such foraging strategies thus allows an optimal exploitation of resources at the population level. This collective notion of optimality (also discussed in [43]) differs from the more usual individual optimality that is studied in search models, which is based on maximizing the rate of prey capture by a single agent in an environment of static prey. In these contexts, interactions between agents and birth/death processes are usually ignored.

The predator abundance represents a natural quantity to measure foraging efficiency from a collective point of view. In the deterministic approach that we use, this quantity evolves

Figure 9. (a) In simulations, space is a 2D discretized square lattice, with some sites forming a patch in the center (green area). Inside the patch, a site can contain at most one prey (blue dots). There is no limitation on the number of predators (red dots) per site. Predators perform independent discrete 2D Lévy flights. When a predator (red dots) arrives at a site containing prey, it consumes it with probability $\lambda'$ = 1 and reproduces with probability $\lambda$. In one Monte Carlo time step, predators die with probability $\mu$ whereas surviving predators perform one movement step. The patch radius is set to $R = 10$. An empty site in the patch next to a prey can become occupied by a new prey with probability $\sigma$. The curves display the predator abundance as a function of the movement parameters $\beta$ and $r$ with (b) $\mu = 0.08$, (c) $\mu = 0.05$, and (d) $\mu = 0.01$, for a fixed $\lambda = 0.1$. 

(a) $\lambda = 0.1$, $\mu = 0.01$, $r = 0.05$, $\beta = 2$

(b) $\lambda = 0.1$, $\mu = 0.08$ and $\sigma = 1$

(c) $\lambda = 0.1$, $\mu = 0.05$ and $\sigma = 1$

(d) $\lambda = 0.1$, $\mu = 0.01$ and $\sigma = 1$
toward a stable steady state solution (there are no oscillations in our model). In a stochastic approach, however, there are other ways of quantifying the efficiency, such as using the mean first passage time to extinction or to a threshold value of prey population that allows the population of predators to survive. Although we did not focus on stochasticity in this work, it is an important aspect deserving future research.

A first category of unfavorable environmental conditions corresponds to predators with high mortality and slow reproduction. In this case, as expected, the foraging strategy consisting of diffusing normally and with a high resetting rate to the prey patch allows a better exploitation of resources and generates more-abundant forager populations (figures 2(a) and (b)). This situation changes when the predator mortality is too low: in this second category, the risk is to overpopulate the prey cell and underpopulate the other cells. In such cases, a low resetting rate is preferable since it gives the time for foragers to diffuse away, thus increasing the prey density on the patch and consequently the reproduction rate per predator. Comparatively, the mobility exponent $\beta$ plays a less prominent role: Lévy and Brownian foragers can reach the same maximal population levels owing to the logistic dependence of $N_p$ on $a_0$, but at different optimum resetting rates (figure 2(c)). In figures 3 and 4, one can appreciate that the abundances at their maximum as a function of $r$ do not depend on $\beta$. At an even smaller mortality rate (compared to the reproduction rate), the optimal resetting rate tends to zero for any value of $\beta$ (figures 3 and 4).

The total predator abundance is more sensitive to the Lévy exponent $\beta$ when $r$ is fixed to some value, which is not necessarily the optimal one (figures 5 and 6). Generally speaking, at a fixed resetting rate, the optimal $\beta$ moves from 1 (highly superdiffusive) to a value $>3$ (Brownian) as the relative mortality rate $\mu/\lambda$ increases. Hence, at small mortality, the overpopulation of the origin is avoided thanks to superdiffusion between resetting events. It is important to note that, when $r = 0$, one would recover the model studied in [43] in the limit of vanishing patch density. However, in this previous work only finite patch densities were considered, and hence the results cannot be directly compared with the currents ones, in particular figures 5(a) and 6(a). However, the nonmonotonic behavior of the predator abundance with $\beta$, when $r$ is different from zero, is similar to the behavior found in figure 5 of [43], where $\beta_{opt}$ could also lie in the Lévy range. It is possible that, in a first approximation, the average distance travelled before resetting in the current model is analogous to the average between-patch distance in [43].

In the particular case corresponding to the absence of resetting ($r = 0$), predators will avoid extinction if $\beta > \beta_c$, i.e. if they are not excessively superdiffusive (figures 5(a) and 6(a)). Otherwise, the probability of returning to the origin by chance during a lifetime $(1/\mu)$ is too small, and this effect is not compensated for by the birth of new individuals within the patch. One of our main conclusions is that setting $r$ different from zero greatly improves the abundance and widens the range of values of $\beta$ allowing survival in one-patch configurations.

Conversely, if $\beta$ is held fixed in the Lévy regime, there is a critical resetting rate $r_c$ below which no population survives (figures 3 and 4). This critical value decreases as foragers become more Brownian, since they become more recurrent and need less resetting to occupy the origin and reproduce. In addition, at small enough $\mu/\lambda$, $N_p$ is nonmonotonous: there exists an optimal resetting rate that maximizes the predator abundance. This finding is reminiscent of the nonmonotonic behavior with respect to $r$ of the first passage time to a target site for a diffusing particle initially located at a given distance [35, 36, 38, 51]. In our context, too much resetting produces excessive concentration on a single patch and resource overexploitation, whereas too few resetting generates little predation and reproduction.

It is satisfying to notice that the conclusions obtained for 1D systems depend little on the spatial dimension, as shown by the 2D stochastic simulation results. We thus expect the 1D
cases to give useful insights into patch configurations that are ecologically more realistic. Future extensions of the present work should consider several prey patches randomly distributed in space, as studied in [43], and where resetting would take place in different places. The exponent $\beta$ could play a significant role in multiple-patch systems, since superdiffusion may allow the colonization of distant patches. In future work, predators could perform Lévy walks instead of Lévy flights, since this former model has been widely used in the context of animal movement and random search problems [14, 15, 52].

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