The influence of turning angles on the success of non-oriented animal searches

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Abstract

Animal searches cover a full range of possibilities from highly deterministic to apparently completely random behaviors. However, even those stochastic components of animal movement can be adaptive, since not all random distributions lead to similar success in finding targets. Here we address the general problem of optimizing encounter rates in non-deterministic, non-oriented searches, both in homogeneous and patchy target landscapes. Specifically, we investigate how two different features related to turning angle distributions influence encounter success: (i) the shape (relative kurtosis) of the angular distribution and (ii) the correlations between successive relative orientations (directional memory). Such influence is analyzed in correlated random walk models using a proper choice of representative turning angle distributions of the recently proposed Jones and Pewsey class. We consider the cases of distributions with nearly the same shape but considerably distinct correlation lengths, and distributions with same correlation but with contrasting relative kurtosis. In homogeneous landscapes, we find that the correlation length has a large influence in the search efficiency. Moreover, similar search efficiencies can be reached by means of distinctly shaped turning angle distributions, provided that the resulting correlation length is the same. In contrast, in patchy landscapes the particular shape of the distribution also becomes relevant for the search efficiency, specially at high target densities. Excessively sharp distributions generate very inefficient searches in landscapes where local target density fluctuations are large. These results are of evolutionary interest. On the one hand, it is shown that equally successful directional memory can arise from contrasting turning behaviors, therefore increasing the likelihood of robust adaptive stochastic behavior. On the other hand, when target landscape is patchy, adequate tumbling may help to explore better local scale heterogeneities, being some details of the shape of the distribution also potentially adaptive.

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1. Introduction

Much of the research in the study of animal movement considers turning angle distributions to be by-products of complex behavioral processes related to orientation mechanisms (Bovet and Benhamou, 1988; Turchin, 1991; Morales et al., 2004; Benhamou, 2006). This is presumably the case when relevant background information drives the movement, such as in oriented searches that use cognitive memory or environmental feed-backs (e.g., taxis, kinesis). As a consequence, the emerging path shows a preferential direction towards the information source, even if a stochastic component is also present (e.g., environmental noise, perceptual errors). Alternatively, when information about targets is poor or lacking, animal movement may be guided only by the “aim” or the “need” of finding a generic target (e.g., mate, resource), without prominent cues orienting the movement.
A way to distinguish between oriented and non-oriented searching is to analyze the spatial structure of the resulting trajectories (Bovet and Benhamou, 1988). For instance, some statistical analysis on angular distributions can: (i) determine whether or not an orientation component exists (Benhamou and Bovet, 1992; Benhamou, 2004, 2006), (ii) estimate quantitatively such component (Coddington and Hill, 2005), and (iii) characterize the orientation component as local or global (Benhamou, 2006).

When performing non-oriented searches, animals face basic behavioral trade-offs at the landscape level. Solving these trade-offs may involve the combination of basic “rules of thumb”, such as modifying the speed of movement according to energetic reserves and risk of predation (Zollner and Lima, 2005) while keeping efficient rules to find the targets. These search rules can be either systematic (Conradt et al., 2003) or stochastic (Bartumeus et al., 2005; Heinz and Strand, 2006). In the latter case, the assumption is that, if global orientation mechanisms cannot be used, yet animals can still improve the chances of locating targets by relying on some statistical properties derived from their motility patterns (Viswanathan et al., 1999; Bartumeus et al., 2002a, b; Raposo et al., 2003; Santos et al., 2004; Bartumeus et al., 2005). In fact, it has been conjectured that the stochastic components of animal movement could be adaptive (Bartumeus, 2007), but a detailed description of the underlying mechanisms remains the subject of ongoing investigations (Viswanathan et al., 1999; Bartumeus et al., 2005; Schimansky-Geier et al., 2004; Visser and Kiorboe, 2006).

Recently, several authors (Komin et al., 2004; Schimansky-Geier et al., 2004; Visser and Kiorboe, 2006) have suggested that the motility behavior of some planktonic species could allow individuals to adjust particular statistical properties of turning angle distributions to different environmental conditions. Specifically, the zig-zag motion of *Daphnia* has been suggested as an optimal strategy for patch exploitation (Komin et al., 2004; Schimansky-Geier et al., 2004). These results suggest that, when exploring patchy resources, animals could adjust turning angle distributions, selecting a preferred turning angle value, which may depend on the size of the patch. Such a mechanism would allow organisms to stay within the patch for a proper (i.e. ideal or optimal) amount of time, maximizing the energetic gain.

In the present work, we address the problem of locating targets in low information-availability/detection-power scenarios. Our aim is to uncover the specific properties through which turning angle distributions can impact on the search efficiency of non-oriented movement. To that aim, we use correlated random walk (CRWs) models assuming a very general family of turning angle distributions, the Jones–Pewsey probability distribution function, which embraces as particular cases some distributions commonly considered in animal search studies (e.g. von Mises (vM), wrapped Cauchy (WCD)). We focus our attention on those particular cases where the search process is not oriented by any prominent environmental cue, and the efficiency in locating the targets is basically determined by the combination of some statistical features of turning angle distributions with some landscape characteristics, such as target density and structure (i.e., homogeneous and patchy landscapes). Specifically, we study how two stochastic traits of turning angle distributions: (i) angular correlations (i.e. directional memory) and (ii) the shape of the distribution, enhance random encounter success in different environments. Finally, we make some considerations on whether evolutionary mechanisms could eventually frame the stochastic aspects of CRWs.

2. A generalized CRW model

CRW models have been successfully used to explore the biological mechanisms of movement in very different ecological contexts (e.g. Kareiva and Shigesada, 1983; Bovet and Benhamou, 1988; Crist et al., 1992; Hill and Hader, 1997; Codling et al., 2004).

The key statistical properties of CRWs arise from a peaked (usually around zero) probability distribution of turning angles, i.e., the relative angles between two successive step vectors. The smaller turning angles are more probable than the larger ones, thus introducing a certain degree of directional memory (i.e., persistence) in the walk (Turchin, 1998). In this class of random walks, the move steps are assumed either to have a fixed length or a Gaussian-like variation, therefore, a characteristic scale for the move lengths always exists. At the macroscopic level, the directional memory (and not the move lengths) controls the spreading rate of the walker, and can have impact on the search efficiency (Bartumeus et al., 2005). For long enough time \( t \), the mean square displacement (msd), a statistical quantity measuring the spreading process, goes as \( t^\alpha \) where the exponent \( \alpha \) characterizes the diffusion process (Berg, 1983; Okubo and Levin, 2002). For the usual case of Brownian motion, whose step increments have finite variance and no correlations, the central limit theorem guarantees \( \alpha = 1 \), i.e., normal diffusion. On the other hand, super(sub)-diffusion corresponds to \( \alpha < 1 \) \((> 1)\). Since CRWs are Markovian in nature (Johnson et al., 1992a), at sufficiently large scales normal diffusion (i.e., Brownian motion) always emerges. However, due to the existence of some directional memory or motion inertia, CRWs can actually maintain super-diffusive properties in a restricted range of spatiotemporal scales, i.e., for \( t \)'s shorter than a determined correlation (time) length \( \tau \), which provides a measure of the directional memory of the walk (Viswanathan et al., 2005) (see also Appendix A).

The novelty of the CRW models considered here is that the turning angles are chosen from a new and generalized circular probability distribution, hereafter called JP distribution. Jones and Pewsey (2005) proposed a whole family of circular symmetric unimodal distributions that generalize some commonly used circular probability density functions (PDFs). Their expression reads \( (\kappa \geq 0 \text{ and } \kappa \in \mathbb{R}^+) \).
We consider four situations. Two of them are CRWs with angular distributions that are very similar in shape (i.e., width) but have different mean cosine angles $\rho$ and hence distinct degrees of correlation $\tau$ (Fig. 1a). The other two are CRWs with the same $\rho$, but considerably distinct shapes for the angular distributions (Fig. 1c). From here onwards, we respectively identify these four cases as: $\rho = 0.97$, $0.86$, $0.94$ and $0.96$. The specific parameters leading to them are listed in Table 1. We notice that the choice $\rho > 0.8$ agrees with empirically observed values (Zollner and Lima, 1999), and it is also closely related to theoretical predictions of optimal inter-patch movements (Zollner and Lima, 1999; Bartumeus et al., 2005).

We perform two sets of simulations. The first is aimed to identify statistical properties related to: (a) the msd; and (b) the first passage time or net-to-gross displacement ratio (NGDR). The second set investigates: (c) the search efficiencies (average and variation) in both homogeneous and extremely patchy landscapes.

The msd is a traditional metric of random walk theory. Its variation with time characterizes the type of diffusion (Berg, 1983; Shlesinger et al., 1995; Okubo and Levin, 2002). The msd is defined as the square of the Euclidean distance between the starting location and the position at a given time, averaged over many different random walks. In the corresponding simulations, we compute the msd as a function of time for 500 different correlated random walkers moving in a two-dimensional arena (i.e., in this case there is no searching). The msd is the adequate measure to study changes in the diffusive properties through time, one of the interests in the present work. In spite of this, it is worth to point out that when the real scales of the spreading process are of interest, the mean net displacements (e.g., meters per day) are a more biologically intuitive metric than the msd (square meters per day) (McCulloch and Cain, 1989; Crist et al., 1992).

The NGDR is computed as the ratio of the shortest linear distance between the start and ending points of a trajectory and the total path length. Of note is the fact that the NGDRs values depend on the time spent observing the trajectory and the linear distance considered. In general, for an observation time going to infinity, the NGDR has a value of 100% when paths are completely straight (i.e., ballistic motion) and a minimum of zero when paths are totally circular. In this sense, the NGDR may also be regarded as an indicator (but not a full measure, see, Bovet and Benhamou, 1988; Benhamou, 2004; Codling et al., 2004; Codling and Hill, 2005) of path sinuosity. Actually, for a more rigorous definition of sinuosity, one should make use of appropriate spatial (Bovet and Benhamou, 1988; Benhamou, 2004) and temporal (Codling and Hill, 2005) sinuosity indexes. In our computations of the NGDR, 500 correlated random walkers (again with no searching) start at the origin and stop once reaching the border of a circumference of radius $r = 2 \times 10^3 l_0$, where $l_0$ is a fixed move step. In this context, the larger the NGDR, the shorter the time to get to $r$ for the first time. The relative values of NGDR for different CRW
models are maintained if we change the scales—the circumference radius. Since in our simulations the spatial scale is fixed and our interest is to study the relative sinuosity of different CRW models (but not their actual sinuosity), we can safely use NGDR for such comparisons.

Indeed, contrary to other NGDR measures, the NGDRs computed here can be directly related to the inverse of first passage times (Okubo and Levin, 2002; Johnson et al., 1992b; Fauchauld and Tveraa, 2003).

Finally, we consider a search model in which random walkers look for fixed, randomly distributed target sites (either homogeneously or in patches) in a two-dimensional space. The walkers perform CRWs with fixed step move lengths $\ell_0$. Taking into account some variability in $\ell_0$—through, e.g., Gaussian or exponential distributions of move lengths—does not change qualitatively the results. The turning angles are sorted from the corresponding JP probability distributions. Along each step, the walker “scans” for circular targets of radius $r_t$ with a detection radius $r_d$. If it finds a target, i.e., if the distance between the walker and the target is equal or less than $R$ (where $R = r_d + r_t$), the step is truncated, the walker proceeds to the target location, and the number of encounters increases by one. If it does not, the step is completed and the number of encounters remains the same. A full run ends after the walker travels a total of $N$ steps. We only focus on destructive searches (targets are depleted once detected) because results in the literature (Bartumeus et al., 2005) show that CRWs cannot optimize non-destructive searches, where re-visitation of previously detected targets is possible. To implement the destructive case and ensure stationary averages throughout the simulations, targets are deleted once found (local depletion) but we maintain global target densities by randomly adding a new target each time an encounter is computed. For the patchy scenario, targets are relocated in such way as to keep both the initial patch structure and the global target density.

In homogeneous landscapes, targets are randomly and uniformly distributed in a two-dimensional space. The whole search process is then scaled in terms of the mean free path $\lambda$, which represents the average distance between
two target sites. The characteristic size of the squared searching arena \( L \), the number of target sites \( N_t \), and the detection distance \( R \), set \( \lambda \), given by (Viswanathan et al., 1999; Bartumeus et al., 2005)

\[
\lambda \approx \frac{L^2}{2RN_t}.
\]

On the hand, to generate patchy landscapes, we first locate 12 source points in a regular arrangement covering the whole landscape. Each of these points acts as a “seed” for building up the patches. The target locations within a patch region are created from an exponentially decaying radial distribution, centered at the seed position. This procedure leads to a regular distribution of patches, all of them having basically the same number of targets. In each patch, the local density is defined by the characteristic scale of the exponential distribution, \( s = 0.025L \), where \( L \) is the side of the squared searching arena. Thus, such local density changes according to the scale of the system \( L \). The global density of targets, as in the homogeneous case, is again fixed by \( \lambda \). We adjust the parameters so to get a determined value for \( \lambda \) given by Eq. (4), but observe that now \( \lambda \) no longer represents a mean free path between targets.

We define the search efficiency function \( \eta = n_e/d_{\text{total}} \) as the ratio of the final number of target sites visited, \( n_e \), to the total distance traversed by the searcher, \( d_{\text{total}} \). Since \( \eta \) scales with \( \lambda^{-1} \), the product \( \lambda\eta \) is a renormalized search efficiency, which assumes values around the interval \((0, 1)\) and allows an appropriate comparison among distinct target densities. We compute the average and the standard deviation of \( \lambda\eta \) over 50 random walks that travel a total of \( N = 10^7 \) steps, for each type of landscape (homogeneous and patchy).

Regarding the target sites, we consider low, \( \lambda = 10^3 \), and high, \( \lambda = 10 \), densities.

In all simulations, we set \( \ell_0 = 0.5 \), \( r_d = 0.5 \), \( r_t = 0.5 \), \( v_d = 1 \), and \( N_t = 5 \times 10^3 \). Furthermore, for \( \lambda = 10^3 \) (\( \lambda = 10 \)) we take \( L = 3162 \) (\( L = 316 \)).

4. Results

4.1. Statistical properties and motility patterns

Plots of msd in relation to time (Figs. 1b and d) show the diffusive properties of the four CRW models selected. In all cases, we observe changes in the local slopes as time increases, indicating a transition from superdiffusive (i.e., msd \( \propto t^\alpha \), with \( \alpha > 1 \)) to normal diffusion (i.e., msd \( \propto t^1 \)).

The larger the mean cosine angle \( \rho \), the longer the correlation length \( \tau \) (Eq. (3)), hence delaying the mentioned crossover. The distributions with \( \rho = 0.9 \) (\( A \) and \( B \)), although having considerably different shapes, result in exactly the same diffusive properties (Fig. 1d).

The mean cosine angle \( \rho \) has strong effects on the motility pattern of the walker at both large and short scales. The larger the \( \rho \), the more ballistic is the path at short scales and the smaller the amount of clogging or overlapped areas at large-scales (see Fig. 2a). The degree of spatial overlap is controlled by \( \rho \) via the correlation length \( \tau \), which determines the diffusive properties of the movement. On the other hand, a strong change in the shape (width) of the distribution involves a conspicuous change in the short-scale motility patterns: from a looping (\( \rho = 0.9A \)) to a zig-zaging (\( \rho = 0.9B \)) type of motion (insets in Fig. 2b). This is so because the wider the distribution, the

![Fig. 2.](image-url) (a) Comparison of CRWs generated by \( \rho = 0.97 \) and 0.86. Blow-up windows on part of the trajectories show the differences in the short-scale motility patterns between the two models. (b) The same as in (a) but for \( \rho = 0.9A \) and 0.9B.
smoother the transition from small to large turning angles ($\rho = 0.9A$ in Fig. 1c), leading to loopy and locally sinuous paths ($\rho = 0.9A$, inset in Fig. 2b). A sharp transition from large to small turning angles ($\rho = 0.9B$ in Fig. 1c) do not favor gradual changes of directions. Instead, it leads to sudden reorientations, which result in a zig-zag-like behavior at short scales ($\rho = 0.9B$, inset in Fig. 2b).

Even though the shapes of the distributions involve short-scale changes in motility patterns, by looking at Fig. 2b one may conclude prematurely that they have no effect on the large-scale properties of the walking paths. However, this is not the case. Fig. 3 shows that, at large scales, the width of the turning angle distributions has a particular impact on the NGDRs. Although a large variation of NGDRs is observed for each of the four studied examples, yet some systematic statistical patterns clearly emerge. We performed inference tests to illustrate this fact. Mann–Whitney tests (Zar, 1999) comparing the average NGDRs values for each of the four parametrized distributions reveal no significant differences between the $\rho = 0.97$ and 0.86 distributions: \(\langle \text{NGDR} \rangle_{\rho=0.97} = 0.50\) and \(\langle \text{NGDR} \rangle_{\rho=0.86} = 0.46\). On the other hand, the average NGDR for $\rho = 0.9B$ is significantly larger ($p<0.0001$) than the one for $\rho = 0.9A$: \(\langle \text{NGDR} \rangle_{\rho=0.9A} = 0.57\) and \(\langle \text{NGDR} \rangle_{\rho=0.9B} = 0.42\). Note also that $\rho = 0.9B$ leads to the largest average NGDR, whereas $\rho = 0.9A$ results in the smallest one (Fig. 3a). In Fig. 3b we display four representative individual paths with NGDRs close to 75% of the overall variability. The figure evidences that large NGDRs (e.g., $\rho = 0.9B$) are associated to asymmetric and strip-like spreading outs from the initial point, whereas small NGDR (e.g., $\rho = 0.9A$) involve propagations that are largely symmetric and more winding. In the latter case, the spreading is fairly equally distributed in space. One can check the degree of strip-likeness of a walk in two dimensions by framing the whole walk within a rectangular box of sides $L_x$ and $L_y$, so to leave as less empty space as possible inside the box. A non-strip-like walk would be that in which the ratio $L_x/L_y \approx 1$, otherwise we find either $L_x/L_y \ll 1$ or $L_x/L_y \gg 1$, meaning that the whole walk is “stretched” towards some biased (and random) direction.

4.2. Search efficiency

In Fig. 4 we compare, for low and high target densities, and in homogeneous and patchy landscapes, the rescaled searching efficiencies $\lambda_t$ of the four CRW models. The large number of time steps considered in the simulations, $N = 10^7$, ensures that the results correspond to the stationary equilibrium regime, i.e., after the transient dynamics. For each of the CRW models, we observed a large variation of $\lambda_t$ (particularly in patchy landscapes). Despite this fact, statistical inferences (Mann–Whitney tests, Zar, 1999) performed on the simulated data show robust and distinguishable statistical features (Fig. 4). In homogeneous landscapes (Fig. 4, first row), the largest differences in the search efficiency (i.e., $\lambda_t$) occur between the two distributions with different mean cosine angles (or equivalently, different correlation lengths), namely, $\rho = 0.86$ and 0.97. This is true at both low ($\lambda = 10^3$) and high ($\lambda = 10$) densities. We also note that, in homogeneous landscapes, the striking different shapes for the wide ($\rho = 0.9A$) and sharp ($\rho = 0.9B$) distributions results in a small variation of $\lambda_t$. Remarkably, the former is only slightly better than the latter. At high densities, the average search efficiency values for the four CRW models tend to be closer to each other. Indeed, by inspecting Fig. 4 (first row) we see that the difference between the largest and the smallest average values ($\rho = 0.97$ and 0.86) is around 0.2 for $\lambda = 10^3$, and just about half of it for $\lambda = 10$. This is so because the CRWs statistical properties associated to $\rho$, i.e., to the diffusiveness, become less important in a...
random search when the availability of target sites increases. Furthermore, Fig. 4 reveals that as density increases, aspects related to the shape of the distribution can become more relevant, in relative terms, than those associated to $r$. For the case of homogeneous landscapes, all the patterns observed were statistically different (Mann–Whitney tests, Zar, 1999).

For patchy landscapes (Fig. 4, second row), the statistical variation (fluctuations) of the search efficiency for all the CRW models considered is much larger than those for homogeneous landscapes. This fact may explain why the Mann–Whitney tests, comparing $r = 0.9A$ and $0.9B$, do not reveal significant differences at low-density landscapes ($\lambda = 10^3$). At these densities, as in the case of homogeneous landscapes, $\rho = 0.86$ and 0.97 present the largest discrepancy between the average efficiencies: the larger the $\rho$, the higher the $\lambda\eta$. Contrary to the observations for homogeneous landscapes, in high-density patchy landscapes ($\lambda = 10$), the shape of the distribution ($\rho = 0.9A$ and $0.9B$) has an impact on the search efficiency similar to the one due to the actual value of $\rho$ ($\rho = 0.97$ and 0.86). Indeed, the sharp distribution ($\rho = 0.9B$) leads to the worst search strategy, with an average efficiency even lower than the one obtained with $\rho = 0.86$.

5. Discussion

Stochasticity can be present in different components of animal movement (e.g., velocity, move lengths, orientations), leading to different encounter rates. Due to the energetic costs of searching, behavioral features favoring more efficient combinations of the above-mentioned random components may represent a real adaptive advantage. Indeed, it has been suggested that animals could increase the chances of locating targets simply by profiting from certain statistical properties of their movements (Bartumeus et al., 2005; Bartumeus, 2007).

The assumption that certain stochastic components of motion could become relevant mechanisms to improve search efficiency may not be particularly realistic in many situations. In general, there is a relative larger benefit for a search outcome when individuals possess good skills in sensing and reacting to simple environmental clues. As an example, Codling et al. (2004) show that an important
evolutionary advantage might exist if fish larvae develop some basic detecting abilities. However, our results may be of interest in those cases where sensory systems are not useful enough, for example, because of their limited action when there are confusing signals in the environment—environmental noise, extremely intermittent signals, etc.—or under particular scaling conditions of the landscape, e.g., when the typical size of the landscape is much larger than the perceptual range (Lima and Zollner, 1996; Bartumeus, 2007). In these situations animals could control movement speed to balance risks of predation or starvation while dispersing (Zollner and Lima, 2005), or else initiate robust systemic to stochastic rules of search (Bartumeus et al., 2005; Bartumeus, 2007). When there are confusing signals in the environment—dependent on the specific JP parametrization) is that very sharp turning angle distributions (therefore probably independent on the specific JP parametrization) is that very sharp turning angle distributions, such as $\rho = 0.9A$, are highly inefficient. In this sense, it is reasonable to believe that, in general, the modulation of the correlation length has larger impacts on search efficiency than the modulation of the shape. Further findings can be resumed as the following: (i) in homogeneous landscapes, the impact in the search efficiency of both the correlation length and the shape of turning angle distributions decreases as target density increases; (ii) in patchy landscapes, the same is true for the correlation length; however, the impact of the distribution shape increases as target density increases.

The fact that the correlation length can be such a major influence in the search efficiency is relevant because individual-based models of animal movement have been considered to be strongly dependent on behavioral details (Turchin, 1998). As a consequence, they would be of limited generalization in a biological evolutionary context. Our results indicate that this may not be the case, at least in random search scenarios. In fact, different behavioral traits can lead (by natural selection) to a same numerical value of the correlation length, and so to a similar fitness (assuming that higher search efficiency implies in higher fitness). For example, behavioral repertoires, associated to distributions as distinct as $\rho = 0.9A$ and $0.9B$, would show identical correlation lengths and hence extremely close search efficiencies.

Although the correlation length seems to be more critical for long-term search efficiency, the shape of the distribution can also influence it. In fact, the shape (width) defines the transition between small and large angle deviations (sinuous versus zig-zag paths), directly altering the geometry of the random walk during the exploration process, regardless the specific correlation length. The sharper the distribution, the thinner the “scanned” region by the walker. A more peaked and sharp distribution increases the $NGDR$s (decreases the first passage time) by reducing the fully bi-dimensional sinuosity component of the trajectory, and forcing the overall spreading of the search to a strip-like configuration (Fig. 3b). As an example, consider a landscape with evenly distributed targets (one can think on a small mammal looking for food in a very well ordered, but relatively sparse, orchard). In this scenario, and provided that ballistic motion is not possible, zig-zagging would be a more efficient behavior than looping, because zig-zags lead to strip-like walks with relatively larger $NGDR$s. However, strip-like walks (larger $NGDR$s) do not allow an appropriate bi-dimensional scanning of homogeneous randomly distributed targets, which intuitively can be thought as if spatial fluctuations were introduced in an originally regular target lattice. Indeed, such type of walks would increase the probability of missing nearby targets, diminishing the global search efficiency. In patchy landscapes, the spatial fluctuations of target densities is much higher than in homogeneous landscapes. So, in the former the ability to exploit local density variations can become relevant at the long-term, and these effects can be amplified as the average density increases. On the other hand, in the latter, the smaller amount of fluctuations in space prevents larger (and statistically significant) changes in the efficiency due to shape effects.

Our simulations show that the relative contribution of both stochastic components (i.e., shape and correlation
length) to search efficiency depends on the specific parameters of the JP distribution, and the density and structure of target landscapes. However, from the above discussion, it is inferred that the shape of the turning angle distribution modulates the ability to exploit the landscape inhomogeneities at short and intermediate scales, whereas the correlation length determines the type of diffusion. More specifically it sets the range of scales where super-diffusive behavior is possible, related to the amount of spatial overlap during the exploration process. So, in this sense we can presume that one of the two optimization processes will gain relevance depending on the type of landscape. Also, the fact that only very “extreme” changes in the shape significantly alter the search efficiencies (sharp distributions often generate highly inefficient searches) makes plausible that correlation length effects could be more important than shape effects in general. Overall, in real heterogeneous landscapes, it may happen that a robust search strategy would be to keep large correlation lengths to minimize the overlap of visited areas, and to avoid peaked or sharp turning angle distributions in order to better exploit the spatial target fluctuations. In this way, the searcher would be able to efficiently scan the “local” landscape, while keeping superdiffusive properties for a large enough range of scales (see Section 5.2). Interestingly, these are the type of turning angle distributions found when analyzing animal paths by means of CRWs (Zollner and Lima, 1999).

5.2. The correlation length: superdiffusive-like behavior in CRWs

In a CRW searching process, superdiffusive features can appear only at limited spatiotemporal scales: the larger the correlation length, the larger the range of such scales (Fig. 1). However, we recall that, at long enough times, CRWs necessarily lead to Brownian motion, presenting a msd which goes linearly with \(t\). This fact reduces their potential to increase the encounter rates in long-term random searches (Bartumeus et al., 2005; Viswanathan et al., 2005). In this sense, genuinely superdiffusive random walks such as Lévy walks (Shlesinger et al., 1995; Klafter et al., 1996; Metzler and Klafter, 2004; West, 2006) differ radically from CRWs. From a pure diffusive perspective, CRWs cannot be as efficient as Lévy or other super-diffusive walks. In fact, any Lévy random walk is super-diffusive at any time scale and has its msd going as \(t^\alpha\) for \(\alpha > 1\), regardless the time interval. But from Eqs. (C1) and (C2) in the Appendix C, one finds that for CRWs the msd scales as \(t^{1+\beta(t)}\), for \(\beta(t)\) a decreasing function of \(t\), vanishing for \(t \to \tau\). So, strictly speaking, even below \(\tau\) CRWs do not show genuine superdiffusion but time-dependent superdiffusion.

Because of all that, the encounter success of CRWs will mainly depend on the relationship between the correlation length and some scale related to the search constrains, like the average patch density and/or time of exploration. The condition for which CRWs can “mimic” superdiffusion in an inter-patch searching process, where patches are uniformly distributed, is derived in the Appendix C. It reads

\[
\lambda \ll \sqrt{2\ell_0 / \ln[p]}.
\]  

(5)

So, if the mean free path \(\lambda\) (or conversely, the patch density \(1/(2R\lambda)\)) satisfies the above relation, then a CRW can generate a superdiffusive random search process.

In more simple terms, Eq. (5) states that fully super-diffusive-like properties can emerge in CRWs only at high densities. But then, we would expect to find a search dynamics essentially constrained by the spatial distribution of distances between targets, and so, the gain in efficiency due to changes in diffusiveness would be very low (Bartumeus et al., 2005). In addition, from a biological point of view, the regime of Eq. (5) represents a situation with so many patches that there is almost no need for individuals to follow any special search strategy. In these situations, animal movement patterns would majorly represent the outcome of constant cue detection of nearby targets, instead of adaptations to the inter-patch search problem itself. Further, at high target densities, the selection pressure to optimize encounter rates should not be as strong as at low target densities, when death by starvation is more likely (Faustino et al., 2007).

Note that the arguments above only hold for pure CRWs in homogeneous or weakly correlated landscapes. Composite CRWs (Morales et al., 2004), representing different behavioral states of exploration processes in heterogeneous landscapes, may involve longer superdiffusive regimes. Thus, they could be much more competitive in terms of random search efficiency than pure CRWs. Further studies are needed to elucidate the diffusive properties of composite CRWs and to compare them with other superdiffusive random walks.

Last but not least, the adaptive adjustment by animals of (i) the correlation length of their walks and (ii) the shape of their turning angle distributions might not be related exclusively to long-term searching. These two factors could become relevant in relation to other trade-offs occurring at shorter scales (Farnsworth and Beecham, 1999), like in foraging processes with clear-cut characteristic spatial lengths (e.g., area-restricted search, patch-exploitation, home ranging). Limited superdiffusive properties, for example, might be useful to safely explore a local space surrounded by predators, to accomplish certain social demands from other individuals in the population during the search (Ramos-Fernández et al., 2004) or to optimally exploit a patch (Komin et al., 2004; Schimansky-Geier et al., 2004; Visser and Kiorboe, 2006). Also, as pointed out in Visser and Kiorboe (2006), different metabolic and ecological constrains could be involved in the adjustment of adequate correlation lengths in the swimming paths of planktonic organisms: food availability, organisms size, searcher/target relative motility patterns, and the ecological...
compromise between being at the same time predator and prey. Finally, specific behavioral details of central foraging or home ranging (Bell, 1991; Turchin, 1998) could also be the basis for correlation length adjustments.

6. Concluding remarks

In summary, we have investigated the importance of two distinct stochastic mechanisms in the outcome of a random search performed by CRWs: (i) the limitation of directional memory; and (ii) the variability arising from differences in the shapes of the turning angle distributions (for fixed correlation times). We have shown that the main contribution to long-term search efficiency comes from directional memory effects, associated to diffusiveness. However, shape effects (closely related to the distribution width) can also play a relevant role, leading to different results for a searcher exploiting environments with different density and spatial structure for the target sites.

It is important to emphasize that: (i) the exact relative contribution to search efficiency of the two stochastic components investigated (i.e., shape and correlations) always depends on the specific parameters of the JP distribution and on the density and structure of the landscape, and (ii) the cases analyzed in the present work are far from exhausting all the possibilities. Indeed, by playing with the parameters of the JP distributions, one can generate many different CRWs, which eventually could display further interesting statistical properties for the searching efficiency. Also, more complicated arenas (inhomogeneous or fractal distributions of target sites) may reveal different $\lambda\eta$ behavior for the present CRWs models. Such an extensive study, however, is beyond the scope of the present work. Even so, here we have shown the essentials of how the two features analyzed (i.e., shape and correlation) contribute to enhance random encounter success in different landscapes.

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Appendix A. The correlation length

A random walk model consisting on increments with finite variance cannot lead to genuinely scale invariant superdiffusion unless the correlations are non-Markovian (i.e., of long range). Therefore, for CRWs a correlation length (or time) $\tau$ necessarily exists beyond which the behavior tends to Brownian motion. An explicit expression for $\tau$ has been derived in detail in Viswanathan et al. (2005). Here we review the main ideas and the final expression.

Suppose that each step $j$ of a CRW is described by the vector position $r_j$. Thus, let us define the correlation between two successive steps as $C(1) \equiv \langle r_{j+1} \cdot r_j \rangle / \langle r_j \rangle^2$, for $r_j = |r_j|$ and $\langle \ldots \rangle$ representing the average over the RW. Now, if the distribution of length steps $r_j$ does not depend on the turning angles or on the other $r_i$'s, then $\langle r_{j+1} \cdot r_j \rangle = \langle r_{j+1} \rangle \langle r_j \rangle \times \langle \cos(\theta_{j+1} - \theta_j) \rangle$.

Furthermore, if we assume that only the relative orientations $\theta = \langle \theta_{j+1} - \theta_j \rangle$, but not the actual turning angles $\theta_j$ and $\theta_{j+1}$, have correlations, we finally can write

$$C(1) = \langle \cos(\theta) \rangle = \int_{-\pi}^{+\pi} \cos(\theta) f_{\text{wrap}} (\theta). \quad (A.1)$$

Here, $f_{\text{wrap}}$ denotes the circular “wrapped” PDF of relative turning angles (Appendix B).

Since our present CRWs are in fact Markovian, it implies that the correlation between $t/\theta_0$ steps apart decay as $C(t/\theta_0) \sim \{C(1)\}^{1/t_0}$, where $\theta_0$ is the typical time of one step (Viswanathan et al., 2005). Taking $\tau$ as the adimensional correlation length (or time), such that $C(\tau) = e^{-1}$, then

$$C(\tau) = \{C(1)\}^{1/\tau} = \langle \cos(\theta) \rangle^\tau = e^{-1}, \quad \text{or}$$

$$\tau = -\ln[\langle \cos(\theta) \rangle]. \quad (A.2)$$

The validity of this expression (Viswanathan et al., 2005) extends to all one-step Markov CRW models, leading to a general expression for the correlation length. An important aspect of Eq. (A.2) is that $\tau$ ends up written in terms of the mean cosine of turning angles, which is a quantity easy to measure in any data set.

Simply speaking, $\tau$ gives an account of how many successive steps are correlated, so giving an idea of what is the “directional memory” of previous steps along a CRW. For any scale two or more orders of magnitude larger than $\tau$ (see the explanation below), the CRW appears Brownian because the model cannot keep the orientations correlated at such relatively large scales. Thus, the above result, Eq. (A.2), can be useful to determine whether a data set contains enough information to adequately predict its long-term diffusive properties. In other words, if the data set either supports genuine superdiffusion or represents a CRW that appears superdiffusive only locally (Viswanathan et al., 2005).

For circular statistics (Jupp and Mardia, 1999; Jammalamadaka and SenGupta, 2001), the first moment of the circular PDF reads $\phi_1 = \rho \exp[i\theta]$, with $\rho$ denoting the mean resultant length and $\bar{\theta}$ the mean direction. When $\bar{\theta} = 0$, the case of symmetric PDFs (and our interest here), we find that $C(1) = \langle \cos(\theta) \rangle = \rho$, thus parameterizing $\tau$ only as a function of $\rho$. From a practical point of view, this fact is a significant advantage since there are efficient
methods to obtain ρ for arbitrary circular data sets (e.g. Ravindran and Ghosh, 2003). Hence, it is useful to rewrite Eq. (A.2) as $τ = -1/\ln[ρ]$. Note that the value $ρ = 1$ leads to deterministic ballistic motion ($τ = ∞$), with $τ$ diverging as $1/(1 - ρ)$ for $ρ \rightarrow 1$. Any value $ρ < 1$ introduces stochasticity, giving rise to true random walks. In particular, for $ρ = 0$ we recover a uniform distribution associated with perfectly uncorrelated Brownian random walks, for which $τ = 0$. Finally, another equally important aspect is that $ρ$, and so $τ$, can be written in terms of the turning angle PDFs parameters used to construct the CRW model.

As a final remark, a question that may arise concerns whether $τ$ is really the correct value for the correlation length, in the sense discussed as follows. For a zero-centered non-wrapped Gaussian distribution, $f(\cos[θ]) = \exp(-σ/2)$, where $σ$ represents the variance of the turning angles $θ$. So, one can correctly note that for small (Gaussian) variances, $τ = 2/σ$. Hence, a variance equal to 1 results in $τ = 2$. But of course the correlations in such a stochastic process cannot vanish just after two steps, thus in apparent contradiction with our definitions. To better illustrate the significance of $τ$, let us consider more carefully in what time scales the correlation function would decay by a satisfactory factor. As discussed in Viswanathan et al. (2005), the real crossover to diffusive behavior occurs on scales at least one order of magnitude larger than that corresponding to $e^{-1} = 1/2.17$ (because then $\exp[-10]$ is small enough, whereas $e^{-1}$ is still rather large). To be on the safe side (see Viswanathan et al., 2005), at least two orders of magnitude of leeway should be given for the motion to converge convincingly to diffusive behavior. Therefore, answering the above question, we state that technically the correlation length $τ$ is defined as the number of steps for the correlation function to decay by the factor $e^{-1}$, in analogy to the time constants used in electronic circuits, the mean life of a radioactive element, and all other exponentially decaying functions of time. However, this does not mean that $τ$ represents the time for the complete crossover. Instead, we need to wait for the function to decay not by a factor $e^{-1}$ but by a factor $e^{-10}$, or even better, $e^{-100}$. By this argument, the time for the correlations to die out in the example given above is $10τ = 20$ or $100τ = 200$ steps. In this way, we may assume safely an effective time to reach the diffusive regime of $t_{eff} = 100τ$.

Appendix B. Turning angle (circular) distributions

Mathematically, angular PDFs must be treated differently from the more common case of distributions on straight intervals (Jupp and Mardia, 1999; Jammalamadaka and SenGupta, 2001). Consider, for instance, the turning angle $θ_j$ of a walk step $j$, which effectively falls in the range $[-π, +π]$. We cannot use the usual methods of probability distributions and characteristic functions on the real line to describe such a variable defined on a finite periodic interval. In fact, angular PDFs belong to the so-called family of circular distributions. They can be constructed by wrapping the usual PDFs on the real line (Coles, 1998; Jupp and Mardia, 1999; Jammalamadaka and SenGupta, 2001; Gatto and Jammalamadaka, 2003; Jammalamadaka and Kozubowski, 2004). Let $x$ denote a random variable on the line and let $f_x$ be its PDF. We obtain the corresponding wrapped (or angular) PDF via

$$f_{wrap}(θ) = \sum_{k=-∞}^{+∞} f(θ + 2πk), \quad θ ∈ [-π, +π). (B.1)$$

Closed form expressions for such constructions exist for a few cases only. The wrapped normal or Gaussian PDF, for example, does not have one. Among the most important circular distributions which do possess such analytical formulas, we cite the von Mises distribution (vMD, which matches reasonably well the wrapped normal distribution) given by

$$f_{vMD}(θ) = \frac{\exp[κcos(θ)]}{2πI_0(κ)}, \quad κ ≥ 0, (B.2)$$

where $I_κ(θ)$ is the modified Bessel function of first kind of order $κ$. There is also the wrapped Cauchy distribution (WCD), given by

$$f_{wCD}(θ) = \frac{1 - ρ^2}{2π(1 + ρ^2 - 2ρcos(θ))}, \quad ρ ∈ [0, 1]. (B.3)$$

Finally, another example is the CD, written as

$$f_C(θ) = \frac{1 + 2ρcos(θ)}{2π}, \quad ρ ∈ [0, 1/2]. (B.4)$$

In the above symmetric distributions $ρ$ or $κ$ fix their width. Among the different circular distributions of turning angles, both the WCD (Zoltnor and Lima, 1999; Morales et al., 2004) and the von Misses (Codling et al., 2004; Codling and Hill, 2005) are commonly used in CRWs models. In particular, some animal movements features can be well described by a WCD. For instance, the peaked behavior of the WCD can account for the high persistence of animals in moving in certain directions. At the same time, the small but non-vanishing tail allows for occasional strong deviations from such directions, a phenomenon observed in real field data.

In fact, by comparing the three distributions for a same $ρ$, we see that in general the WCD has the most pronounced peak around $θ = 0$, and also the fattest tails (Jones and Pewsey, 2005).

Of particular interest for circular distributions are the circular characteristic functions, given in terms of the $nth$ order expectations $φ_n ≡ \exp[imθ] = z_n + iβ_n$. For the symmetric case, these functions become equal to the cosine moments, i.e. $φ_n = z_n ≡ \cos[nθ]$. The first cosine moment, $z_1 = \cos[θ]$, is especially relevant to characterize the diffusive properties of random walks (Kareiva and Shigesada, 1983; Bartumeus et al., 2005; Viswanathan et al., 2005), as we discuss along this work.
Appendix C. Superdiffusive-like behavior in CRWs

For discrete CRWs, it has been derived (Kareiva and Shigesada, 1983) that the msd from a certain start point is given by (see also Komin et al., 2004)

\[ \langle R^2(n) \rangle = \ell^2 \left( \frac{1 - \rho^2}{(1 - \rho)} \right) \left[ n - \frac{2 \rho}{(1 - \rho^2)} (1 - \rho^n) \right]. \]  

(C.1)

Here, \( n \) is the number of steps taken by the walker, \( \ell \) is the average length of each step, and \( \rho = \langle \cos \theta \rangle \), with \( \theta \) the angle between two successive steps (drawn from a certain circular distribution function). On the other hand, by assuming a random walk model in a continuous time dimension, the msd reads (Taylor, 1921; Visser and Kiorboe, 2006)

\[ \langle R^2(t) \rangle = 2v^2 t \left[ 1 - \exp \left[ -\frac{t}{\bar{t}} \right] \right]. \]  

(C.2)

In Eq. (C.2), \( v \) is the mean velocity of the walker and \( \bar{t} = \tau t_0 \), for \( \tau \) our adimensional correlation length and \( t_0 \) the typical time of one step. Note from Eq. (C.2) that \( \sqrt{\langle R^2(t) \rangle} \) goes as \( vt \) for \( t \ll \bar{t} \) and as \( \sqrt{2v^2\bar{t}} t^{1/2} \) for \( t \gg \bar{t} \). Thus, the two limiting behaviors, ballistic and normal diffusion, are obtained, respectively, for short and long times.

Assuming that \( \bar{t} \gg 1 \), which is one of the conditions necessary for any CRW to present anomalous diffusion at large enough times, we can easily derive Eq. (C.2) directly from Eq. (C.1). Indeed, recalling the definition of the correlation length, we have \( \bar{t} = -t_0 / \ln |\rho| \), so \( \rho = \exp[-\bar{t}/t_0] \). Then, if we set \( n = t / t_0 \) we can write in Eq. (C.1) that \( \rho^n = \exp[-t / \bar{t}] \). Furthermore, one has that \( 2\rho/(1 - \rho^2) \approx \bar{t}/t_0 \) and \( (1 - \rho^2)/(1 - \rho^2) \approx 2\bar{t}/t_0 \), which are good approximations when \( \bar{t}/t_0 = \tau \approx 1 \). Finally, since \( t_0 = \ell_0 / v \), by putting all this together we get Eq. (C.2): both the continuous and discrete random walk models are equivalent, provided the correlation length is much larger than the time of a single step.

Now, consider our situation of a complete random distribution of target sites in a two-dimensional arena. The mean free path between targets is given by Eq. (4) in the main text, or \( \lambda \approx L^2 / (2RN) \) (note that the target density is \( N / L^2 \)). Therefore, in average a searcher with a radial detection distance \( R \) should travel (in a straight line) a distance \( \lambda \) to find a target site (Viswanathan et al., 1999). The key point is that if a searcher spends in average a time \( \bar{t} \) looking for successive target sites, where \( \sqrt{\langle R^2(\bar{t}) \rangle} = \lambda \) in Eq. (C.2), and \( \bar{t} \) satisfies the condition \( \bar{t} \leq \bar{t} \), then the CRW can mimic a superdiffusive process. In fact, by using Eq. (C.2) we obtain

\[ \langle R^2(\bar{t}) \rangle = \lambda^2 = 2v^2 \bar{t} \left[ 1 - \exp \left[ -\frac{\bar{t}}{\bar{t}} \right] \right] \approx 2v^2 \bar{t} \bar{t}. \]  

(C.3)

Now, once \( \bar{t} = -t_0 / \ln |\rho| \) and recalling that \( v = \ell_0 / t_0 \), we find from the above relation \( \lambda^2 \bar{t}^2 |\rho| / (2v_0^2) \approx \bar{t}/\bar{t} \). Finally, as \( \bar{t} / \bar{t} \ll 1 \), we obtain the result

\[ \lambda \approx \sqrt{\frac{\sqrt{2} t_0}{|\rho|}}. \]  

(C.4)

References


