A random walk model to study the cycles emerging from the exploration-exploitation trade-off

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We present a model for a random walk with memory, phenomenologically inspired in a biological system. The walker has the capacity to remember the time of the last visit to each site and the step taken from there. This memory affects the behavior of the walker each time it reaches an already visited site modulating the probability of repeating previous moves. This probability increases with the time elapsed from the last visit. A biological analog of the walker is a frugivore, with the lattice sites representing plants. The memory effect can be associated with the time needed by plants to recover its fruit load. We propose two different strategies, conservative and explorative, as well as intermediate cases, leading to non intuitive interesting results, such as the emergence of cycles.

I. INTRODUCTION

The movement of animals in search for food, refugia or other resources is nowadays the subject of active research trying to unveil the mechanisms that give rise to a wide family of related complex patterns. In particular, physicists find in these a fruitful field to explore reaction-diffusion mechanisms [1, 2], to apply the formalism of stochastic differential equations [3–5] and to perform simulations based on random walks [6–9].

One of the key aspects of this phenomenon is the fed back interaction between the individual and the environment [10]. These interactions may involve intra and inter specific competition that, together with previous experience [11, 12] and the search for resources, drive the displacement of the individuals. In particular, when animals move around in order to collect food from patches of renewable resources, their trajectories depend strongly on the spatial arrangement of such patches [13]. This observation has motivated a large collection of studies focused on finding optimal search strategies under different assumptions of animal perception and memory [14, 15]. A related open question is that of the origin of home ranges, a concept introduced in [16] to characterize the spatial extent of the displacements of an animal during its daily activities. Many species perform bounded explorations around their refugia, even though the available space and resources extend far beyond. There are several hypotheses that try to explain this phenomenon, which could be only an emergent behavior associated to very simple causes [17]. The review by Börger et al. [9] is an exhaustive compilation of the state of the art. There, the authors point out that movement models not always lead to the formation of stationary home ranges. Still, home ranges arise, for example, in biased diffusion [3], in self-attracting walks [18] and in models with memory [19]. Nevertheless, the quest to unveil and characterize the underlying weave of causes and effects behind the emergent patterns is not over. How do these emerge as the result of the interaction between the behavior of an organism and the spatial structure of the environment?

In this context, the venerable symmetrical random walk has been the subject of many studies, with a large collection of applications and characterizations that include aspects beyond the simple walker capable of only uncorrelated short-range steps. Just to focus on what we want to present here, let us restrict the examples to random walks on discrete lattices where the walker can gather information to build up a history. One such case is the self avoiding walk (SAW), where the walker builds up its trajectory by avoiding to step onto an already visited site [20, 21]. A characteristic result corresponds to the walker running into a site with all its neighboring sites already visited and being blocked. The converse case occurs when the walker prefers sites visited earlier.

Previous works have shown that introducing long-range correlations into a random walk may lead to non trivial effects translated into drastic changes in the asymptotic behavior. The usual diffusive dynamics can evolve into sub-diffusive, super-diffusive or persistent. Such random walks with long-range memory have been extensively studied in recent years [19, 22–28].

In [29–31] a behavior that can be interpreted as memory has been explored. These works analyze a self attracting walk where the walker jumps to the nearest neighbor according to a probability that increases when the site has already been visited. A generalization that includes an enhancement of this memory with the frequency of visits, but also with a degradation with time, was proposed in [18].

In this work we propose a random walk with a specific memory that induces local correlations at long times. The rationale for this model is to mimic the movement of a foraging animal, e.g. a frugivore, going from one plant to another in order to feed. We show that the emergence of looped walks, that can be associated with home ranges, can be promoted by very rudimentary capacities of the individual together with a natural dynamics of the environment.

II. THE MODEL

For a forager the proximity of a plant is not enough to make it attractive for a future visit: the plant must also have a visible and interesting load of fruit. Moreover, when visiting a plant the animal usually takes only part of the available fruit and moves on. After this, the plant needs some time to recover its fruit load. Such a model was analyzed in [17]. We attempt here a further simplification, coding the complex interaction of memory, consumption and relaxation in the probabilities defining the random walk from each site of the lattice.

As a first simplification, consider that the animal eats all the available ripe fruit in the visited plant and leaves. Let us say that a walker moving in such a substrate has a memory, allowing it to remember the time of visit to every site and the step taken from there. When revisiting a fruitful plant the animal will consider it a success and repeat the step taken from there, "remembering" its previous visit. When returning to a plant before its recovery the walker takes a random step. This unlimited memory is not necessary associated to an extraordinary skill of the forager. It could be stored in the environment as the state of each plant, which proximity and fruit load can trigger on the forager the inclination to choose a specific direction. Thus, the memory of having visited a site once, needs not to be stored on the animal but recorded on the topology of the environment (as is the case in [17]). Also, we can anticipate here that when a home range emerges the walker effectively uses a bounded amount of memory.

Besides this, imagine two possible strategies for the *update* of the memory, the details of which will be given below. A *conservative* walker will keep in memory the time in which the visit to that site was successful and the step taken on that occasion. An *exploring* walker, instead, will update the memory of the visit to the current time and the step to the randomly chosen one. Between these two strategies there might be intermediate ones, all of which will be explored below.

Now, with the motivation just exposed, let us define a random walk that modifies the probabilities of steps from each site according to the time since the last visit and a parameter defining the strategy. The rules of the walk can be summarized as follows:

- When visiting a new site, take a random step in either of the four directions. Store in memory the time of visit t_v and the step.

- When returning at time t to a site previously visited at time t_v:

  - With probability $p_r(t - t_v)$ repeat the step stored in memory. Update the visit time stored in memory.

  Or:

  - With probability $1 - p_r(t - t_v)$ take a random step and:

    * With probability ρ, update in memory the time of visit and the step taken.

  Or:

    * With probability $1 - \rho$, keep the memory unmodified.

The probability distribution used to repeat the step taken in the previous visit is used to model the replenishment of the fruit mentioned above. It can be simply a Heaviside step function $p_r(t - t_v) = \theta(t - t_v - \tau)$, where τ is a parameter representing the recovery time of the plants. It is equivalent to the memory of the *elephant walk* [19], but used in a different way. Contrary to the usual memory that makes the probability of revisiting a site fade out with time, here we are considering a probability of revisiting a site that increases with time. In such a case the walker will always repeat its step when returning after τ steps, and always take a random step when returning earlier. This strict condition can be relaxed by modeling p_r with a smooth step function. In the results shown below only the Heaviside step distribution will be used, since, as we will show later, no significant differences where found when using a smooth distribution. In such a case, the walks are characterized by two parameters, τ and ρ.

Our results show the emergence of closed circuits in non trivial ways. To characterize the behavior of these we analyze both the duration of the transient elapsed until the walker enters the closed circuit, as well as the length of such cycles.

The emergence of such circuits is reflected in the fact that during the initial stages the mean square displacement exhibits a diffusive behavior whereas for longer times it reaches a plateau. Such a behavior has been already reported in previous works [23, 24] where due to a fed back coupling between a particle and its environment, it gains experiences with modified surroundings, resulting in a bounded walk.

III. RESULTS

The results presented below correspond to mean values taken over 10^3-10^4 realizations, on a 2 dimensional lattice, large enough to avoid that the walker reaches the borders. The simulations were done for 10^5 and 10^6 time steps, showing no significant dependence between them.

One of most revealing features of any sort of walk, be this random, self avoiding, self attracting, etc. is its mean square displacement (MSD). The behavior of the MSD in the present model shows rather interesting features. Figure 1 displays the MSD as a function of time for a range of values of ρ, from 0 to 1, and for $\tau = 20$. Recalling that ρ is the probability that the walker updates the information, stored in its memory, regarding the time of visit to a site and the step taken from there, we associate $\rho = 1$ with the *exploring* behavior and $\rho = 0$ with the *conservative* one. We observe that for $\rho = 0$ the behavior is clearly diffusive, while for $\rho = 1$ the MSD reaches
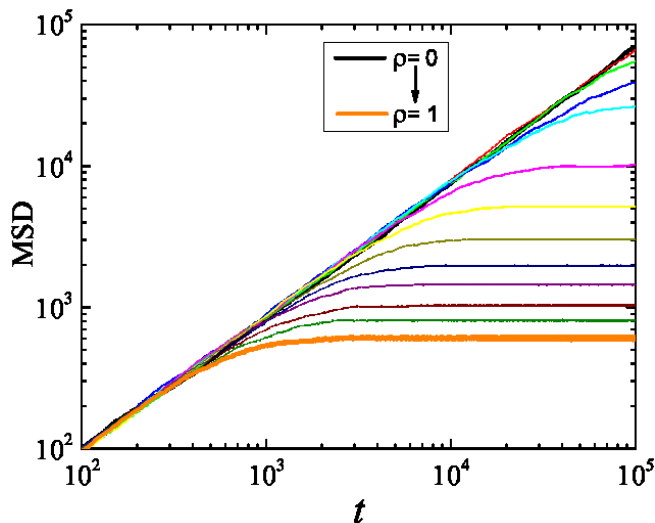
FIG. 1: Mean square displacement vs. time for probability $\rho = 0$ (black), $\rho = 1$ (orange) and intermediate values, and corresponding to recovery time of the plants $\tau = 20$. Simulations performed in a square lattice of 5000×5000 sites, 10^5 time steps and 10^3 realizations. (Color on line.)

FIG. 2: Contour plot of the fraction of realizations that end in a cycle, as a function of parameters ρ and τ. Simulations performed in a square lattice of 5000×5000 sites, 10^5 time steps and 10^4 realizations. The gray region corresponds to realizations that do not end in cycles due to finite observation time.

a plateau indicating that the walker remains trapped in a bounded region. Contrary to the intuitive guess, this shows that it is the exploring behavior the one which allows the walker to find closed circuits more easily, while the conservative behavior leads to a diffusive walk. Intermediate values of ρ generate intermediate behaviors. We have analyzed the model for values of τ ranging from 5 to 150, finding analogous results for all of them.

These results rise several questions about the dependence of the the emergence of cycles on each parameter. Even though all two-dimensional walks (including the case $\rho = 0$) eventually return to a site in a condition that allows the settling of a cycle, the time necessary to fulfill this condition can vary greatly. As a result of this, after a fixed number of steps only a fraction of the walkers are able to do so. In the following we proceed to characterize the statistical behavior of these walkers by measuring several relevant quantities.

Figure 2 shows a contour diagram representing the fraction of realizations that end in a cycle, as a function of the parameters ρ and τ. We observe that this fraction increases both for decreasing τ as well as for increasing ρ. Consistently, mapping this situation to the biological scenario, when plants take too long to recover (large τ), or when the foragers are not exploring enough (too small ρ), there is no formation of home ranges.

Another informative aspect of the walks that needs characterization is the length of the cycles. The concept of a home range is always associated to the measurement of the amount of space utilized. Sometimes it is measured through the utilization distribution [32], that represents the probability of finding an animal in a defined area within its home range. In this case, once the cycle is
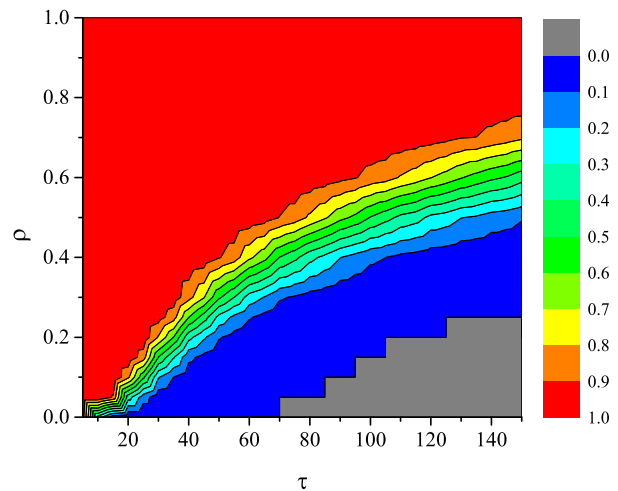
established, the animal will visit each site within the cycle only once at each turn, so the utilization distribution will be uniformly distributed among the sites within the cycle. Still we can have an estimation of the amount of used spaced by measuring the longitude of the cycle. A priori we know that τ is the greatest lower bound (infimum) for the average cycle length. This average is shown in Fig. 3. We can conclude that the mean length of the cycles is very close to this bound for all parameters sets, showing a very weak dependence on ρ for the largest values of τ, undoubtedly due to the undersampling arising from the finite simulation runs. Observe, nevertheless, the wedge shaped region of very conservative walkers that never find a cycle, which grows with the recovering parameter τ.

Let us now focus on the extreme cases of $\rho = 0$ and $\rho = 1$. When $\rho = 0$ we found that the behavior is diffusive for all values of τ, so that $\langle x^2 \rangle = D(\tau)\,t$. As shown in Fig. 5, $D(\tau)$ depends on τ approaching 1 from below as τ increases. On the other hand, perfect explorers—those with $\rho = 1$—always find a cycle. We have found that the average length of the transient depends quadratically on τ.

The transient regime is longer as the value of τ is larger, i.e., for short recovery times, the walker finds a cycle easier (and faster). If τ is very large, it may happen that the walker returns successive times to the same site earlier than τ, and randomly choose the next step, losing the possibility of repeating the last steps and thus entering a cycle.

Observe that the exploring walker is the one that continuously updates the stored information. An intuitive guess of the resulting dynamics, analyzed in terms of the intensity of exploring activity of the individual, may lead us to think that such walker would have a higher difficulty
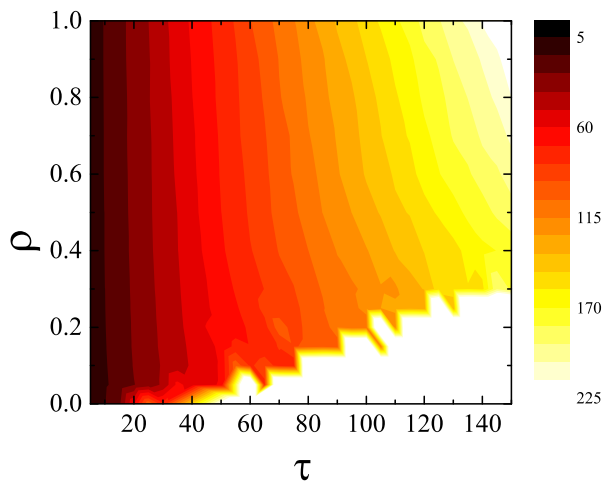
FIG. 3: Contour plot of the mean cycle length as a function of ρ and τ. Simulations performed in a square lattice of 5000×5000 sites, 10^5 time steps and 10^4 realizations.
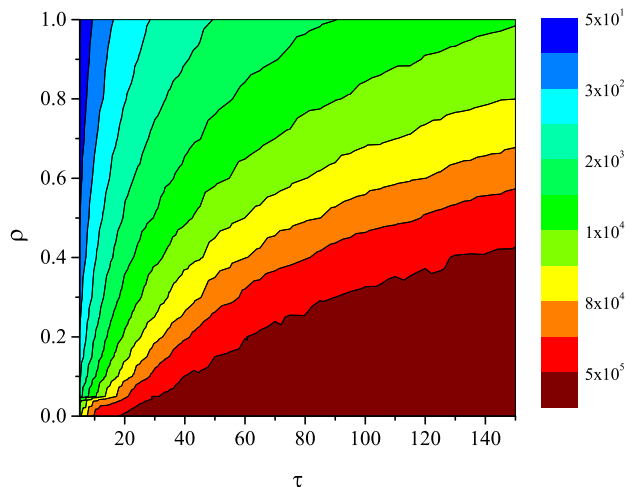

FIG. 4: Contour plot of the mean transient length as a function of parameters ρ and τ. The color scale is logarithmic. Simulations performed in a square lattice of $10^4 \times 10^4$ sites, 10^6 time steps.

in establishing a walking pattern and finding a closed circuit. Also, for those who maintain the stored information (the conservative walkers), finding an optimal closed circuit would be a relatively simple task. However, our results show that this intuition is wrong.

Relevant insight on the mechanisms that give rise to the observed behavior of the forager walk can be obtained from well known results of conventional random walks. A random walk in one and two dimensions is recurrent, i.e. the probability that the walker eventually returns to the starting site is 1. (In higher dimensions, the random walk is transient, the former probability being less than 1 [33].) So, in principle, for any value of τ and $\rho = 0$ the forager walk eventually ends up in a cycle. However, this
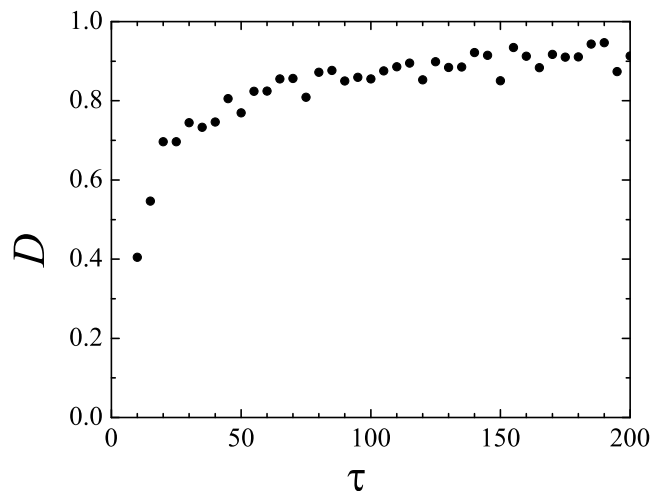

FIG. 5: Diffusion coefficient of the $\rho = 0$ case (slope of the average MSD curves for each value of τ). Forty uniformly distributed values of τ were considered between 5 and 200.

asymptotic behavior of the system may not be the most relevant one in many contexts. In the biological scenario, for example, one would be interested in the possibility of finding cycles in relatively short times.

Our results can be explained by considering the so called *Pólya problem* or first return time. The probability that a simple random walk in one dimension returns for the first time to a given site after $2n$ steps is

$$\binom{2n}{n} \frac{1}{(2n-1)2^{2n}}. \tag{1}$$

In two dimensions the probability that a simple random walk returns to a given site after $2n$ steps is the square of the previous probability [33] as a simple random in two dimensions can be projected into two independent one-dimensional walks on the x and y axes. The probability given by Eq. (1) asymptotically decays as $n^{-3/2}$, indicating that returning to the initial site is increasingly improbable with the elapsed time. The forager walk can be interpreted in the following way. Until the moment that the walker gets trapped in a cycle, it performs a random walk. Afterwards, the behavior is deterministic. That very moment corresponds to the first time a cycle is completed, so it is a return to the initial step of the cycle after $\tau_c \geq \tau$ time steps, where τ_c is the period of the cycle of an individual realization for a given choice of τ. Let us assume that the transient walk executed up to this first return can be used to estimate a probability analogous to Eq. (1). We can do this from the length of the transient and the fraction of realizations that successfully ended in a cycle. The transient can be thought of as consisting of successive realizations of walks of length τ_c that were *not* successful in returning to the starting point. We have verified this algebraic dependence.

The immediate question about the validity of the present results for higher dimensions can be answered by

invoking the recurrence theorem presented by G. Pólya in 1921 [34], where he. shows that a random walk is recurrent in 1 and 2-dimensional lattices, and that it is transient for lattices with more than 2 dimensions. The emergence of home ranges as presented in this work is strongly dependent of the probability of eventual returns to already visited places. Thus, for dimensions higher than 2 the expected cycle lengths will be longer and their very existence less probable, as can be deduced from the calculated probabilities of returns to the origin in these cases [35].

Besides, the fact that increasing ρ produces an increase in the probability of finding a cycle can be understood in the following way. The probability of returning to a given site decreases as the walker moves away. When ρ is small the walker can move increasingly farther away from the stored site, making it rather difficult to return to it and enter a cycle. When ρ is high the foraging walker constantly updates its memory, in a way that it is always relatively close to the most recently stored site. This increases the probability of returning to it and triggering a cycle.

For completeness, we include a plot showing results based on the use of a smoother distribution. The smooth step depends on two parameters, τ and w. The limit $w \to \infty$ tends to a Heaviside step function at $t = \tau$. Figure 6 displays the behavior of the walk for three values of ω (10, 2 and 0.5), exemplifying the typical behaviors for a fixed value of $\tau = 20$. The MSD's are averages over 1000 realizations. The black curves correspond to $\omega = 10$, which is very similar to a step, and gives an MSD almost identical to the one shown in Fig. 1, with $\rho = 1$ (orange curve). While smoother curves tend to plateaus at higher values no qualitatively differences are observed in the behavior.

IV. CONCLUSIONS

One of the important aspect related to animal movement is the effect that spatial heterogeneities have on the observed patterns. When the spatial heterogeneity is manifested through the distribution of resources, the link between resource dynamics and random walk models might be the key to answer many of open questions about the emergence of home ranges. Another route to explore this problem is by accounting for learning abilities and spatial memory [37].

The formation of a home range has previously been investigated with models in which a single individual displays both an avoidance response to recently visited sites and an attractive response toward places that have been visited sometime in the past [15, 38]. An animal searching for food would choose its movements based not only on its internal state and the instantaneous perception of the environment, but also on acquired knowledge and experience. Animals use their memory to infer the current state of areas not previously visited. This memory
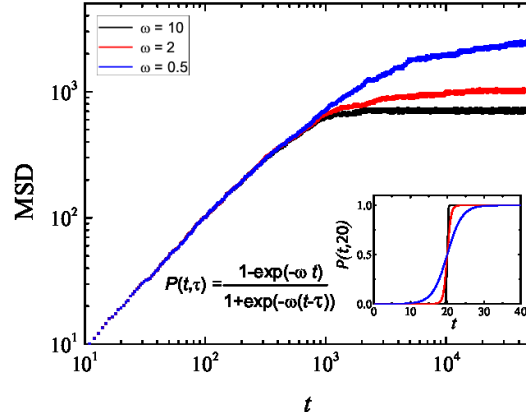

FIG. 6: Mean square displacement vs. time considering a smooth function for the probability to repeat the step taken in the previous visit. $\omega = 10$ (black), $\omega = 2$ (red), $\omega = 0.5$ (blue) and $\tau = 20$ (color on line). Simulations performed in a square lattice of 5000×5000 sites, 10^5 time steps and 10^3 realizations. The inset shows the functional expression and shape of the probability distribution.

is build up by collecting information remembered from previous visits to neighboring locations [39].

Although the emergence of home ranges is crucial in understanding the patterns arising from animal movement, there are few mechanistic models that reproduce this phenomenon. Traditional random walks, widely used to describe animal movement, show a diffusive behavior far from displaying a bounded home range. However, the addition of memory capacity has proven to predict bounded walks [19, 23, 24]. Home ranges also arise in biased diffusion [3] and in self-attracting walks [18]. The interest aspect of the results presented here is that they not only reveal the non trivial behavior of the so called *frugivore walk* but also contribute to a deeper understanding of the causes underlying the constitution of home ranges as an emergent phenomenon, among which we highlight the foraging strategy. By considering a minimal model we have shown that a walker with rudimentary learning abilities, together with the feedback from a dynamic substrate, give rise to an optimal foraging activity in terms of the usage of the spatial resource. Indeed, neither a foraging strategy based just on diffusion (a random walk without memory), nor a walk strongly determined by memory (like our conservative walker), are optimal. A better strategy is one that combines the use of memory with an exploratory behavior, such as our *explorative* walker.

There is evidence supporting that precisely this combined strategy may be the one favored by evolutionary mechanisms [40, 41]. Foraging activity must balance between exploration and exploitation: on the one hand, exploring the environment is crucial to find and learn about the distributed resources; on the other hand, exploitation of known resources is energetically optimal. Indeed, this

trade-off is a central thesis in current studies of foraging ecology, as it is apparent in the thorough work by W. Bell [42], in Lévy flight models [6] and others. The simple mechanism analyzed here contributes with theoretical support to these ideas. We have shown that the balance between exploration and exploitation not only provides an optimal use of resources. It may also be responsible for the emergence of a home range. The balance between exploration and exploitation appears as the road to successful foraging.

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