

# Intermittent random walks: transport regimes and implications on search strategies

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**Abstract.** We construct a transport model for particles that alternate rests of random duration and flights with random velocities. The model provides a balance equation for the mesoscopic particle density obtained from the continuous-time random walk framework. By assuming power laws for the distributions of waiting times and flight durations (for any velocity distribution with finite moments) we have found that the model can yield all the transport regimes ranging from subdiffusion to ballistic depending on the values of the characteristic exponents of the distributions. In addition, if the exponents satisfy a simple relationship it is shown how the competition between the tails of the distributions gives rise to a diffusive transport. Finally, we explore how the details of this intermittent transport process affect the success probability in an optimal search problem where an individual searcher looks for a target distributed (heterogeneously) in space. All the results are conveniently checked with numerical simulations.

**Keywords:** stochastic processes (theory), dynamics (theory), population dynamics (theory), diffusion

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**1. Introduction**

Transport processes are widespread and common in many fields of physics, chemistry and biology [1]. Traditionally, the Brownian motion has been considered as the underlying microscopic dynamics for transport processes. Thus, diffusion has been used to characterize most movement patterns in biological and ecological systems [2]. As is widely known, diffusive transport is characterized by a mean square displacement which increases linearly with time,  $\langle x^2(t) \rangle \sim t$ . However, there are a lot of systems that do not follow this behavior [3]–[12]. In these cases the mean square displacement is a power law with time rather than a linear dependence,  $\langle x^2(t) \rangle \sim t^\gamma$ , where  $0 \leq \gamma \leq 2$ . This regime is known as anomalous diffusion and has received much attention in recent decades. The continuous-time random walk (CTRW) framework has been used to describe anomalous diffusion from a mesoscopic level [3, 13, 14] (albeit other formalisms have also been provided in the literature to explain this behavior). In this scheme the random walkers are assumed to perform jumps of random lengths distributed according to a probability density function (PDF) frequently called the dispersal kernel. These jumps are alternated with resting phases of random duration, which are also distributed according to a function known as the waiting time PDF. Using different distributions for the jump lengths and waiting times it is possible to generate all the possible transport regimes above. However, the model has the unphysical microscopic feature that jumps are performed instantaneously. In order to overcome this problem Zaburdaev *et al* [15] presented a new model where the particles are permanently flying with random velocities. This model is also proposed within the formalism of the CTRW and it is more realistic from a microscopic point of view since there are many non-biological systems where the particles are continuously moving.

However, in many biological systems it is common to find that the individuals present an intermittent behavior, in which episodes of high activity (flights) are alternated with episodes of inactivity. Intermittent movement is widely observed in animals and in cells [16]–[18]. Theoretical studies have shown that intermittent behavior is an efficient search strategy (see below) but little attention has been paid to incorporating the intermittent movement into a mesoscopic description. In order to cover this gap, we generalize here the velocity version of the CTRW scheme (sections 3–5) to incorporate the intermittency. We point out that similar ideas have been explored recently in the context of cell migration [19] or nanoparticle movement [20], but the models in those works are far less general than the one we shall present here.

According to the ubiquity of intermittent strategies observed in animal motion patterns, there has also been recently an emerging interest in the study of optimization problems regarding intermittent search. In [21] it was shown that when the distributions of random times spent by the individual waiting at a position (*scanning phase*) and flying (*relocation stage*) are exponential, then there exists an optimal relation between the two characteristic times of the distributions, for which the mean search time to detect a randomly localized target gets minimized. Moreover, the agreement found between this relation and the foraging data recorded for different species is overwhelming [21]. At the sight of this, many extensions and modifications of the original problem were proposed; at this stage the number of papers published on this topic is too large to provide an exhaustive review here, but the reader can find in [22]–[27] some of the latest advances made. Along the lines of these works, in the present paper we address a characteristic search problem where the targets are assumed to be continuously distributed throughout the whole spatial domain (though a certain scanning time is required to detect them). While the case of homogeneous target distribution has been already explored by different authors, there is little knowledge of the results arising when targets are allocated heterogeneously according to a given density function. In [28] the authors considered the case of targets distributed according to a Poisson distribution, but introduced several assumptions to avoid the mathematical difficulties of dealing with quenched disorder. As we will try to show here, the spatial heterogeneities mean that the properties of the transport pattern followed by the individuals become essential in order to define an optimal strategy. Our main objective here (section 6) is then to explore the role that these motion patterns play on the mean search time needed to detect the target.

## 2. Previous models

Let us start by introducing the traditional and well-known CTRW framework [29]. For simplicity, consider a one-dimensional and infinite continuous medium where there is a set of non-interacting particles. Each particle performs instantaneous jumps from one position to another. Before jumping, particles must wait at their position a random time distributed according to the waiting time PDF  $\varphi(t)$ . On the other hand, the jump lengths are distributed according to the dispersal kernel  $\Phi(x)$  which is assumed symmetric. Then, we define  $J_j(x, t)$  as the density of particles arriving at the position  $x$  at time  $t$ , which is given by the mesoscopic balance equation

$$J_j(x, t) = \delta(x)\delta(t) + \int_{\mathbb{R}} \int_0^t J_j(x - x', t - t')\varphi(t')\Phi(x') dt' dx', \quad (1)$$

where the subscript  $j$  means jump and refers to the jump model. The first term on the right-hand side is the contribution from the initial condition and the second term stands for the density of particles that arrived previously at a different position at a previous time and have waited a time  $t'$  to perform a jump of length  $x'$  to reach the point  $x$ . Let us define  $\varphi^*(t) = \int_t^\infty \varphi(t') dt'$  as the survival probability, which gives us the probability that a particle has not jumped within the period  $[0, t]$ . Using this function, the density  $P_j(x, t)$  of particles at the position  $x$  at time  $t$  is given by

$$P_j(x, t) = \int_0^t J_j(x, t - t') \varphi^*(t') dt'. \quad (2)$$

Equations (1) and (2) define completely the jump model. Transforming equations (1) and (2) by Fourier–Laplace it is possible to solve for  $P_j(k, s)$ ,

$$P_j(k, s) = \frac{\varphi^*(s)}{1 - \varphi(s)\Phi(k)}, \quad (3)$$

where  $k$  and  $s$  are the corresponding arguments in the Fourier and Laplace space. Although this model has been used in several applications, it presents some unphysical features such as, for example, that the mean square displacement becomes infinite for dispersal kernels with heavy tails [30, 31]. This problem arises because the model assumes a flight time equal to zero or, in other words, an infinite jumping velocity. Although this is not realistic, it is a good approach for systems with typical waiting times larger than flight times. There are some ways to deal with this kind of problem, for example by assuming correlations between waiting times and jump lengths [31, 32]. In particular, Ziburdaev *et al* [15] have recently proposed a new model that introduces a finite flight velocity for particles. They considered that particles fly with random velocities chosen from a velocity distribution function  $h(v)$ . The flight duration is a random variable distributed according to the PDF  $\phi(t)$ . When the waiting time finishes, the particles randomly change their velocity and the process starts again. In order to express this idea they introduced the density function  $J_f(x, t)$  of particles changing their velocity at position  $x$  at the time  $t$  as

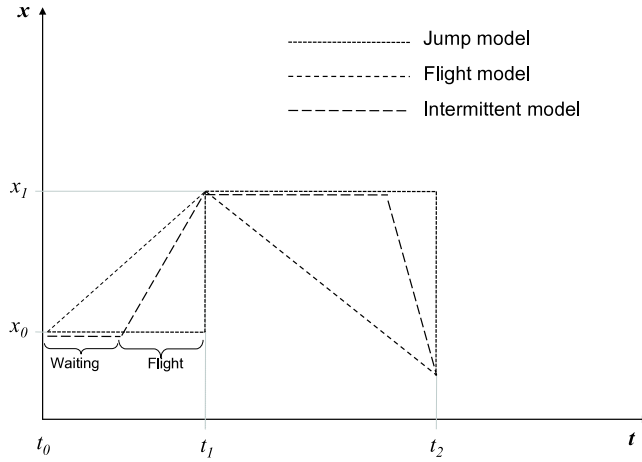
$$J_f(x, t) = \delta(x)\delta(t) + \int_{\mathbb{R}} \int_0^t J_f(x - vt', t - t') \phi(t') h(v) dt' dv, \quad (4)$$

where the subscript  $f$  refers to the flight model. In analogy with the jump model, it is possible to define the density of particles located at position  $x$  at time  $t$  as

$$P_f(x, t) = \int_{\mathbb{R}} \int_0^t J_f(x - vt', t - t') \phi^*(t') dt' dv, \quad (5)$$

where  $\phi^*(t)$  provides the probability that the velocity of a particle does not change until a flight time  $t$ ; this is defined by  $\phi^*(t) = \int_t^\infty \phi(t') dt'$ . It is possible to solve the model in Fourier–Laplace space:

$$P_f(k, s) = \frac{\mu_2(k, s)}{1 - \mu_1(k, s)}, \quad (6)$$



**Figure 1.** Schematic picture of the trajectories of a particle for the three models discussed in the text. For the intermittent model, the first waiting and flight periods are explicitly indicated to facilitate understanding.

where

$$\mu_1(k, s) = \int_0^\infty e^{-st} \int_{\mathbb{R}} e^{-ikt v} h(v) \phi(t) dv dt, \quad (7)$$

$$\mu_2(k, s) = \int_0^\infty e^{-st} \int_{\mathbb{R}} e^{-ikt v} h(v) \phi^*(t) dv dt. \quad (8)$$

Zaburdaev *et al* [15] showed that there is a connection between the flight time and velocity distributions with the dispersal kernel of the traditional (jump-based) CTRW given by

$$\Phi(x) = \int_0^\infty \int_{\mathbb{R}} \delta(x - vt) \phi(t) h(v) dv dt. \quad (9)$$

Although equation (9) tells us that there is a connection between both descriptions, the macroscopic behavior presents fundamental differences [33], which will become accentuated for heavy-tailed distributions. In the jump model, when the waiting time PDF lacks a finite first moment and the dispersal kernel has a finite second moment, the waiting time dominates the macroscopic behavior and the transport regime of the system is subdiffusive. This behavior cannot be recovered from the flight model since the particles there are always in motion. On the other hand, when the flight times of the particles are large enough, the shape of the density profile obtained from the flight model is drastically different from that obtained from the jump model due to the fact that the dynamics of the flight model is faster than that of the jump model.

### 3. The model with intermittency

We propose here a model that takes into account both waiting times between successive jumps and jumps with finite velocity (or, equivalently, flights of non-zero duration). This is the main goal of this work. In figure 1 we have drawn the trajectories of a particle for each model: the jump model, the flight model and the intermittent model. The particle

starts at  $t_0$  at  $x_0$  and reaches the point  $x_1$  at time  $t_1$  by performing an instantaneous jump after waiting a time  $t_1 - t_0$  (jump model) or traveling directly from  $x_0$  to  $x_1$  at constant velocity without waiting (flight model) or waiting first at  $x_0$  and then jumping with constant velocity to reach  $x_1$  at time  $t_1$ . In our model, each particle waits some random time distributed by the waiting time PDF  $\varphi(t)$ , and then the particle starts to fly with some random velocity distributed according to the velocity PDF  $h(v)$  during a random time distributed by the PDF  $\phi(t)$ . Let us define  $J_w(x, t)$ , the density of particles that were flying but now are waiting at position  $x$  at time  $t$ , as

$$J_w(x, t) = \delta(x)\delta(t) + \int_{\mathbb{R}} \int_0^t J_f(x - vt', t - t')h(v)\phi(t') dt' dv, \tag{10}$$

where the subscript  $w$  refers to waiting particles. In consequence, the density of particles that were waiting and start to fly at position  $x$  at time  $t$  after the waiting period of duration  $t'$  is given by

$$J_f(x, t) = \int_0^t J_w(x, t - t')\varphi(t') dt'. \tag{11}$$

Now, we can define the density of waiting particles at position  $x$  at time  $t$ , namely  $P_w(x, t)$ , and the density of particles flying at position  $x$  at time  $t$ , namely  $P_f(x, t)$ , as

$$P_w(x, t) = \int_0^t J_w(x, t - t')\varphi^*(t') dt', \tag{12}$$

$$P_f(x, t) = \int_{\mathbb{R}} \int_0^t J_f(x - vt', t - t')h(v)\phi^*(t') dt' dv, \tag{13}$$

respectively. The Fourier–Laplace transform of (10) reads

$$J_w(k, s) = 1 + J_f(k, s)\lambda_1(k, s), \tag{14}$$

where

$$\lambda_1(k, s) = \int_0^\infty e^{-st} \int_{\mathbb{R}} e^{-ikt} h(v)\phi(t) dv dt, \tag{15}$$

and the corresponding Fourier–Laplace transform of (11) is

$$J_f(k, s) = J_w(k, s)\varphi(s). \tag{16}$$

By combining equations (14) and (16) we get

$$J_w(k, s) = \frac{1}{1 - \lambda_1(k, s)\varphi(s)}, \tag{17}$$

$$J_f(k, s) = \frac{\varphi(s)}{1 - \lambda_1(k, s)\varphi(s)}. \tag{18}$$

Finally, inserting (17) and (18) into the Fourier–Laplace transforms of (12) and (13) one finds

$$P_w(k, s) = \frac{\varphi^*(s)}{1 - \lambda_1(k, s)\varphi(s)}, \tag{19}$$

$$P_f(k, s) = \frac{\lambda_2(k, s)\varphi(s)}{1 - \lambda_1(k, s)\varphi(s)}, \tag{20}$$

where

$$\lambda_2(k, s) = \int_0^\infty e^{-st} \int_{\mathbb{R}} e^{-ikt v} h(v) \phi^*(t) dv dt. \quad (21)$$

The total density of particles at position  $x$  at time  $t$ , namely  $P(x, t)$ , is the sum

$$P(k, s) = P_w(k, s) + P_f(k, s). \quad (22)$$

#### 4. Relation between models

Now we want to show that under the appropriate limits our model reduces to the flight model or to the jump model. To recover the flight model we consider  $\varphi(t) = \delta(t)$ , which means that the waiting time is zero. In this case  $\varphi(s) = 1$  and the survival probability  $\varphi^*(s) = 0$ , therefore  $P_w(k, s) = 0$  and  $P_f(k, s) = (\lambda_2(k, s))/(1 - \lambda_1(k, s))$ , which corresponds to equation (6). On the other hand, to recover the jump model we set  $\phi(t) = \delta(t)$ , which means that the flight time is zero. Introducing this into equation (20) we find  $P_f(k, s) = 0$ , since  $\phi^*(s) = 0$ . To show that equation (19) equals equation (3), we need to prove that  $\lambda_1(k, s)$  is equal to  $\Phi(k)$ . To this end we introduce the identity  $e^{-ikt v} = \int_{\mathbb{R}} e^{-ikx} \delta(x - vt) dx$  into (15) to obtain

$$\lambda_1(k, s) = \mathcal{F} \left[ \int_0^\infty e^{-st} \int_{\mathbb{R}} \delta(x - vt) h(v) \phi(t) dv dt \right], \quad (23)$$

where  $\mathcal{F}$  means the Fourier transform. Now, introducing the Taylor expansion of  $e^{-st}$  and taking into account the identity  $\delta(x - vt) = \delta(v - x/t)/t$ , equation (23) becomes

$$\lambda_1(k, s) = \Phi(k) + \mathcal{F} \left[ \sum_{n=1}^{\infty} \frac{(-s)^n}{n!} \int_0^\infty t^{n-1} h\left(\frac{x}{t}\right) \phi(t) dt \right], \quad (24)$$

where we have assumed absolute convergence of each term in the sum. The term inside the brackets is equal to zero when  $\phi(t) = \delta(t)$  for any distribution  $h(v)$  and therefore  $\lambda_1(k, s) = \Phi(k)$ .

#### 5. Mean square displacement

The transport process is commonly characterized by the asymptotic ( $t \rightarrow \infty$ ) behavior of the mean square displacement (MSD) as a function of time. This characterization is given through the exponent  $\gamma$  that rules the asymptotic MSD. When  $\langle x^2(t) \rangle \propto t^\gamma$  with  $\gamma = 1$ , the transport regime of the system under study is the standard (normal) diffusion, if  $\gamma < 1$  the transport is subdiffusive, and if  $1 < \gamma < 2$  it is superdiffusive; finally  $\gamma = 2$  corresponds to the ballistic transport. We recall that we are concerned here with unidimensional and symmetric dispersal kernels. Mathematically the MSD of a number density of particles  $P(x, t)$  is defined by

$$\langle x^2(t) \rangle = \int_{\mathbb{R}} x^2 P(x, t) dx, \quad (25)$$

which in the Fourier–Laplace space reads

$$\langle x^2(s) \rangle = -\frac{\partial^2}{\partial k^2} P(k, s)|_{k=0}. \quad (26)$$

Now, applying to equation (22), we obtain

$$\langle x^2(s) \rangle = \langle v^2 \rangle \left\{ \frac{\varphi(s)\mathcal{L}[t^2\phi^*(t)]}{1-\phi(s)\varphi(s)} + \frac{\phi^*(s)\varphi^2(s)\mathcal{L}[t^2\phi(t)]}{[1-\phi(s)\varphi(s)]^2} + \frac{\varphi^*(s)\varphi(s)\mathcal{L}[t^2\phi(t)]}{[1-\phi(s)\varphi(s)]^2} \right\}, \quad (27)$$

where  $\mathcal{L}$  means Laplace transform. We have assumed for convenience that the second moment  $\langle v^2 \rangle$  of the velocity distribution exists, since we are basically interested in how the distributions  $\phi(t)$  and  $\varphi(t)$  affect the macroscopic behavior of the system.

To calculate the MSD explicitly let us take for the waiting time distribution and the flight time distribution

$$\varphi(t) = \frac{\alpha}{(1+t)^{1+\alpha}}, \quad \phi(t) = \frac{\beta}{(1+t)^{1+\beta}}, \quad (28)$$

respectively, with  $\alpha > 0$  and  $\beta > 0$ . The values of  $\alpha$  and  $\beta$  determine the existence of finite moments. In order to calculate the MSD we need to work with the Laplace transform of the distributions (28) but, as we are interested in asymptotic properties ( $s \rightarrow 0$ ), we only keep the lowest orders of the expansion of  $\varphi(s)$  and  $\phi(s)$  in powers of  $s$  as follows:

$$\varphi(s) \sim \begin{cases} 1 - s^\alpha, & 0 < \alpha < 1, \\ 1 - s + s^\alpha, & 1 \leq \alpha < 2, \\ 1 - s + s^2, & \alpha \geq 2, \end{cases}$$

and the same holds for  $\phi(s)$  but replacing  $\alpha$  by  $\beta$ . Introducing these expansions into equation (27) and applying the inverse Laplace transform, we obtain the following results for the MSD in the limit  $s \rightarrow 0$ :

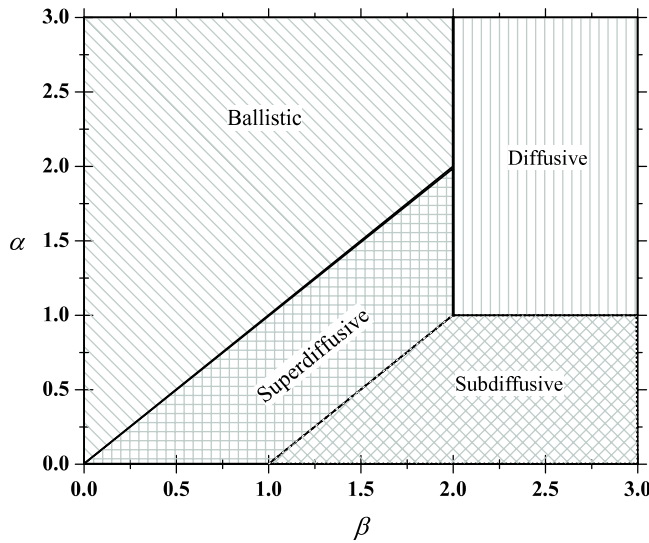
$$\langle x^2(t) \rangle \sim \begin{cases} t^2, & 0 < \beta < \alpha, \quad \alpha > 0, \\ t^{2-\beta+\alpha}, & \alpha \leq \beta < 2, \quad 0 < \alpha < 1, \\ t^{3-\beta}, & \alpha \leq \beta < 2, \quad \alpha \geq 1, \\ t^\alpha, & \beta \geq 2, \quad 0 < \alpha < 1, \\ t, & \beta \geq 2, \quad \alpha \geq 1. \end{cases} \quad (29)$$

In figure 2 we plot a diagram for the parameter space  $\alpha - \beta$  where the corresponding transport regions are specified. On the dashed line separating the regions of subdiffusion and superdiffusion it holds that  $\alpha = \beta - 1$ , and then the transport regime is diffusive. This clearly illustrates the competition between the tails of the waiting time and flight time PDFs.

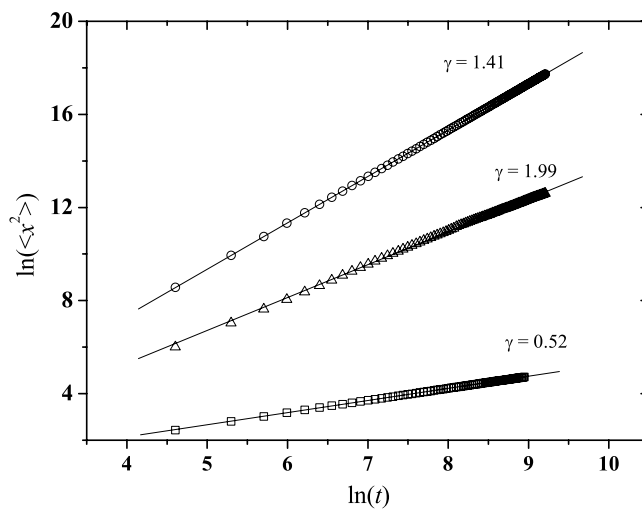
In order to prove our analytical predictions we have made Monte Carlo simulations of the random walk process, averaged over a large number of realizations. Our numerical simulations collapse perfectly with the analytical predictions as is shown in figure 3 proving not only the validity of our analytical results, but also the suitability of the model itself since we did not make explicit use of the equations above in the simulations.

As shown in (29), our model is able to reproduce all transport regimes ranging from subdiffusive to ballistic. When  $0 < \alpha \leq 1$  and  $\alpha \leq \beta < 2$  the asymptotic behavior of the





**Figure 2.** Transport regions for the possible values of the characteristic exponents  $\alpha$  and  $\beta$ . On the dotted line the transport regime is diffusive.



**Figure 3.** MSD versus time in a log–log plot. The symbols correspond to the numerical simulations and the straight lines are the linear fit. The slope provides the numerical value of the exponent  $\gamma$  of the expression  $\langle x^2(t) \rangle \sim t^\gamma$ . The theoretical prediction for the case with  $\alpha = 0.6$  and  $\beta = 1.2$  (circles) is  $\gamma = 1.4$ , for the case  $\alpha = 1$  and  $\beta = 1/2$  it is  $\gamma = 2$  (triangles) and for the case  $\alpha = 0.3$  and  $\beta = 1.8$  it is  $\gamma = 1/2$  (squares).

MSD presents a particular behavior given by  $t^{2-\beta+\alpha}$ , a proof of the competition between the tails of the PDFs  $\varphi(t)$  and  $\phi(t)$ . In some cases ( $\alpha < \beta - 1$ ) the waiting times govern the dynamics of the system and its heavy-tailed distribution induces a subdiffusive regime; in the opposite case ( $\alpha > \beta - 1$ ) the flight times dominate the dynamics of the system and superdiffusion is obtained. Interestingly, the competition between the tails is equilibrated when  $\alpha = \beta - 1$ . This competition allows us to obtain any transport regime with the

same formal shape as the distribution's shape. This feature cannot be found either in the jump model or in the flight model, where the transport regime is fully determined by the order of the largest finite moment of  $\varphi(t)$  or  $\phi(t)$ , respectively.

## 6. Implications on search strategies

Now we will explore how the details of the motion patterns considered here may affect the success of a search process. To do this we will adopt the same approach as the authors in [22]. Consider an individual performing an intermittent motion across an infinite one-dimensional domain, such as that we have implemented here. As usual in intermittent search strategies, it is considered that resting periods correspond to a scanning phase during which the searchers can perceive the target, while flights are used as a relocation phase that the searchers employ to reach a new position in order to start a new scanning phase. So, searchers are not able to detect the target during flights. The target is assumed to be distributed throughout the whole domain, so when the searcher reaches a new position  $x$  there is a probability  $\beta$  that the target can be effectively found there. In that case, the probability that the searcher has not been able to detect the target after a scanning period of duration  $\tau$  is denoted by  $p(x, \tau)$ . The function  $p(x, \tau)$ , in consequence, must be a monotonically decreasing function which satisfies  $p(x, 0) = 1$ ,  $p(x, \infty) = 0$ . Besides, the probability that the target has not been detected in a single scanning phase of duration  $\tau$  will be  $q(x, \tau) \equiv (1 - \beta) + \beta p(x, \tau)$ .

### 6.1. Homogeneous target distribution

If all the positions in the domain are considered equivalent (that is, if  $\beta$  and  $p$  are independent of space), it is possible to provide an exact expression for the mean search time; this result has been derived in several works [21, 23, 22]. We define  $S(t)$  as the overall probability that the target has not been detected by a searcher after a time  $t$ . Then the Laplace transform of this function can be written in terms of the Laplace transforms of the flight and waiting time distributions,  $\phi(t)$  and  $\varphi(t)$ , respectively [22]:

$$S(s) = \frac{\mathcal{L}[\varphi^*q] + \mathcal{L}[\varphi q]\phi^*(s)}{1 - \mathcal{L}[\varphi q]\phi(s)}. \quad (30)$$

Note that here again we use either the Laplace argument  $s$  or  $\mathcal{L}$  to denote that a function is being defined in the Laplace space.

The mean search time can be computed from the previous expression through

$$\langle T \rangle = \int_0^\infty t \frac{d}{dt} S(t) dt = \lim_{s \rightarrow 0} S(s). \quad (31)$$

This result allows us to study the success of a search strategy (in terms of minimizing  $\langle T \rangle$ ) as a function of the mean waiting and mean flight times. In general, when the target is homogeneously distributed we should expect that it is more profitable to spend most of the time in the scanning phase in order to detect the target as quickly as possible. However, it is risky to carry out too long a scanning phase since there is a finite probability  $1 - \beta$  that the target is not present, so the searcher could be wasting its time there. In consequence, it is often found from (30) and (31) that if the waiting time and flight time distributions have finite first moments, then there exists an optimum waiting (scanning) time that minimizes  $\langle T \rangle$ .

## 6.2. Heterogeneous target distribution

As far as we are concerned, there are no previous studies that have addressed the previous search problem for the case when the target is not homogeneously distributed in space. Introducing a heterogeneous target distribution poses a new dilemma to the searchers. Now they have to choose between spending a long time in the scanning phase in order to detect (sooner or later) the target, or switching to the relocation phase and wasting some time in order to reach a new position where the probability of succeeding can be higher. So, the details of the motion pattern become essential in order to determine what the optimal strategy is.

Let us assume that the searcher starts a new relocation phase at the origin at  $t = 0$ . The successive random durations of the relocation phases are denoted by  $\tau_1, \tau_3, \tau_5, \dots$  while random durations of the scanning phases read  $\tau_2, \tau_4, \tau_6, \dots$ . Moreover, we introduce the random variables  $z_1, z_2, z_3, \dots$  to specify the positions at which the successive scanning phases will take place. With all this, we can write an expression for the probability  $S_n^{(1)}(t)$  that the target has not been detected yet by the searcher when it is performing its  $n$ th scanning phase:

$$\begin{aligned}
 S_n^{(1)}(t) = & \int_{\tau_1 + \tau_2 + \dots + \tau_{2n} \leq t} d\tau_1 d\tau_2 \dots d\tau_{2n} \int_{-\infty}^{\infty} dz_1 \dots \int_{-\infty}^{\infty} dz_n \left[ \prod_{k=0}^{n-1} \phi(\tau_{2k+1}) \right] \\
 & \times \left[ \prod_{k=1}^{n-1} \varphi(\tau_{2k}) q(\tau_{2k}, z_k) \Lambda_k(z_1, \dots, z_k, \tau_1, \tau_3, \dots, \tau_{2k-1}) \right] \\
 & \times [\varphi^*(\tau_{2n}) q(\tau_{2n}, z_n) \Lambda_n(z_1, \dots, z_n, \tau_1, \tau_3, \dots, \tau_{2n-1})], \quad (32)
 \end{aligned}$$

where  $\Lambda_i$  stands for the probability that the  $i$ th scanning phase will take place at position  $z_i$  conditioned on the previous trajectory followed by the searcher, so in general  $\Lambda_i$  can depend on all the previous flight times and scanning positions. Note also in (32) that the probability  $q$  that the target is not detected during a single scanning phase is now space-dependent, in contrast with the homogeneous case above.

The main problem with expression (32) is that the probabilities  $\Lambda_i$  depend on the flight times  $\tau_1, \tau_3, \tau_5, \dots$ , which makes the analytical treatment almost impossible. So, in order to reach some exact results we will consider here a simplified situation in which flight times have fixed duration  $t_f$  (albeit they can still be performed at different speeds). This removes the explicit dependences of the functions  $\Lambda_i$  on time, so (32) will read now

$$\begin{aligned}
 S_n^{(1)}(t) = & \int_{\tau_1 + \tau_2 + \dots + \tau_{2n} \leq t} d\tau_1 d\tau_2 \dots d\tau_{2n} \int_{-\infty}^{\infty} dz_1 \dots \int_{-\infty}^{\infty} dz_n \left[ \prod_{k=0}^{n-1} \delta(\tau_{2k+1} - t_f) \right] \\
 & \times \left[ \prod_{k=1}^{n-1} \varphi(\tau_{2k}) q(\tau_{2k}, z_k) \Lambda_k(z_1, \dots, z_k) \right] [\varphi^*(\tau_{2n}) q(\tau_{2n}, z_n) \Lambda_n(z_1, \dots, z_n)]. \quad (33)
 \end{aligned}$$

Moreover, since we are basically interested in the effects of motion on the search success, we will consider for simplicity that the target can be present at any position, so  $\beta = 1$ . Then, the function  $q$  takes the decoupled form

$$q(t, x) = p(t)m(x), \quad (34)$$

where the function  $1 - m(x)$  can be interpreted as a normalized target density.

Similarly to (33), we can write the probability  $S_n^{(2)}(t)$  that the target has not been detected yet after the searcher has finished its  $n$ th scanning phase and is performing its  $(n + 1)$ th relocation phase. This will read

$$S_n^{(2)}(t) = \int_{\tau_1 + \tau_2 + \dots + \tau_{2n} + \tau_{2n+1} \leq t} d\tau_1 d\tau_2 \dots d\tau_{2n+1} \int_{-\infty}^{\infty} dz_1 \dots \int_{-\infty}^{\infty} dz_n \left[ \prod_{k=0}^{n-1} \delta(\tau_{2k+1} - t_f) \right] \times \left[ \prod_{k=1}^n \varphi(\tau_{2k}) q(\tau_{2k}, z_k) \Lambda_k(z_k) \right] [1 - H(\tau_{2n} - t_f)], \tag{35}$$

where  $H$  represents the Heaviside function.

Finally, the overall probability that the target has not been detected at time  $t$  is obtained through

$$S(t) = \sum_{n=0}^{\infty} [S_n^{(1)}(t) + S_n^{(2)}(t)]. \tag{36}$$

The Laplace transform of this probability, from (33)–(35) and using the convolution theorem, is

$$S(s) = \sum_{n=0}^{\infty} (e^{-t_f s})^n \lambda_n \left( \mathcal{L}[\varphi p]^{n-1} \mathcal{L}[\varphi^* p] + \mathcal{L}[\varphi p]^n \frac{1 - e^{-t_f s}}{s} \right), \tag{37}$$

where we have defined

$$\lambda_n \equiv \int_{-\infty}^{\infty} dz_1 \dots \int_{-\infty}^{\infty} dz_n \left[ \prod_{k=1}^n m(z_k) \Lambda_k(z_1 \dots z_k) \right]. \tag{38}$$

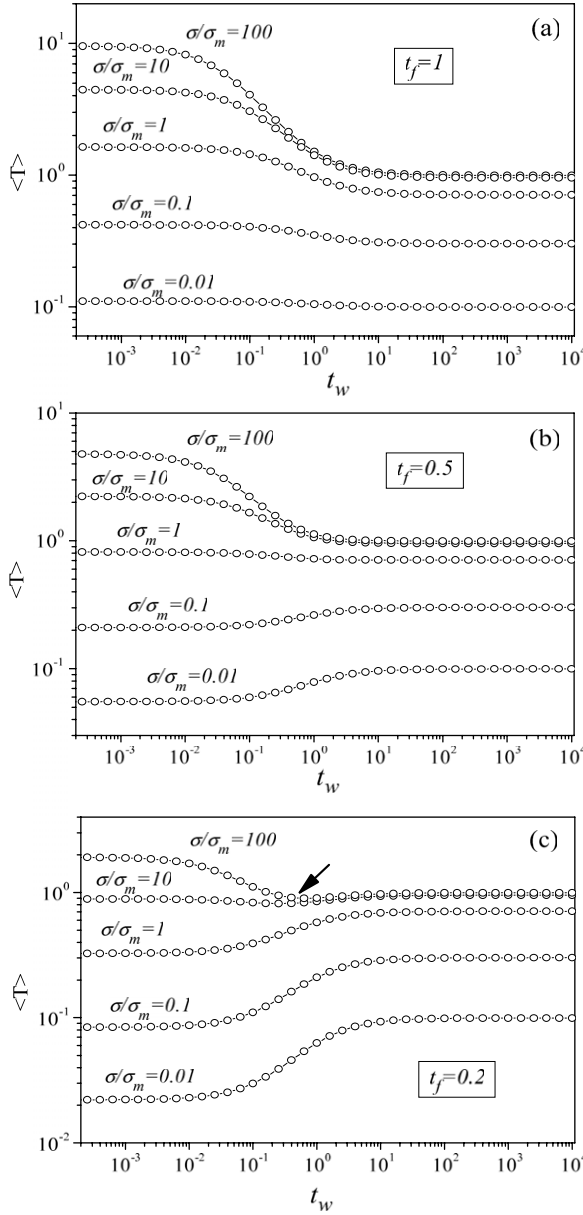
The equations (37) and (38) represent our main result, from which the mean search time  $\langle T \rangle$  can be computed through (31). Note that for  $m(x) = 1$  (which indeed leads to  $\lambda_n = 1$ ) we recover the case of homogeneous target distribution, and then (37) reduces to (30).

Unfortunately, it is not possible to find a non-trivial case for which the sum in (37) can be computed analytically. However, the rate of convergence for this sum will be rather fast, so in practice it is not difficult to determine the mean search time directly from (37). Here we will explore a simple example in which the waiting (or scanning) time distribution and the survival probability are exponential, so  $\varphi(t) = t_w^{-1} e^{-t/t_w}$ ,  $p(t) = e^{-t/t_s}$ . Moreover, we will take  $m(x) = e^{-\sigma_m x^2}$ , which means that the target is easier to detect as long as we depart from the origin; this is to ensure that initially the relocation phase will tend to increase the success probability of the searcher. Finally, we also choose a Gaussian shape for the speed distribution  $h(v) \sim e^{-\sigma_t^2 v^2}$ . This last choice leads us, from (9), to

$$\Phi(x) = \sqrt{\frac{\sigma}{\pi}} e^{-\sigma x^2} \tag{39}$$

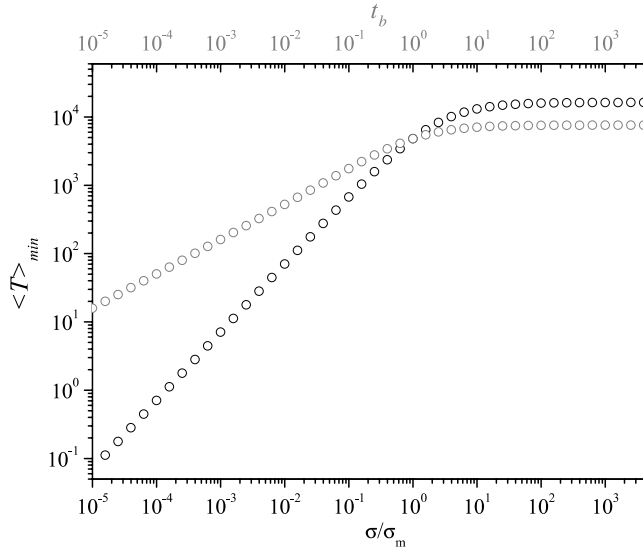
for the case of flight times with fixed duration  $\phi(t) = \delta(t - t_f)$ . From this result we can determine the functions  $\Lambda_i$  appearing in (38); these are nothing but the probabilities to relocate to position  $x_i$  provided that the previous scanning phase occurred at  $x_{i-1}$ , i.e.

$$\Lambda_i(x_1 \dots x_i) = \Phi(x_i - x_{i-1}). \tag{40}$$



**Figure 4.** Theoretical results for the mean search time from (31) and (37). The values of the parameters are shown in the legends, except for the survival time  $t_s = 1$ . Each one of the three plots tries to characterize a different regime for  $\langle T \rangle$ . (a) The mean search time is always a decreasing function of  $t_w$ , despite  $\sigma/\sigma_m$  reducing to 0. (b) The mean search time is a decreasing function of  $t_w$  for large values of  $\sigma/\sigma_m$  and an increasing function of  $t_w$  otherwise. (c) The same as in the previous case, but now an optimal mean search time arises for large values of  $\sigma/\sigma_m$  (as indicated by the arrow).

Introducing (38)–(40) into (37) we can determine the exact form of  $S(s)$ . In figure 4 we plot some results for the mean time  $\langle T \rangle = S(s = 0)$  obtained for the functions  $\varphi(t), p(t), m(x), h(t)$  chosen as mentioned above. It is seen that the shape of the speed distribution  $h(v)$  is critical to determine the behavior of  $\langle T \rangle$ . Specifically, the mean search

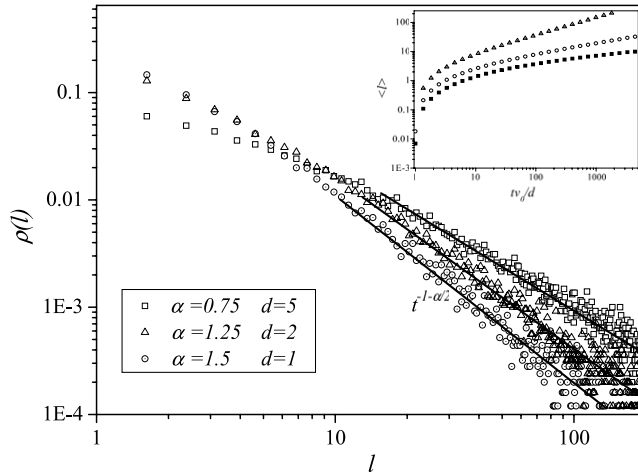


**Figure 5.** Minimum mean search time (minimized with respect to  $t_f$ ) as a function of  $t_b$  (top axis, in gray) and  $\sigma/\sigma_m$  (bottom axis, in black). The value  $t_w = 1$  has been used for the waiting time distribution in all cases.

time is found to depend on the quotient  $\sigma/\sigma_m$  in the specific case considered here, rather than on  $\sigma, \sigma_m$  separately. For low values of this quotient, the benefits from relocation are large, so the mean search time is reduced for small values of the mean scanning time  $t_w$ . This occurs unless the flight time  $t_f$  is too large and so relocation is always unproductive (as happens in figure 4(a)). On the contrary, large values of  $\sigma/\sigma_m$  mean that relocation will be almost useless and so the searcher will perform better by increasing its mean scanning time  $t_w$  (figures 4(b) and (c)). Interestingly, we find that there often exists (provided that the survival time  $t_s$  is large compared to the flight time  $t_f$ ) an optimal scanning time for which  $\langle T \rangle$  gets minimized (see arrow in figure 4(c)). All this confirms our idea above that a heterogeneous target distribution introduces a competition between the benefits of relocation and those of scanning for longer times.

### 6.3. Comparison with other search strategies

Finally, we think it could be of interest to compare the performance of our search strategies with those obtained from intermittent strategies based on Levy flights, which have attracted great interest during recent years [34]–[36]. One interesting result found recently is that search strategies based on Levy flights have been shown to be quite insensitive to some parameters such as the target density [35]; this makes these strategies more robust to external conditions. In the situation presented here it is not easy to explore the sensitivity of our model, since we do not explicitly have an optimal choice of parameters that minimizes  $\langle T \rangle$  except for some cases (see figure 4). However, we can try to study how the minimum search time  $\langle T \rangle_{min}$  (minimized with respect to the range of  $t_f$  values) depends on the target density. Intuitively, the difference between high or low densities will appear in our model by modifying the probability  $q(t, x)$ , which in turn depends on the parameters  $t_b$  and  $\sigma_m$ . The two cases are shown graphically in figure 5.



**Figure 6.** Asymptotic leapover distribution for different values of the target position  $d$  and the exponent  $\alpha$  (see legend); in all the cases  $v_0 = 1$  has been used. The solid lines represent, for each of the three cases plotted, the asymptotic scaling  $\rho(l) \sim l^{-1-\alpha/2}$  derived in [34]. Inset: average leapover as a function of the renormalized time  $tv_0/d$  for the three cases studied.

There it can be seen that the minimum search time remains constant for large values of either  $t_b$  or  $\sigma/\sigma_m$ . Both situations lead to  $q(t, x) \rightarrow 1$ , so this means that under unfavorable conditions (or, equivalently, low target densities) our search strategy is quite robust. On the contrary, when  $t_b$  and  $\sigma/\sigma_m$  are small, then  $q(t, x) \rightarrow 0$  and the minimum search time decreases monotonically.

On the other side, leapover distributions play an important role in strategies based on heavy-tailed distributions. Provided that the target is unique and it is located at position  $d$ , the leapover  $l$  is defined as the distance by which the position  $d$  is overshoot once the target passes through that point for the first time (see [34] for details). So, the leapover distribution  $\rho(l)$  serves to measure to what extent the searcher can miss the target due to long relocation events. In our case, we have used a power-law distribution for flight times, as in (28), and a delta Dirac distribution for speeds  $h(v) = 1/2[\delta(v + v_0) + \delta(v - v_0)]$ . Waiting times were taken as exponentially distributed for simplicity. With all this, the dispersal kernel reads, from (9),  $\Phi(x) \sim |x|^{-1-\alpha}$ , which allows a direct comparison with the Levy flight case studied in [34]. As expected, the asymptotic shape of the leapover distribution coincides with that found for Levy flights (since the dispersal kernel is the same in both cases) and scales as  $l^{-1-\alpha/2}$  for long values of  $l$  (figure 6). This result was derived analytically in [34] and it implies that dispersal kernels with finite mean can lead to leapover distributions whose first moments diverge. Note that the values of the parameters shown in figure 6 are the same as those used in figure 3 of [34] to facilitate comparison. There is, however, an important difference between our results and those for the Levy flight case: since larger leapovers require now larger times to be completed (due to the finite speed of particles in our model) then the average leapover will grow monotonically with time. This is shown in the inset of figure 6. Besides, if the leapover distribution does not have a finite mean (as happens for  $\alpha \leq 2$ ) then the average leapover will grow indefinitely.

## 7. Conclusions

We have presented a transport model where the particles have an intermittent behavior between random waiting phases alternated with flights of finite random velocities. Dividing the total population into two subpopulations (flying and waiting particles) we have obtained balance equations for the mesoscopic densities of particles within the framework of the CTRW.

We have found an analytical solution in the Fourier–Laplace space and have shown the conditions under which our model is reduced to the jump model and the flying model. From this, we have calculated the MSD, which shows that our model is able to reproduce all the transport regimes ranging from subdiffusion to ballistic. This is done by assuming PDFs of waiting times and flight durations as power laws. The explicit competition between the tails of both PDFs is highlighted when (for a specific relationship between the exponents) the transport becomes diffusive. Our results have been checked with numerical simulations of the stochastic process, exhibiting a perfect agreement.

Note that extensions of our results to two or three dimensions are possible, but this would require the introduction of additional assumptions regarding the reorientation process of individuals (i.e. how the direction of motion changes from one flight to the next). Actually, we have studied recently a particular case of the model in 2D [19]. Also, we could relax the assumption made here that dispersal kernels are symmetric. It is interesting to note that, if asymmetries are introduced in the speed distribution  $h(v)$ , our results for the MSD regimes (summarized in figure 2) would not change, since the MSD only depends on  $h(v)$  through  $\langle v^2 \rangle$ , as seen in equation (27). On the other hand, asymmetries in the distributions of flight times or waiting times will necessarily lead to explicit dependences of these distributions in space. That case, which is out of the scope of the present work, would not allow us to reach an analytical expression for  $\langle x^2 \rangle$  except for some trivial cases.

Finally, we have shown how the details of the transport process considered here can affect the mean search time for an intermittent searcher looking for a heterogeneously distributed target. In agreement with intuitive understanding, we find that fast and efficient transport is preferred if this can take one to new locations with a higher target density, while transport should be suppressed to optimize the mean search time if the benefits from relocation are low. We stress that while search problems on homogeneous media have become better and better understood in recent years due to the effort of many researchers, ours represents one of the first attempts to analyze search problems on a heterogeneous domain. We claim that this may be an extremely attractive topic to explore in forthcoming years due to the broad importance that spatial problems have in ecology and biology.

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