HOW MANY ANIMALS REALLY DO THE LÉVY WALK?

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Abstract. Lévy walks (LW) are superdiffusive and scale-free random walks that have recently emerged as a new conceptual tool for modeling animal search paths. They have been claimed to be more efficient than the “classical” random walks, and they also seem able to account for the actual search patterns of various species. This suggests that many animals may move using a LW process. LW patterns look like the actual search patterns displayed by animals foraging in a patchy environment, where extensive and intensive searching modes alternate, and which can be generated by a mixture of classical random walks. In this context, even elementary composite Brownian walks are more efficient than LW but may be confused with them because they present apparent move-length-heavy tail distributions and superdiffusivity. The move-length “survival” distribution (i.e., the cumulative number of moves greater than any given threshold) appears to be a better means to highlight a LW pattern. Even once such a pattern has been clearly identified, it remains to determine how it was actually generated, because a LW pattern is not necessarily produced by a LW process but may emerge from the way the animal interacted with the environment structure through more classical movement processes. In any case, emergent movement patterns should not be confused with the processes that gave rise to them.

Key words: diffusive walks; Lévy flight; optimal foraging; path modeling; search pattern.

INTRODUCTION

The various versions (possibly correlated and/or biased) of “classical” random walks have been shown for a long time to be very useful to model animal paths in a homogeneous environment (see review in Turchin 1998). In more complex environments, where animals have to adapt their behavior to the local conditions encountered, movements can be modeled as mixtures of such “classical” walks (Benhamou 1992, 1994, 2004, Morales et al. 2004). Recently, however, various species (fruit fly [Cole 1995], Wandering Albatross [Viswanathan et al. 1996], jackals [Atkinson et al. 2002], reindeer [Márell et al. 2002], dinoflagellates [Bartumeus et al. 2003], spider monkey [Ramos-Fernández et al. 2004], but see Austin et al. [2004] on grey seal) have been claimed to display search or activity patterns that may be accounted for as Lévy walks (LW). LW have also been claimed to be more efficient than classical random walks (Viswanathan et al. 1999, Bartumeus et al. 2002, 2005). Together, these empirical and theoretical findings suggest that many animals may move using a LW process. If so, this would have major consequences for numerous spatial ecology studies, where null hypothesis models for the way animals redistribute in the environment rest on “classical” random walks, which are either diffusive and non-oriented (e.g., dispersal studies) or superdiffusive and oriented (e.g., migration studies), whereas LW are both non-oriented and superdiffusive. LW are also of general interest in various fields because they may be involved each time a random variable obeys a power-law distribution.

“Classical” random walks are characterized by a step length distribution whose variance is finite. In their simplest form, both step orientations (moving directions) and changes of direction (turning angles) are uniformly distributed (mere random walks, MRW). More sophisticated models involve some forward persistence propensity (correlated random walks, characterized by a non-uniform distribution of changes of direction), some directional bias due to a preferred moving direction (biased random walks, characterized by a non-uniform distribution of step orientations) or both (biased correlated random walks; see Benhamou [2006] for a recent account). Like MRW, LW are uncorrelated and unbiased, but their step lengths, called Lévy flights, are characterized by an infinite variance (i.e., they are drawn from a “heavy tail” distribution): the probability density function \( f(l) \) of the largest flights \( l \) (i.e., those occurring in the tail) decreases as \( l^{-\mu} \) with \( 1 < \mu < 3 \), or equivalently, the “survival” probability function \( S(l) = 1 - F(l) \), i.e., the probability of occurrence of flights longer than \( l \), decreases as \( l^{-\alpha} \), with \( 0 < \alpha = \mu - 1 < 2 \) (the exact forms of \( f(l) \) and \( S(l) \) for the shortest lengths \( l \) do not matter). Thus, long steps, although they are scarcer than short ones, remain relatively frequent. The simplest example is provided by the Pareto distribution (e.g., see Newman 2005), which
can be defined for any $\mu > 1$ and minimum step length $l_m > 0$ acting as a scaling factor, but presents a heavy tail only for $\mu < 3$ ($f(l) = kl^{-\mu}$ and $S(l) = (l_m/l)^{\mu}$, with $k = 2l_m^\mu$ and $\alpha = \mu - 1$). Because of the infinite step length variance, the asymptotic distribution of the location coordinates (on any arbitrary axis) of a Lévy walker is not Gaussian but a Lévy symmetric $\alpha$-stable distribution (a special case of Lévy skew $\alpha$-stable distributions, corresponding to a Cauchy distribution when $\alpha = 1$; e.g., Weron [2001]). There is no gap between classical and Lévy walks, however, because any Lévy $\alpha$-stable distribution, which presents heavy tails and an infinite variance for $\alpha < 2$, reduces to a Gaussian distribution for $\alpha > 2$. LW are also known to be scale-free, i.e., self-similar at various spatial scales: the set of sites visited by a Lévy walker has a fractal dimension equal to $\alpha$ (Shlesinger et al. 1993).

In this paper, I show that composite Brownian walks (CBW) used by a predator looking at random for prey items in a patchy environment generates search patterns that mimic those generated by LW, and that they can be much more efficient than LW in this type of environment. The step length “survival” distribution, i.e., the cumulative frequency of lengths greater than any given threshold, makes it possible to clearly identify true LW patterns, but is unfortunately rarely used in animal path studies. Finally I emphasize the fact that a LW pattern is not necessarily generated by a LW process, but may also emerge from the way an animal interacts with its particular environment through classical movement processes. This suggests that many actual animal search patterns may look like LW, but that very few animals are likely to move using a LW process.

**Lévy Walk vs. Composite Brownian Walk**

**Search patterns, step length distributions, and diffusivity**

LW patterns (Fig. 1A) look like the patterns expected for an animal which searches for patchily distributed resources by performing a composite classical walk, where intensive (area-concentrated) search mode within patches and extensive (ranging and relocation) search mode between patches alternate (Fig. 1B). Let us consider here the very simple example where such a two-search-mode pattern emerges although the animal relies on an elementary single search mode process—moving in a straight line in a random direction until a prey item is found—because of the patchy structure of the environment. For this purpose, let us assume that two-search-mode pattern emerges although the animal considers here the very simple example where such a pattern between patches alternate (Fig. 1B). Let us consider that step lengths are drawn at random from a Pareto distribution with $\mu = 2$; (B) composite Brownian walk simulated by drawing step lengths at random from two exponential distributions, one for inter-patch movements with mean $\lambda_{\text{inter}}$ used with a 0.1 probability, the other for intra-patch movements with mean $\lambda_{\text{intra}}$ used with a 0.9 probability, with a ratio $\lambda_{\text{inter}}/\lambda_{\text{intra}} = 15$. In both types of search, turns between steps were drawn at random from a uniform angular distribution.

Straight line until it finds an item and reorienting at random afterwards, an animal will perform a composite Brownian walk (CBW), i.e., a mixture of two MRW, one made of relatively sporadic exponentially distributed steps with a relatively large mean $\lambda_{\text{inter}} = [\delta_{\text{patch}}(W_{\text{patch}} + W_{\text{item}})]^{-1}$ and the other made of much more frequent exponentially distributed steps with relatively small mean $\lambda_{\text{intra}} = (\delta_{\text{item}}W_{\text{item}})^{-1}$, where $W_{\text{patch}}$ is the mean patch width and $W_{\text{item}}$ is the item detection width.

The ratio between the mean step lengths $\lambda_{\text{intra}}$ and $\lambda_{\text{inter}}$ hence depends on the patchiness of the environment, and the ratio between the frequencies of inter-patch and intra-patch movements depends on the mean number of prey items per patch. As a simple numeric example, let us consider that step lengths are drawn at random with a 0.1 probability from an exponential distribution with mean $\lambda_{\text{inter}} = 15$ and with a 0.9 probability from another exponential distribution with mean $\lambda_{\text{intra}} = 1$ (global mean step length equal to 2.4; Fig. 1B). The resultant observed step length frequency distribution plotted using a linear binning seems to obey a power law with exponent $\mu = 2$, so that this CBW may be erroneously rated as a LW (Fig. 2). If a logarithmic binning is used (Newman 2005, Sims et al. 2007), however, the log–log relationship obtained for the CBW is less linear (with $r^2$ dropping from 0.94 to 0.90), provided frequencies have not been bin-width normalized ($r^2 = 0.97$ otherwise). In addition, the step length survival distribution of a LW should also display a
linear log–log relationship (with a slope equal to 1 – \(\mu\)). It is clearly not the case for the CBW. The survival distribution is therefore much more reliable than the observed frequency distribution for identifying true power-law distributions, but most published studies that focused on animal LW rest on linear bin-based observed frequency distributions: the logarithmic binning was used infrequently (e.g., Viswanathan et al. 1996) and the survival distribution not at all to my knowledge.

An important property of random walks concerns the evolution of the mean squared net displacement (MSND), i.e., the mean squared beeline distance between the starting and last locations (see Turchin 1998). In correlated random walks, the MSND is asymptotically proportional to the step number, with a convergence speed inversely related to the amount of forward persistence (the location coordinates on an arbitrary axis then obey a Gaussian distribution centered on the starting point with a variance equal to MSND/2; see Bovet and Benhamou [1988]). This type of relationship still holds true when the MSND is expressed as a function of the path length \(L\) (or the traveling time if the speed is constant) rather than the step number (Bartumeus et al. 2005). Because they have an infinite variance, the MSND after a discrete number of \(L\)evy flights does not converge towards a finite value. This is why the MSND of LW is systematically expressed as a function of continuous time (i.e., path length \(L\), as flight speed is assumed to be constant [Shlesinger et al. 1993]). LW are known to be superdiffusive (Fig. 3): the MSND increases as \(L^a\) with \(a > 1\) (Shlesinger et al. 1993, Bartumeus et al. 2005), or equivalently, the root mean square of the net displacement fluctuations (RMS) increases as \(L^b\) with \(b > 1/2\) (Viswanathan et al. 1996). The evolution of the net displacement of the CBW also suggests some superdiffusivity: the MSND and the RMS seem to increase as \(L^{1.26}\) and \(L^{0.64}\), respectively. The computer simulations used in Fig. 3 also showed that the coefficient of variation of the squared net displacement is close to 1 for the CBW (as expected, since the distribution tends asymptotically toward a scaled \(x^2\) law) and is even higher for the LW, with a value that can be approximated as 0.52 \(L^{0.23}\).

Searching efficiency

I relied on computer simulations to compare the search efficiency of LW with that of CBW when resources are patchily distributed. The environment was defined as a square of 500 × 500 \(u^2\), where \(u\) is an arbitrary unit length, with wrap-around margins (so that its size was virtually unlimited). A total of 2500 (poor habitat, P; overall mean density = 0.01) or 10 000 prey items (rich habitat, R; overall mean density = 0.04) were randomly allocated to 125 (P) or 250 (R) circular patches without detectable boundaries, whose center coordinates were randomly drawn from a uniform distribution: the number of patches per habitat unit...
area (mean: 0.0005 [P] or 0.001 [R]) and the total number of prey items per patch (mean: 20 [P] or 40 [R]) obeyed Poisson distributions. In addition, the prey items were also randomly located within their respective patches: the number of prey items per patch unit area also obeyed a Poisson distribution with a mean set to 0.25 (P) or 0.5 (R). Patches were therefore twice more numerous and opulent in R than in P, but their mean sizes did not differ. For simplicity, I assumed that the animal moved at a constant speed and could detect any prey item located at less than 0.5u from the path (i.e., \( W_{\text{item}} = 1u \); see Benhamou [1992] for a more realistic model where the detection probability is inversely related to the speed). The prey item was then removed, involving a local depletion of the patches, but replaced to its initial location after the animal has traveled 500u, to keep the overall prey distribution constant. The results were obtained with a simulated path of \( 1 \times 10^7u \) in each case, and the foraging efficiency was expressed relatively to that of a straight line search (equal either to 0.01 [P] or 0.04 [R] item harvested per unit length traveled).

The efficiency of an animal performing a MRW with constant step length \( l \) did not depend on the habitat richness. It was found to be only 0.35 with \( l = 1u \) (Fig. 4). It increased with \( l \) and converged toward 1 (which is reached with \( l \geq 500u \), as any harvested item had then enough time to renew). The CBW considered here rested on a true two mode search process. It consisted of the animal moving in a straight line until it detected a prey item (and thereby a patch), then performing a MRW with constant step length \( l = 1u \), and finally resuming the straight line movement in a random direction once it has moved a certain distance \( g \) (the “giving-up length”) without detecting any item. This CBW hence corresponded to a mixture of two MRW, one with large steps obeying an exponential distribution, characterizing the inter-patches movements, and the other one with short constant steps \( l = 1u \), characterizing the intra-patch movements. The optimal values of giving-up length were found to be \( g \approx 50u \) in P, or \( g \approx 20u \) in R, leading to
Introducing some forward persistence in the intensive search mode (i.e., converting the intra-patch MRW into a CRW) only slightly increased the efficiency. In contrast, if the intensive search mode consisted in performing search loops around the memorized location of the last item detected (see Benhamou 1994), the efficiency reached 3.35 (with $\mu = 50$) in P and 2.69 (with $\mu = 20$) in R, with the search loop parameters set at their optimal values.

Two types of LW can be considered. Full LW, in which prey items are harvested during the flights without involving a reorientation at this level, cannot be very efficient because the series of short flights occur at random with respect to the patch locations. Their dynamics are dominated by very long flights, so that the efficiency was found to be very close to 1, whatever the habitat richness and the value of the exponent $l = 2.7$. Above this value, the efficiency tended to decrease, reaching 0.83 for $l = 3$ (which is the limit beyond which a LW reduces to a MRW). In truncated LW (TLW), harvesting a prey item forces the animal to stop its flight there and to draw a new moving direction at random. Hence, the series of short flights tend to occur in the vicinity of the patches because the long sporadic flights, which correspond to relocation phases, tend to be truncated at the patch locations. The best efficiency for a TLW with a minimum step length set to $l_{min} = 0.5$ was found to be equal to 1.21 for an exponent $\mu = 1.7$ in P, and 1.15 for an exponent $\mu = 1.6$ in R (Fig. 4). With higher values of $\mu$, a TLW converges to a MRW and is therefore less efficient. With lower values of $\mu$, the series of short flights are probably too small to allow for an efficient searching. It is worth noting that a TLW with $\mu = 1$ cannot be formally defined, but can be assimilated to a CBW with $\mu = 0$, i.e., an elementary single mode search process able to generate a composite search pattern when items are aggregated. It is the simplest way to model the composite search path of an animal looking for resources in a patchy environment but it is not more efficient than a straight line search (Fig. 4).

**DISCUSSION**

Recent work has suggested that animals from various species (mainly mammals and birds, see references in Introduction) act as Lévy walkers, based primarily on the apparent power law of the observed step length frequency distribution, and sometimes on an additional superdiffusivity criterion. I have shown that using the same criterions, a composite Brownian walker looking for resources that are patchily distributed may be erroneously rated as a Lévy walker. More generally, mixtures of random walks where area-concentrated phases within patches alternate with large distance relocation phases between patches, whatever the precise rules that control them, are liable to mimic to some extent the characteristics of LW, and appeared to be more efficient to harvest aggregated prey items. Distinguishing between these two types of walks when
studying animal actual movements is therefore clearly necessary.

Diffusivity is not likely to be a discriminative property. First, it depends to a large extent on the scale at which the path is studied. At short scale, correlated random walks seem to be superdiffusive because the convergence toward the asymptotic diffusive behavior can be very long (see Benhamou 2006). The CBW also appeared to be superdiffusive at the scale used in Fig. 3 (although no forward persistence was involved), yet less than expected for a LW. More fundamentally, large parts of animal movements encompass some orientation component and are therefore better modeled as biased correlated random walks, which can be highly superdiffusive: when the preferred direction is constant (goal located at infinity), the MSND of such walks tends to increase quadratically with the path length because the advection process dominates over the diffusion process in the long term (Marsh and Jones 1988, Turchin 1998, Benhamou 2004, 2006). On the other hand, the actual habitat used by an animal is not infinitely large. In particular, numerous species restrict their movements by themselves within limited areas (home ranges) and so return more or less regularly to the same places. This movement behavior, which can also be modeled as a biased correlated random walk (the goal being a central place rather than located at infinity; e.g., Benhamou 1989), is highly subdiffusive in the long term. A subdiffusive behavior may also appear at short scale due to the obstacles encountered in heterogeneous landscapes (Johnson et al. 1992). Another reason making the diffusivity results very difficult to interpret is the huge variability of the squared net displacement, with a coefficient of variation close to 1 for classical unbiased random walks and even higher for LW. The linear bin-based observed frequency distribution of step lengths also does not provide a discriminative criterion. Hence, numerous animal paths may have been erroneously rated as LW because of the unreliability of the analysis tools used. The survival distribution, and possibly the nonnormalized logarithmic bin-based observed frequency distribution, appears to be the best means to distinguish between LW and mixtures of classical random walks, but they are rarely used. Other methods (e.g., Benhamou 2004, Morales et al. 2004) should also be used to determine whether the movement patterns recorded would be suitably accounted for as a mixture of classical random walks.

The recent fascination with LW is undoubtedly due to their assumed optimizing potential. Cole (1995) showed that LW are more efficient than MRW for foraging on prey items uniformly distributed in a bounded area. MRW are known to be very inefficient, however, as they lead the predator to search too many times at the same places. Their efficiency can be easily increased by introducing some forward persistence as a correlation in the successive moving directions (e.g., Bovet and Benhamou 1991). Recently, Bartumeus et al. (2005) showed that a truncated LW with \(1 < \mu < 3\) is more efficient than a correlated random walk with a forward persistence \(0 < P = 1.5 – \mu/2 < 1\) for foraging on prey items uniformly distributed over an infinitely large environment. The search efficiency increases as \(P\) increases or as \(\mu\) decreases, and the best moving strategy in this context is obviously the straight line (corresponding to the extreme values \(P = 1\) or \(\mu = 1\)). Truncated LW have been shown to be more efficient than correlated random walks for foraging on sparse, motionless (or slow moving) resources that are uniformly distributed in space and that renew immediately (“non-destructive” foraging), with an optimal value of \(\mu\) close to 2 (Viswanathan et al. 1999, Bartumeus et al. 2005, Reynolds 2006). In this peculiar context, however, the best searching strategy consists in either not moving at all or in shuttling back and forth between two close sites, if the renewal process requires that the predator leaves the target site. Although many foragers, such as nectar-feeding insects, do not literally destroy the target sites they exploit, they tend to lower the local resources to a minimum level (predicted by the marginal value theorem; e.g., Pleasants [1989]) and should therefore, to be efficient, avoid these sites for a while. In most natural environments, resources are not uniformly distributed but aggregated in patches which renew only progressively. Non-destructive foraging on uniformly distributed prey items hence seems to be a quite unrealistic situation. It has been claimed by Viswanathan et al. (1999) to act as a proxy for usual (destructive) foraging on prey items that are patchily distributed but, then, LW are unsurprisingly surpassed by CBW. Indeed, once a patch has been reached, both a truncated Levy walker and a composite Brownian walker will tend to perform a tortuous path, but only the latter is able to control the duration of its area-concentrated search mode as a function of the local patch richness (through the giving up length). It is also worth noting that composite walks seem also to be a valuable alternative to LW for maximizing the probability of finding a cryptic item in a fixed time (Bénichou et al. 2006, Shlesinger 2006). It is therefore somewhat dubious that, maybe except in some particular situations, optimizing search efficiency acts as an evolutionary pressure toward relying on LW processes in animal movements.

In most cases, the movement patterns classically observed, where relatively frequent and short steps are interspersed with relatively scarce and large ones, are likely to correspond to an adaptation of movements to the patchiness of the environment (rather than to a spontaneously generated power–law distribution of step lengths). Patterns should not be confused with processes (Chapleau et al. 1988). To be useful, a movement model should be able not only to account for the patterns observed but also, and more fundamentally, to throw some light on the processes that generates them from the way an animal is assumed to interact with its environment. Because of the existence of multiple spatial scales
(Wiens 1989), animals may adapt to their environments by performing either scale-free or multiple scale-specific movements, depending on the landscape nature. When an animal moves through a fractal landscape (e.g., corresponding to a hierarchical patch system; see Fauchald [1999]), an LW pattern may result from an efficient search for resources that are distributed in self-similar ways across various environmental scales, as illustrated by a very interesting twofold study on spider monkeys. Ramos-Fernández et al. (2004) provided some evidence that these primates displayed LW patterns when searching for fruits in their tropical forest. In a second round, Boyer et al. (2006) showed that the search patterns observed may be generated by an optimal foraging movement model that does not rest on a LW process: the animals were assumed to have memorized the values and the locations of the fruit trees, and to choose the next tree to visit based on a ranking of the profitability (tree value per traveling distance). This optimal strategy resulted in a LW search pattern because of the power–law distribution of tree sizes. In patchy but non-fractal environments, a seemingly LW pattern may also emerge. LW hence may act as a more or less useful way to model animal search patterns in patchy environments (e.g., Gautestad and Mysterud 2005), like the negative binomial distribution provides a simple way to model resource patterns. Understanding the processes giving rise to the latter patterns rests on a composite approach specifying how patches occur in the environment and how resources are distributed between and within patches. Similarly, in most cases, the movement processes involved may be better understood through composite models based on mixtures of classical random walks (e.g., Benhamou 1990, 2004, Zollner and Lima 1999, Johnson et al. 2002, Morales et al. 2004), which can highlight scale-specific decision rules, such as those specifying when to leave a patch or return to a central place, or how to allocate global search effort in the various parts of a home range, to name a few ones that have been addressed in the framework of optimal foraging theory.

Determining whether a given animal really moves using a LW process eventually requires a two-level procedure. First, one has to ascertain whether the movement pattern observed corresponds to a true LW pattern, i.e., the survival distribution of step lengths obeys an inverse power law with an exponent $\alpha < 2$ (rather than their linear bin-based observed frequency distribution obeys an inverse power law with an exponent $\mu < 3$, as usually done). Second, one has to ascertain whether the pattern observed may be intrinsically generated (e.g., Cole 1995) rather than being the by-product of the way the animal interacts with its particular environment through some classical movement process (e.g., Boyer et al. 2006). If the pattern observed is just a seeming LW pattern, it was likely to have been generated by a mixture of classical movement processes. Otherwise, it would be necessary to check whether the environment structure does not present some free-scale properties liable to force some classical movement process to generate a LW pattern. To attempt to identify the movement process actually involved, one should first consider carefully how the emergent movement pattern was recorded and analyzed. Location data are often discrete sample points of curvilinear paths, i.e., do not correspond to behaviorally significant events. The turning angle and step length distributions obtained are therefore arbitrary, but the way the sampling rate affects them in classical random walks is known (Bovet and Benhamou 1988, Benhamou 2004, Codling and Hill 2005). In contrast, Lévy flights are assumed to correspond to actual moves between true reorientation events rather than to arbitrary steps. This holds true in the study by Viswanathan et al. (1996), where data corresponded to actual behavioral changes (the times when an albatross “landed” on the sea, presumably to eat), although no locations were recorded (the resultant walk was inferred by assuming a constant moving speed and a random reorientation process between flights). In most other field studies focusing on LW, in contrast, location data were recorded at fixed time intervals, so that the “flight lengths” corresponded to speeds rather than to distances between biologically significant events. Much more care than usually done is therefore required before claiming that a given animal did the Lévy walk.

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**Literature Cited**


