Lévy or Not? Analysing Positional Data from Animal Movement Paths

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Abstract The Lévy walk hypothesis asserts that the optimal search strategy for a forager under specific conditions is to make successive movement steps that have uniformly random directions and lengths drawn from a probability distribution that is heavy-tailed. This idea has generated a huge amount of interest, with numerous studies providing empirical evidence in support of the hypothesis and others criticising some of the methods employed in these. The most common method for identifying Lévy walk behaviour in movement data is to fit a set of candidate distributions to the observed step lengths using maximum likelihood methods. Commonly used candidate distributions are the exponential distribution and the power-law (Pareto) distribution, both on an infinite and a finite (truncated) range. Data sets for which the relative fit of a power-law distribution is better than that of an exponential are typically classified as Lévy walks. However, the movement pattern of the Lévy walk is similar to that of an animal that switches between two behavioural modes in a composite correlated random walk (CCRW) movement process. Recent studies have shown that standard approaches can misidentify the CCRW process as a Levy walk. This misidentification can be due to the methods used to sample and process the data, a failure to assess the absolute fit of the candidate distributions, or the lack of a strong alternative model. In this chapter, we simulate a CCRW process and show that including a composite exponential distribution in the set of candidate

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distributions can alleviate the problem of misidentification. However, in some cases sampling and processing of the CCRW data can cause a power-law distribution to have a better fit than a composite exponential. In such cases, the absolute goodness-of-fit of the power-law distribution is typically poor, indicating that none of the candidate distributions are a good model for the data. We discuss the relevance of these results for the analysis of empirical movement data.

1 Introduction

1.1 Lévy Walks

The Lévy walk hypothesis, originally posed by Klafter et al. and Cole [19, 34] and subsequently by Viswanathan et al. [64], asserts that the optimal search strategy for a forager with limited perceptive range and no prior knowledge of the distribution of food in the environment is to move according to a Lévy walk (LW). This means taking a series of steps of (uniformly) random direction and of length l drawn from a probability distribution that is heavy-tailed, meaning that it does not have finite variance [55]. The most commonly used such distribution is the Pareto distribution, with probability density function

$$p(l) = Cl^{-\mu}, \qquad l > l_{\min}, \tag{1}$$

where $1 < \mu \leq 3$ and C is a normalization constant given by $C = (\mu - 1)l_{\min}^{\mu-1}$. Note that, in genral, there may also be steps of length $l < l_{\min}$, but the distribution of these step lengths is not important and it is the power-law tail described by (1) that characterises a Lévy walk.

In foraging models, steps are truncated at points where the forager finds a food item [64] and so the search strategy is sometimes referred to as a truncated Lévy walk (TLW). Note that a 'pure' Lévy walk where steps are not truncated after encounters is no more efficient as a search strategy than movement in a straight line, as demonstrated in [10]. Similarly, almost all theoretical LW search models rest on the assumption that each new search begins with a food item just outside the perceptive range of the forager [64]. This can be thought of as representing a highly patchy distribution of food. However, the advantage of any LW strategy is rapidly diminished when each search begins with the nearest food item significantly further away than the forager's perceptive range [31, 51].

The original Lévy hypothesis was motivated by the presence of heavy-tailed power-law distributions in empirical movement data from plankton [34], fruit flies [19] and albatrosses [64]. The Lévy walk hypothesis has since generated a huge amount of interest, with numerous studies providing empirical evidence in support of the hypothesis [1, 3, 6, 15, 20, 30, 40, 48, 53, 57], and others criticising some of the methods employed in these [22–24, 56]. In tandem with the empirical evidence, several studies have investigated the efficiency of Lévy walks in various theoretical search scenarios. For recent reviews of Lévy walks as models of animal movement, see [31] and [67].

A key property of a non-truncated Lévy walk is that it is scale-free, meaning that the sampling scale used by the observer should not affect the observed properties [52]. In particular, a Lévy walk (LW) is known to be superdiffusive at all scales [65, 66]. However, a truncated Lévy walk cannot be truly scale-free at all spatial scales given the truncation inherent in the process when food items are encountered. Similarly, when considering an environment of finite size or the upper limit to the speed an animal can achieve, it is not possible to have arbitrarily large step lengths as could (theoretically) be generated in both the pure LW and the TLW. Hence the scale-free nature of Lévy walks is perhaps over-emphasised and looking for scale-free characteristics in observed movement data may not be a reliable way of detecting Lévy walk behaviour.

1.2 Correlated Random Walks and Composite Strategies

A more classical approach for modelling movement behaviour is the correlated random walk (CRW), in which there is some directional persistence from one step to the next [18, 42]. In a CRW, step lengths are drawn from a distribution with finite mean and variance, such as an exponential distribution. An important property of such distributions is that they satisfy the conditions of the central limit theorem, which implies that the random walk is diffusive in the long-term. Changes in direction between successive steps are not uniformly distributed, but are drawn from some circular distribution that is typically peaked about 0, for example the von Mises distribution [39]. The more concentrated this turning angle distribution is about 0, the more directional persistence the CRW will have in the short term.

In contrast to a Lévy walk, a simple CRW is not scale-free and the sampling rate used by the observer is known to have a significant effect on the apparent properties of the movement pattern in a CRW [14, 16, 28]. Although CRWs are always diffusive over sufficiently long timescale, they can appear superdiffusive over short timescales, depending on the level of persistence in the movement [5,63,65]. In this context, it should be noted that a TLW will also appear diffusive at large timescales due to the truncation of long steps.

The basic CRW essentially assumes that movement is modelled as a stationary process, meaning that the parameters governing the persistence in movement do not change with time or space. However, many animals have been observed to display intermittent behaviour, where the forager's movements consist of a mixture of movement strategies (possibly different types of CRWs) [7, 32, 35, 37, 41]. One approach to modelling this behaviour is to use a composite random walk. This is a random walk consisting of more than one distinct behavioural phase, e.g. an extensive phase, in which the forager covers large distances with relatively little turning, and an intensive phase, in which the forager searches a smaller area with a more tortuous path. (Intensive searching is sometimes termed an area-restricted search [36].) A composite random walk model was first proposed as an alternative to the Lévy walk strategy by Bénichou et al. [12, 13]. Benhamou [10] proposed a composite two-phase random walk model for a forager searching for food in a patchy food environment based on memory of encounters. In the first phase, termed the intensive phase, the forager moves according to a Brownian random walk. If after a predetermined amount of time (called the giving-up time) the forager has not located a food item, it switches to a ballistic (straight line movement) strategy until it finds a food item. It then reverts to the intensive strategy to begin the next search. Benhamou [10] showed that this simple composite strategy can be more efficient (i.e. the mean distance travelled between food items is lower) than a truncated Lévy walk.

Reynolds [49, 50] subsequently showed that in certain contexts an even higher efficiency could be obtained by switching to a TLW in the second phase of the composite process, rather than to ballistic motion (which can be viewed as a special case of a LW with $\mu \to 1$). Bartumeus and Levin [5] considered a "Lévy modulated" correlated random walk (CRW), where random reorientations, which break the short-term directional persistence of the CRW, occur after periods of time drawn from a power-law distribution. It was shown that this can increase the efficiency of the search strategy in certain contexts.

1.3 Determining Movement Processes from Observational Data

Given the current interest and the potential implications of Lévy walks being observed in real animal movement data, it is important to be able to determine robustly that: (i) the observed data set is well represented by a heavy-tailed distribution, and (ii) that the movement mechanism giving rise to this observed pattern is actually a LW process and not some other mechanism. It is the interpretation and validity of these two points across a range of studies that had caused much of the current controversy and discussion in the recent movement ecology literature. For example, with respect to (i), [22, 24] and [23] have demonstrated that many (but not all) of the recent studies that have reported LW behaviour in animal movement data may have been flawed or have wrongly interpreted the data. Similarly, with respect to (ii), a number of recent studies have shown that there are variety of movement mechanisms far removed from a LW that can give rise to heavy-tailed or scale-free characteristics in empirical observations of the movement process [17, 27, 31, 44, 45, 49]. Hence, although the the Lévy walk may be a suitable phenomenological description for a wide variety of movement processes, it may have limited relevance as an underlying mechanistic process in all but the simplest of biological scenarios.

2 Sampling and Processing of Movement Path Data

Standard techniques for analysing movement data are usually based on an arbitrary (spatial or temporal) discretization of the observed movement path [8, 9, 14, 16, 33, 59]. This discretization may be due to experimental constraints (as discussed in the next sections) or may be deliberate in order to determine how particular path properties change at different scales [e.g. 16, 28]. By considering features such as the distributions of turning angles and step lengths across the movement path, it is possible to determine the most likely underlying behavioural process(es) that generate the observed pattern, e.g. distinguishing taxis from kinesis [11, 18]. More sophisticated statistical techniques such as hidden Markov models (HMMs) and state-space models (SSMs), as reviewed in [43], have recently been developed to directly infer underlying behavioural processes and parameters from movement data sets. In contrast, many of the recent studies that look for LW characteristics in observed movement data are often based only on a simple analysis of the observed step lengths where a power-law and exponential distribution are the only candidate models considered in a maximum likelihood test [2, 22, 23].

2.1 Discrete Time Sampling

Animal foraging paths are often observed by recording the forager's position at equally spaced time intervals [e.g. 3, 40, 48]. The distances between successive positional fixes are then used to provide a sample of observed step lengths. Much of the empirical evidence for the Lévy walk hypothesis stems from fitting probability distributions to step length data obtained in this way and testing whether a power-law distribution provides a better fit than other candidate distributions. However, it is important to understand how the sampling rate imposed by the observer may affect the data that is subsequently generated. In most empirical studies the aim is to collect data with as high a resolution as possible and this sampling rate is, therefore, not imposed by choice but is due to experimental or technological limitations, e.g. a limited number of signals per day from a GPS tracker.

In such studies, the forager's path is sampled at discrete time points and this imposes a sampling scale on the random walk. Although true LW are scale-invariant, the question of whether truncated LW, composite CRW, or indeed other random search models are invariant to the sampling scale used by the observer has received relatively little attention. Reynolds [49] looked at the effect of subsampling a LW and analysing the rediscretised data. However, this study only examined the difference in the value of the exponent between the original step length distribution and the distribution fitted to the rediscretised data. No comparison was made between the power-law distribution and any other candidate distribution, nor was the dependence on the sampling rate or the exponent of the underlying LW investigated.

Studies on the scale-invariant properties of movement paths, in particular the scaling of mean squared displacement with respect to time, have compared LW to simple CRW observed over different time scales [5, 65], but have not looked at composite CRW.

Plank and Codling [45] considered a composite CRW model in which the forager has two behavioural phases: an extensive phase characterised by a high speed and low tortuosity; and an intensive phase characterised by low speed and high tortuosity. The forager's position was recorded using a range of different sampling frequencies. A power-law distribution and an exponential distribution were fitted to the resulting data and the relative goodness-of-fit of these two distributions compared. It was shown that the sampling scale can have a dramatic effect on the observed data and that this standard fitting method can produce potentially misleading results. At certain sampling scales, the composite CRW model (where the original step length distribution is not heavy-tailed) can produce data for which a power-law distribution fits better than an exponential distribution. This occurs more frequently when there are significant differences between the movement characteristics of the two phases. Plank and Codling [45] also simulated truncated Lévy walks and found that, whilst less sensitive to sampling scale, these can produce step length data for which an exponential distribution fits better than a power law. Similarly, Codling and Plank [17] demonstrated how the use of different sampling scales can cause the step length distribution in different types of movement data to fit a power-law better than an exponential distribution. This applies particularly to data from a set of CRWs with different levels of persistence or from a three-dimensional CRW viewed in one dimension.

2.2 *Identification of Turning Points*

A further issue with movement path sampling is that the sampling points do not necessarily correspond to actual turning or decision-making points in the underlying movement process. The discretisation of the movement path and the subsequent position of the turning points within the observed path is essentially an arbitrary choice imposed by the observer [8, 14] and hence it is often difficult to interpret true biological meaning from any subsequent analysis of the discretised path. To overcome this issue, attempts have been made to identify turning events as points where the forager undergoes a significant change of direction. There are many different ways in which this can be done. The most common is based on the method of [60] of splitting an observed path into a series of straight-line moves. The direction is monitored at each sampling point and a turning event is registered if the current direction deviates from the direction at the previous turning event by more than a specified threshold angle. This is a "non-local" or "cumulative" identification method as it allows a gradual accumulation of change in direction to be eventually registered as a turning event (Fig. 1a). An alternative is to use a "local" identification method, which only considers the change in direction

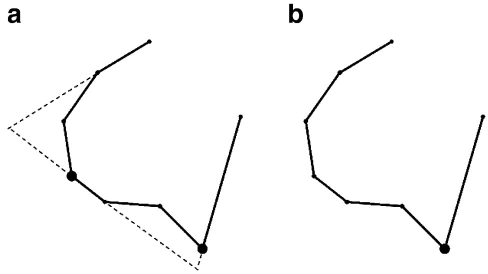

Fig. 1 Diagram illustrating: (**a**) non-local turn identification; (**b**) local turn identification. Identified turning points are indicated by *large solid circles*. With non-local turn designation, turns are identified when the cumulative change of direction from the previous turning event exceeds some threshold angle θ_0. In contrast, local turning identifies turns when the angle between two successive observed random walk steps exceeds some threshold angle θ_0. In this example a threshold angle of 90° is used. A gradual change in movement direction is not identified as a turning event using the local turn designation. Note that with both processing methods, small turns are removed from the data set, while the number of observed steps decreases but the lengths of these observed steps typically increase

between successive observations [17,53] (Fig. 1b). However, this method is sensitive to the sampling scale imposed by the observer. For example, at a high-resolution sampling scale, a local method may fail to identify large changes in direction if they are spread over several observations. For this reason, we will focus primarily on the non-local turn identification method in the rest of this chapter. The identification of turning events can be thought of as a post-processing step on sub-sampled data of the type considered by Turchin [58]. The straight-line distances between the identified turning points become the new "step lengths" and these data can be analysed using standard statistical methods. Reynolds and Frye [53] used a local and a non-local turn identification method to infer movement mechanisms from tracking data for honey bees. An alternative method for identifying turning points was used by de Jager et al. [20]: the autocorrelation between movement directions was monitored over a number of successive steps and once this autocorrelation reduced below some pre-defined threshold level, a turning point was identified. Results produced using this method are qualitatively similar to the non-local turn identification described above.

Codling and Plank [17] considered the effect of turn identification on data from a composite CRW model. The threshold angle used to identify turning events is essentially arbitrary and the sensitivity of results to this parameter, as well as to the sampling scale, was investigated. The results of [17] show that turn-identification can alter the results of a relative goodness-of-fit test of the power-law and exponential distributions. In some scenarios it was shown that the less sensitive the turn identification method used (i.e. the larger the threshold angle for registering a turn), the more likely the relative test is to favour a power-law distribution.

Note that processing of the movement data set to identify turning points using any of the methods described above will typically remove a large number of small turns from the data set; these small turns are usually assumed to be noise or minor directional corrections that do not correspond to a global reorientation event in the movement path [e.g. 6]. However, this sort of processing will clearly produce a non-uniform distribution of turning angles since small turning angles will have been removed. In contrast, a theoretical LW or TLW should have a uniform distribution of turning angles. However, as we show later, a true LW processed in the above manner would also produce a non-uniform distribution of turning angles. Hence, it remains unclear whether studies that identify a power-law distribution of step lengths should be classified as Lévy walks if the turning angles are non-uniform; there does not currently appear to be a robust method of using turning angle data to help identify LW patterns in movement data.

3 Analysing Data from a Composite Correlated Random Walk

In this section, we consider data generated using a composite CRW model and post-processed using a range of sampling scales and threshold angles for turn identification as described above. Motivated by the discussion in [2] and [46], our aim is to determine whether a composite exponential distribution will fit the data generated from a composite CRW better than a simple exponential or a power-law distribution, given that the data is sampled and processed in a similar way to [45] and [17]. In particular, we are interested to see if there are certain sampling and processing scenarios where the generated data fits a power-law distribution better (which may consequently be (mis)interpreted as the data having come from a Lévy walk process).

We also examine the distribution of observed turning angles, i.e. the changes in direction between successive sample points. This is motivated by the fact that LW have a uniform distribution of turning angles, whereas CRW (or any movement process incorporating directional persistence) have a turning angle distribution that is peaked around zero. In principle, this theoretical difference in the turning angle distribution could be used to distinguish LW from other movement processes and we investigate the efficacy of turning angle tests.

3.1 The Composite Correlated Random Walk Model

We use the composite CRW model of [45], which consists of two phases (note that other alternative models for a composite random walk are possible and we only consider a very simple case here). Phase 1 (the intensive phase) is characterised by small mean step length and a lack of directional persistence. Phase 2 (the extensive phase) is characterised by high mean step length and high directional persistence. At each step in phase i, the forager has a fixed probability $p_{\text{switch},i}$ of switching to

Table 1 Parameter values for composite CRW model

Parameter	Phase 1 value	Phase 2 value
Mean step length $\bar{l}$	1	10
Turning angle concentration κ	0	50
Probability of switching phases p_{switch}	0.01	0.01

Step lengths l are drawn from an exponential distribution with mean $\bar{l}$: $p(l) = \exp(-l/\bar{l})$. Turning angles ϕ are drawn from a zero-centred von Mises distribution with concentration parameter κ: $p(\phi) = Ce^{\kappa \cos\phi}$, where C is a normalization constant. All simulated random walks have a total of $N_{\text{RW}} = 1,000$ steps

the other phase. Thus the number of consecutive steps in phase i is geometrically distributed with mean $1/p_{\text{switch},i}$. The random walk is initialised in a statistically stationary state with respect to the two phases, i.e. the forager starts in phase i with probability $p_{\text{switch},i}/(p_{\text{switch},i} + p_{\text{switch},j})$. The parameter values and step length and turning angle distributions used in the simulations are given in Table 1.

In each case, N_{RW} steps of the composite CRW model were simulated, giving positional data (x_i, y_i) for $i = 0, \ldots, N_{\text{RW}}$. As in [17], these positional data were first sampled with a fixed sampling time step δ. This leads to a subsample of positions $(x_{j\delta}, y_{j\delta})$ for $j = 1, \ldots, N_{\text{RW}}/\delta$. This subsample was then subjected to a turn identification algorithm with threshold angle θ_0 [see 17, for full details], giving a sample of turning point locations. The cosine of the threshold angle θ_0 is denoted by c_0. Note that $\delta = 1$ corresponds to complete sampling (every step of the random walk is recorded) and $c_0 = 1$ (equivalent to $\theta_0 = 0$) corresponds to no turn identification (every recorded location is defined to be a "turning point"). The combination $\delta = 1$, $c_0 = 1$ is therefore a control case in which there is "perfect information". From the turning point location data, a sample of observed step lengths d_i and a sample of observed turning angles ϕ_i are constructed. An example realisation of the composite CRW model and illustration of the effects of sampling and turn identification are shown in Fig. 2.

3.2 Fitting a Composite Exponential Distribution

Auger-Méthé et al. [2] criticised the work of Plank and Codling [45] on the grounds that a simple exponential distribution should not be expected to provide a good fit to data from a process consisting of two distinct types of behaviour. Instead, it was suggested that the absolute goodness-of-fit of candidate distributions should be assessed, rather than simply conducting a relative test of two potentially poor models. This is certainly true and this motivates us to fit a composite exponential distribution to data generated from the composite CRW model of [45]. However, because of subsampling and turn identification, the observed data may not always be well described by a composite exponential distribution [46].

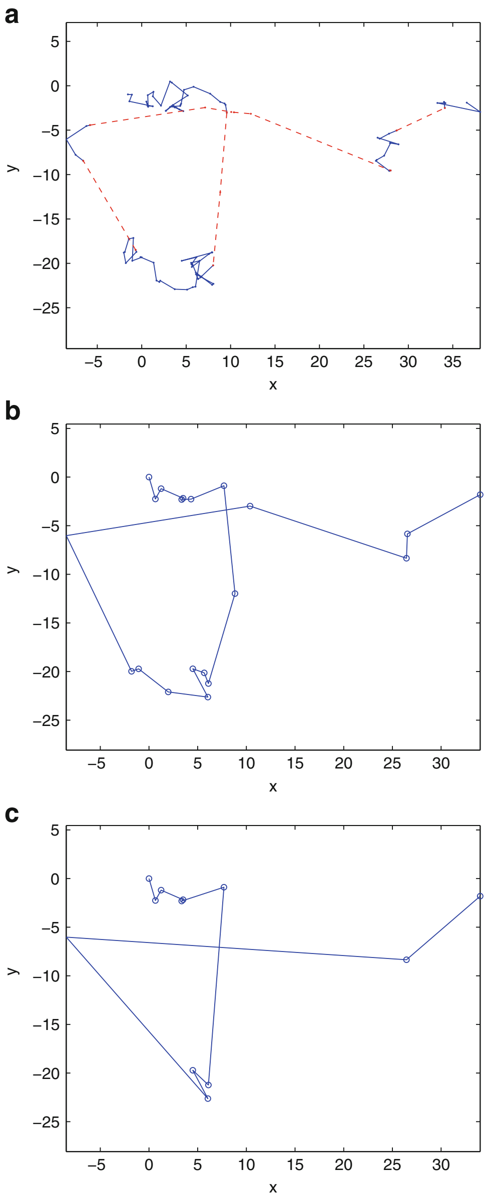

Fig. 2 An example realisation of the composite CRW model: (**a**) the actual path (*solid* and *dashed lines* indicate steps from the extensive and intensive phases respectively); (**b**) the observed locations with a sampling step of $\delta = 5$; (**c**) the identified turning points of the subsampled path shown in (**b**), using a threshold turning angle cosine of $c_0 = 0.5$. Parameter values for the composite CRW are as given in Table 1 except for the switching probabilities $p_{\text{switch1}} = 0.05$ and $p_{\text{switch2}} = 0.4$

A composite exponential distribution is simply a combination of n exponential distributions, each with its own parameter λ_i and its own probability weighting P_i ($i = 1, \ldots, n$), such that

$$\sum_{i=1}^{n} P_i = 1. \tag{2}$$

This is an example of a mixture model. A random deviate from the composite distribution is simply a random deviate from the ith individual distribution with probability p_i. The composite distribution thus has probability density function (PDF)

$$p(d) = \sum_{i=1}^{n} P_i \lambda_i e^{-\lambda_i d}.$$

Since we are fitting data from a composite CRW model with two phases, we consider a double exponential distribution ($n = 2$). This distribution has three parameters: the parameter for each of the two exponential distributions, λ_1 and λ_2, and the proportion P_1 of step lengths that are drawn from the first exponential. (The parameter P_2 is then determined by the constraint (2).) Note that the simple exponential distribution and the power-law distribution each have just one fitted parameter.

In the "perfect information" case ($\delta = 1$ and $c_0 = 1$), the double exponential distribution provides an exact fit to the composite CRW model. The parameters λ_1 and λ_2 correspond to the mean step lengths in the two phases ($\lambda_i = 1/\bar{l}_i$) and the parameter P_1 corresponds to the proportion of steps that are in phase 1 ($P_1 = p_{\text{switch},1}/(p_{\text{switch},1} + p_{\text{switch},2})$). When there is imperfect sampling, the double exponential distribution will provide an imperfect fit and the fitted parameters will deviate from the underlying random walk parameters.

The log-likelihood of a sample $\{d_1, \ldots, d_N\}$ is

$$L = \sum_{i=1}^{N} \ln\left(p(d_i)\right). \tag{3}$$

The maximum likelihood estimates for the three model parameters $\mathbf{v} = \{\lambda_1, \lambda_2, P_1\}$ are found by solving the three simultaneous equations

$$\frac{\partial L}{\partial v_i} = 0, \qquad \text{for } i = 1, 2, 3. \tag{4}$$

These equations are highly nonlinear and must be solved numerically. This was achieved using Newton's method, taking care to ensure solutions satisfy $\lambda_1, \lambda_2 > 0$ and $0 \leq P_1 \leq 1$. Once the maximum likelihood values for the parameters have been calculated, these are substituted into (3) to calculate the log-likelihood. The Akaike information criterion (AIC) is then calculated according to

$$\text{AIC} = -2L + 2K,$$

where K is the number of fitted parameters ($K = 3$ for the double exponential distribution). The AIC therefore penalises the double exponential distribution relative to the single exponential and power-law distributions in accordance with its additional fitted parameters. The AIC was calculated for each of the three candidate models (power law, single exponential and double exponential) and these were used to calculate the Akaike weights w_{pow}, w_{exp1} and w_{exp2}. The Akaike weights sum to 1 and the weight for a given model measures the likelihood of that model being the best representation of the data out of the candidate models tested. In addition to the relative test based on AIC, we also carried out a G-test [see for example 21, ch. 11] to test the absolute goodness-of-fit of the preferred distribution, as advocated by Auger-Méthé et al. [2].

Note that although the composite exponential distribution is a more accurate representation of the composite CRW than the simple exponential distribution often used as an alternative to the Lévy walk, it is not the full representation of the composite CRW model used to simulate the data. While the behavioural phases represented in the composite exponential distribution are independent of one another, the behavioural phases of the composite CRW are related to one another through the Markov switching probability, p_{switch}. The full likelihood of the composite CRW would be a hidden Markov model (HMM) incorporating the Markovian dependencies between the behavioural phases. The composite exponential distribution, which is an independent mixture model, is the marginal distribution of the HMM [68] and thus can be an appropriate approximation of the full likelihood [62]. However, the AIC for the composite exponential distribution may differ from that for the full HMM. This potential discrepancy in AIC requires further investigation that is beyond the scope of this chapter. Here we will restrict ourselves to verifying that the AIC will select the composite exponential over the power-law or single exponential distributions for movement data produced by a composite CRW.

3.3 Testing Step Length Data

For each combination of sampling parameter values (δ and c_0), $M = 200$ replicate random walks, each with $N_{\text{RW}} = 1,000$ steps, were simulated. The Akaike weights presented in this section were obtained by averaging the Akaike weight across the M replicate simulations.

For all cases tested, the Akaike weight of the single exponential distribution w_{exp1} was always zero, indicating that this distribution is never the best fit of the three distributions tested. From here on, we only consider the Akaike weights for the double exponential and power-law distributions.

When there is no subsampling or turn identification ($\delta = 1$ and $c_0 = 1$), the Akaike weight for the double exponential distribution is always 1 (and the weight for the power-law distribution is 0). The absolute goodness-of-fit of the double exponential distribution is also good (G-test gives $P \gg 0.05$). These results are not surprising as, provided that the number of random walk steps is large enough so that the two phases of the composite random walk both occur within the movement path, the observed data will be drawn from a double exponential distribution. The underlying random walk parameters are almost exactly recovered by the maximum

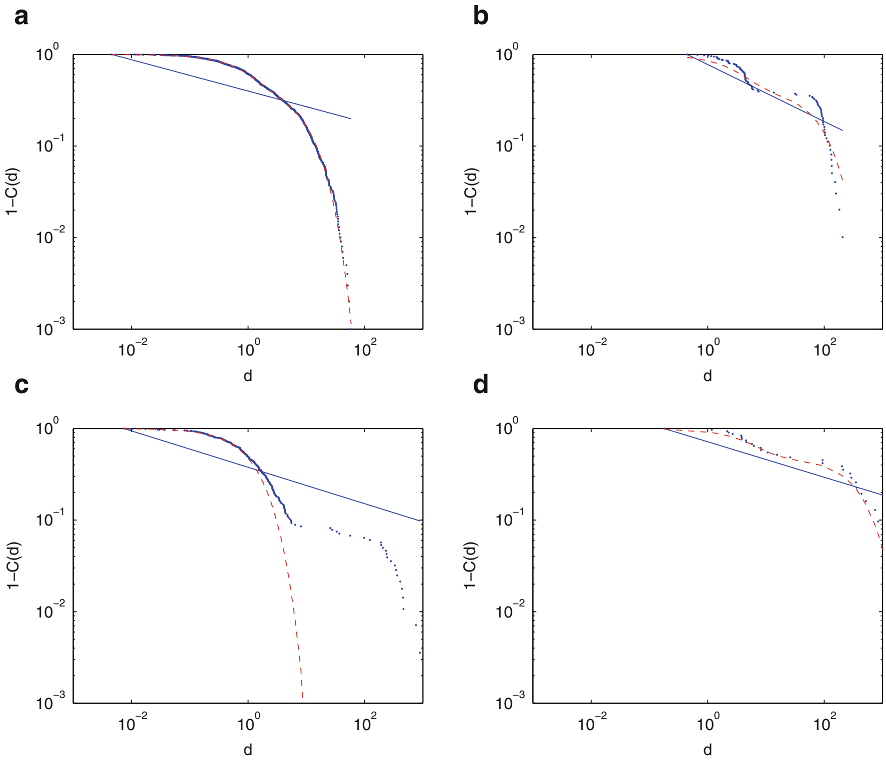

Fig. 3 Survival function $1 - C(d)$, where $C(d)$ is the cumulative distribution function, for observed step length data (*points*) together with the best-fit power-law distribution (*solid curve*) and double exponential distribution (*dashed curve*): (**a**) raw composite CRW data ($\delta = 1, c_0 = 1$); (**b**) subsampling but no turn identification ($\delta = 10,\ c_0 = 1$); (**c**) turn identification but no subsampling ($\delta = 1,\ c_0 = 0.5$); (**d**) subsampling and turn identification ($\delta = 10,\ c_0 = 0.5$). In (**a**), (**b**) and (**d**), the double exponential has the highest Akaike weight; in (**c**) the power-law has the highest Akaike weight ($\mu = 1.2$). Parameter values as in Table 1; $n = 1,000$ random walk steps

likelihood estimation (4) (i.e. $P_1 = 0.5$, $\lambda_1 = 1/\bar{l}_1$ and $\lambda_2 = 1/\bar{l}_2$). An example of the step lengths and fitted distributions for $\delta = 1$ and $c_0 = 1$ is shown in Fig. 3a.

Figure 3b–d show examples of the observed step lengths and fitted distributions for cases where there is either some subsampling of the forager's location or some turn identification (or both). In (b) and (d), where there is some subsampling, the double exponential distribution fits better than the power law. However, in (c), where there is turn identification but no subsampling, the power-law distribution provides the better fit. This is due mainly to the existence of a small number of very large step lengths (up to 10^5 times longer than the smallest observations), although it is clear in this case that neither model provides a good absolute fit to the data (G-test gives $P < 10^{-8}$ for both models).

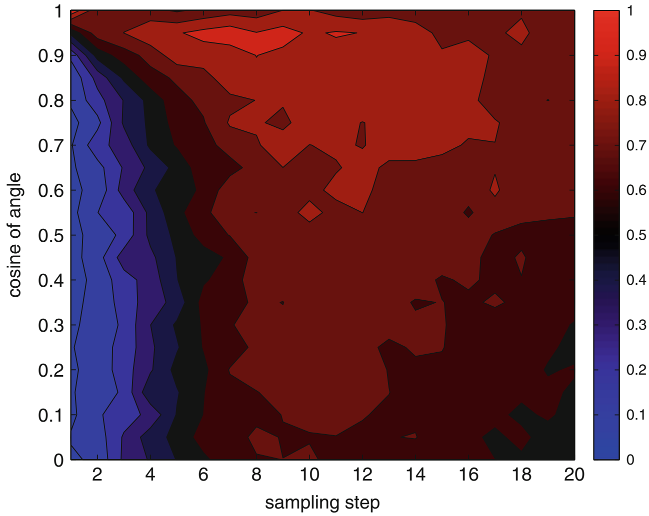

Fig. 4 Average Akaike weight for the double exponential distribution against sampling step size δ and cosine of threshold turn identification angle c_0. *Red areas* indicate cases where the double exponential distribution has the better fit ($w_{\text{exp2}} > 0.5$); *blue areas* indicate cases where the power-law distribution has the better fit ($w_{\text{exp2}} < 0.5$)

Figure 4 shows the outcome of the AIC test (Akaike weight w_{exp2} averaged over $m = 200$ realisations of the random walk model) for the double exponential distribution for a range of values of the sampling step size δ and cosine of threshold angle c_0. For most combinations of these two sampling parameters, the double exponential distribution is favoured over the power-law distribution ($w_{\text{exp2}} > 0.5$). However, as seen already in Fig. 3, when the sampling step δ is small (i.e. the sampling frequency is high) and some degree of turn identification is used ($c_0 < 1$), the power-law distribution is favoured ($w_{\text{exp2}} < 0.5$). This shows that, even when fitting candidate distributions that are a good representation of the underlying movement mechanism, the inclusion of a turn identification processing step can make the results of a relative goodness-of-fit test misleading.

The absolute fit of the candidate models was also assessed using a G-test. In cases where the double exponential distribution had a better fit than the power law, the double exponential distribution was not rejected at the 1 % level ($P > 0.01$). In all cases where the power-law has a better fit (blue areas of Fig. 4), the power-law was rejected at the 1 % level, indicating that neither distribution is a good model for the observed data. It should be noted, however, that the results of the G-test are sensitive to the sample size [46] and that if the sample size is sufficiently small, the power-law model is not rejected. Furthermore, because turn identification reduces the number of observed step lengths, this process tends to increase the likelihood of a given candidate distribution providing an acceptable fit to a given movement path.

Table 2 Results of the Rayleigh test of uniformity for a composite CRW and LW subsampled and processed to identify turning events

Random walk	(a) Control	(b) Subsampling	(c) Turn ID	(d) Subsampling and turn ID
Composite CRW	$R = 0.510$ $P = 0$	$R = 0.438$ $P = 0$	$R = 0.374$ $P = 0$	$R = 0.279$ $P = 0$
Lévy walk	$R = 0.001$ $P = 0.738$	$R = 0.006$ $P = 0.502$	$R = 0.400$ $P = 0$	$R = 0.406$ $P = 0$

For uniformity we expect $R \approx 0$; the P value gives the probability that the generated turning angle data comes from a uniform circular distribution. All values are given to three decimal places

3.4 Testing Uniformity of Turning Angles

To test for uniformity in the turning angles and to determine the effect that sampling and processing of the observed data may have, we complete a Rayleigh test for uniformity on the distribution of turning angles that is generated after sampling and processing (turn identification). The Rayleigh test is the simplest possible test of uniformity for circular data and is based on testing the mean resultant length, R, of the set of angles. A uniform distribution of angles should have $R \approx 0$ and hence the Rayleigh test considers the probability of a given R value being produced given the size of the data set and the assumption of uniformity. For further details see [39] and [61]; for our generated data we used the Rayleigh test that forms part of the CircStats package in R [47].

We considered three different sampling and turn processing scenarios and completed a Rayleigh test of uniformity for the generated turning angles from a composite CRW, with parameter values as in Table 1, and a LW with $\mu = 2.25$. In each case, the data from $M = 200$ replicate random walk simulations, each with $N_{\mathrm{RW}} = 1,000$ random walk steps, were pooled into a single sample of $N_{\mathrm{RW}}M = 200,000$ steps. The scenarios considered were: (a) no subsampling or turn processing (control); (b) subsampling only with $\delta = 10$; (c) non-local turn identification only with cosine threshold angle $c_0 = 0.5$; (d) both subsampling ($\delta = 10$) and turn identification ($c_0 = 0.5$). Although these choices of δ and c_0 are arbitrary, the results are not highly sensitive to variations in either of these parameters (Table 2).

The Rayleigh test demonstrates that the turning angles in a LW with or without subsampling, but with no turn processing, (scenarios (a) and (b)) would not be rejected as coming from a uniform distribution ($P > 0.5$ in both cases). However, any form of turn processing will clearly remove small turns from the data set and hence make the observed distribution of turn angles non-uniform. Hence, a LW that is processed in this manner no longer appears to have a uniform distribution of turning angles (scenarios c and d have $P \approx 0$). In all scenarios, the composite CRW has $P \approx 0$ and the assumption of uniformity of turning angles is rejected in all cases. These results illustrate how data on turning angles would only be useful to distinguish between a LW and a composite CRW if there is no turn identification mechanism in the analysis of the data.

4 Discussion

In this chapter, we have shown how the analysis of step-length data collected from regular sampling of an animal's movement path can be extended to include fitting a composite exponential distribution. In the case of a composite random walk movement process [e.g. 10,17,45], one would expect this to provide a better fit to the data than a simple exponential distribution, which is commonly used as an alternative candidate to the power-law distribution associated with a Lévy walk [23,31].

For the two-phase movement model considered here, the results show that a double exponential distribution always provides a better fit to observed step length data than a simple exponential. Furthermore, in most cases, the double exponential provides a better fit than a power-law distribution. However, this method is not foolproof and there are cases where the power-law fits better than the double exponential distribution, despite the fact that the movement process is not a Lévy walk. Of the scenarios considered here, the power-law has a better fit than the double exponential when using a relatively high-resolution sampling scale (small sampling time step) and performing turn identification. This is largely insensitive to the choice of threshold angle. Nevertheless, the absolute fit of the power-law distribution in these cases is poor, although if the sample size is small there may be insufficient evidence to reject the power-law.

A related issue is that the weight that AIC gives to simplicity decreases as sample size increases [25]. Therefore, the AIC comparison may be biased towards the composite exponential (with three fitted parameters) and away from the power-law (with one fitted parameter) for large sample sizes. Preliminary tests with data generated from a LW nevertheless indicate that the power-law distribution is correctly selected by the AIC test over the composite exponential. However, a thorough investigation of the dependency of this bias on sample size is still needed. The same applies to an investigation of the discrepancy between the AIC resulting from composite exponential likelihood function (4) and that of the full hidden Markov model of the composite CRW model.

Overall, the results presented in this chapter highlight the fact that commonly used sampling and data processing techniques can have a significant impact on the distribution of observed step lengths. The distribution that actually describes the underlying random walk step lengths (the double exponential distribution in the example considered here) may not provide a good fit to the observed data.

Not all movement data are collected by recording spatial locations at equally spaced time intervals. For example, smart position or temperature-transmitting tags (SPOT tags) function through radio transmissions and hence require the tag to have contact with air to send data [38]. These tags are often used to track marine mammals or marine predators [29, 54] and hence spatial location is only recorded when the animal is at the surface. Consequently, it is likely that any data collected on the movements of these animals have been sampled at irregular intervals that depend on the frequency and distribution of times between surfacing for the particular species of interest. Techniques based on continuous-time random walks may aid in the analysis of this type of data set where the times between recordings are themselves a stochastic process. In this chapter, we have only looked at the effect of regular sampling and we have not considered irregular sampling. However, future studies with irregularly sampled positional data should consider this point in more detail.

We have also shown how analysing turning angle data can help distinguish between a Lévy walk, which has a uniform distribution of turning angles, and a random walk with directional persistence, which has a turning angle distribution peaked about zero. If an observed data set was closely approximated by a power-law distribution of step lengths and a uniform distribution of turning angles, it would be a convincing case for a Lévy walk. However, a turning angle test is not useful if a turn identification method, which removes small turning angles, has been applied to the data. In such a scenario, it would be possible for the original process to be a Lévy walk, but for the uniformity of the turning angle distribution to have been lost through turn identification.

A key feature of the Lévy walk hypothesis is that the animal is undergoing a purely random search (rather than interacting with the environment or relying on memory of encounters for example). In most biological scenarios this is unlikely to be true and hence the Lévy walk is arguably more useful as a descriptive tool for classifying particular types of movement process where both small and large steps (intensive and extensive phases) occur, rather than as a true mechanistic model for animal movement (although in very simple biological search scenarios it may be more appropriate). If foragers are performing a random Lévy search (or any other 'purely random' search), then one would expect bouts of intensive searching to occur at random in the environment (corresponding to a typical sequence of short steps in the LW). Conversely, if intensive searching behaviour is correlated with resource-rich areas of the environment, this would suggest that the forager is interacting with the environment. Unfortunately, most movement studies only record the movement data of the animal(s) of interest and do not collect information about the food distribution. However, if data on the occurrence of intensive movement periods can be combined with information about the distribution of resources then it may be possible to determine if the movement process really is a Lévy walk, or whether the path is generated by a composite movement process where the animal interacts with the environment [4, 5, 26].

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