A new approach for objective identification of turns and steps in organism movement data relevant to random walk modelling

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Summary

1. A first step in the analysis of complex movement data often involves discretisation of the path into a series of step-lengths and turns, for example in the analysis of specialised random walks, such as Lévy flights. However, the identification of turning points, and therefore step-lengths, in a tortuous path is dependent on *ad-hoc* parameter choices. Consequently, studies testing for movement patterns in these data, such as Lévy flights, have generated debate. However, studies focusing on one-dimensional (1D) data, as in the vertical displacements of marine pelagic predators, where turning points can be identified unambiguously have provided strong support for Lévy flight movement patterns.

2. Here, we investigate how step-length distributions in 3D movement patterns would be interpreted by tags recording in 1D (i.e. depth) and demonstrate the dimensional symmetry previously shown mathematically for Lévy-flight movements. We test the veracity of this symmetry by simulating several measurement errors common in empirical datasets and find Lévy patterns and exponents to be robust to low-quality movement data.

3. We then consider exponential and composite Brownian random walks and show that these also project into 1D with sufficient symmetry to be clearly identifiable as such.

4. By extending the symmetry paradigm, we propose a new methodology for step-length identification in 2D or 3D movement data. The methodology is successfully demonstrated in a re-analysis of wandering albatross Global Positioning System (GPS) location data previously analysed using a complex methodology to determine bird-landing locations as turning points in a Lévy walk. For this high-resolution GPS data, we show that there is strong evidence for albatross foraging patterns approximated by truncated Lévy flights spanning over 3·5 orders of magnitude.

5. Our simple methodology and freely available software can be used with any 2D or 3D movement data at any scale or resolution and are robust to common empirical measurement errors. The method should find wide applicability in the field of movement ecology spanning the study of motile cells to humans.

Key-words: albatross, cell tracking, correlated random walk, fractal path analysis, Lévy flight, optimal foraging theory, power-law distribution, random walk, satellite tracking, scale-free movement

Introduction

A recent advance within the field of movement ecology that aims to progress our understanding of the mechanisms underpinning search behaviour of diverse organisms has focused on the identification of specialised random walks, such as Lévy flights, principally through the analysis of move step-length distributions arising from recorded movement paths

(Viswanathan *et al.* 1996). A Lévy flight is a special category of super-diffusive random walk where the distribution of move step-lengths fits an inverse power law such that $P(l) \approx l^{-\mu}$ where $1 < \mu \leq 3$ where l is the move step-length and μ the power-law exponent. These movement patterns are characterised by clusters of short move steps connected by rare long relocations, with the pattern being repeated at all scales. Lévy flights (or walks) have generated interest because they have been shown theoretically to optimise searches for sparse resources such as prey, when located beyond an organism's

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sensory range (Viswanathan *et al.* 1999, 2011). Empirical studies have now identified movement patterns consistent with Lévy flights (walks) in individuals from diverse species including insects (Maye *et al.* 2007; Reynolds *et al.* 2009; Bazazi *et al.* 2012; Reynolds 2012), jellyfish (Hays *et al.* 2012), sharks, bony fish, turtles and penguins (Sims *et al.* 2008, 2012; Humphries *et al.* 2010) and seabirds (Humphries *et al.* 2012), as well as from single cells such as *E. coli* and T-cells (Korobkova *et al.* 2004; Harris *et al.* 2012).

Arguably, the most robust evidence for Lévy flight movement patterns in animals has come from studies of pelagic marine predators where move step-lengths have been derived from the depth recordings of electronic tags (Sims *et al.* 2008, 2012; Humphries *et al.* 2010; Hays *et al.* 2012). In one-dimensional (1D) data such as this, vertical displacement step-lengths are straightforward to compute because putative turning points are simple to identify and are unambiguous, being the points where there is a change of direction (i.e. diving or ascending) between consecutive steps. While the 1D turning points identified in this way do not correspond exactly to the actual turning points in the original 3D movement of the animal, the overall scaling properties of Lévy flights are preserved. The step-lengths are analysed using maximum likelihood estimation (MLE) to estimate exponents and goodness-of-fit (GOF) for power-law or exponential distributions (Clauset, Shalizi & Newman 2009; Humphries *et al.* 2010). Testing of the Lévy flight foraging (LFF) hypothesis (Viswanathan, Raposo & da Luz 2008; Viswanathan *et al.* 2011) is mainly concerned with power-law and exponential distributions because the LFF hypothesis predicts that Lévy flight searching is optimal when prey is sparse, whereas simple Brownian (exponential) movements are expected when prey is abundant.

The analysis of horizontal movement paths – in terms of a discrete random walk – for the presence of Lévy or Brownian patterns using MLE requires the identification of turning points in order for the step-lengths to be computed. While Lévy walk characteristics can be identified using functions such as root mean square fluctuation, or mean square displacement, these methods do not provide estimates of exponents and cannot be used to test fully the LFF hypothesis. Turning points are relatively straightforward to identify in the low spatial resolution datasets of animals tracked using Argos satellite transmitters, but the large and variable error fields make such data unsuitable for rigorous testing for Lévy flight behaviour (Bradshaw, Sims & Hays 2007). In some movement data, such as from bacteria, T-cells or desert locusts, the recorded movements are essentially discrete, comprising, for example in the case of *E. coli*, runs and tumbles; in these cases, turn identification is also straightforward. This is also true of some lower resolution data, which is already closer to a discrete approximation of the original movement path.

Tags equipped with Global Positioning System (GPS) sensors now provide data with high spatial accuracy and temporal resolution (Weimerskirch *et al.* 2002; Sims *et al.* 2009); however, testing high-resolution GPS data for Lévy flight patterns has proved problematic because of the difficulties in objectively identifying turning points in a tortuous path (Codling & Plank 2011; Humphries *et al.* 2012). Various methods have been proposed for the identification of turning points, for example, the location of acute turning angles (e.g. Reynolds *et al.* 2007), or the deviation of the movement path from an arbitrary corridor encompassing the trajectory (Turchin 1998; de Knegt *et al.* 2007). However, while the results are dependent on the parameters chosen (Plank & Codling 2009), it can be difficult to set a threshold turning angle, or corridor width, that have a sound basis in the biology of the animal and which are not to some degree contentious. Consequently, the discretisation of the path into steps is in some cases somewhat arbitrary (Reynolds 2010) and parameter choices and the results of the analysis are sometimes difficult to justify. To illustrate the problems, the consequences of differing turn-angle thresholds in GPS data are explored in a sensitivity analysis of wandering albatross data presented in Appendix S1 (section 2). In summary, we found that the number of truncated Pareto-Lévy (TP) distribution fits to the 27 datasets was 4, 17 and 25, for the turn angles 45, 90 and 135°, respectively. While both the number of fits, and the closeness of the fit in many cases, make the results of the analysis using 135° compelling, there is no clear biological justification for that choice of angle. Therefore, it appears that there are potentially significant amounts of 2D data, from diverse species, that at present cannot be used reliably in either Lévy flight or any other random walk movement analysis (e.g. correlated random walks), severely limiting widespread testing of these ideas in ecology.

A study by Sims *et al.* (2008) showed mathematically that a Lévy flight can be projected from 3D to 2D and to 1D with preservation of the power-law exponent. From this, it was suggested that the power-law-distributed 1D vertical displacements of marine predators were indicative of an overarching 3D Lévy flight movement pattern. However, no empirical study has yet shown this to be the case, nor has the dimensional symmetry of a Lévy flight been demonstrated for the TP-Lévy distribution, which was found to be the most common power-law distribution to best fit animal movement data (Humphries *et al.* 2010).

Here, we verify the purported dimensional symmetry of Lévy movement patterns using simulated 3D Lévy distributed move step-length datasets, with a range of exponents, from which any one of the dimensions can be used to form a 1D dataset. The conditions under which the symmetry holds are explored and compared with the results from exponential and composite Brownian (CB) datasets. We examine the effects that tag measurement errors, such as low spatial or temporal resolution, would have on the reliability of identifying move step-lengths, and detecting Lévy flight behaviour, in naturally complex datasets. By extending the symmetry paradigm, we then present a methodology for the identification of step-lengths that can be applied to 2D or 3D data and demonstrate the utility of this methodology in a re-analysis of wandering albatross (*Diomedea exulans*) GPS location data previously analysed for the presence of Lévy flight patterns in the distribution of landing sites (Humphries *et al.* 2012). Software developed to test these ideas is freely available to download with this study.

Materials and methods

SIMULATED DATA

Simulated move step-length datasets for Lévy, Exponential (Brownian) and CB distributions were generated with a range of parameters as described in Appendix S1 (section 1).

EMPIRICAL DATA

High-temporal resolution GPS location data were recorded using GPS loggers attached to 27 *D. exulans* incubating or brooding chicks at the Crozet Islands, Southern Indian Ocean (Weimerskirch, Gault & Cherel 2005; Humphries *et al.* 2012). Adhesive tape was used to attach GPS loggers to each bird's back feathers (Weimerskirch, Doncaster & Cuenot-Chaillet 1994). The tags returned a time series of geographical locations at intervals of between a few seconds to several minutes. Locations were converted to x y coordinates using a plate carrée projection prior to analysis.

DATA ANALYSIS

To test the hypothesis that a Lévy flight exponent (μ) should be symmetrical in all dimensions, data from each dimension were converted to step-lengths by computing the displacement in that dimension between consecutive data points. Maximum likelihood estimation (MLE) analysis was performed on the simulated datasets using the methods described by Clauset, Shalizi & Newman (2009) and Humphries *et al.* (2012) (and Appendix S1, section 9). To verify the GOF, *P*-values were computed using the Monte-Carlo method described by Clauset, Shalizi & Newman (2009). The empirical data model selection, using both Akaike weights and the GOF, was performed as described in Appendix S1 (section 9) and Humphries *et al.* (2012).

Results

ANALYSIS OF SIMULATED DATA

A simulated 3D Lévy dataset ($x_{min} = 1$, $\mu = 2.0$, $x_{max} = 2500$; Fig. 1a) was first analysed with MLE using the step-lengths in
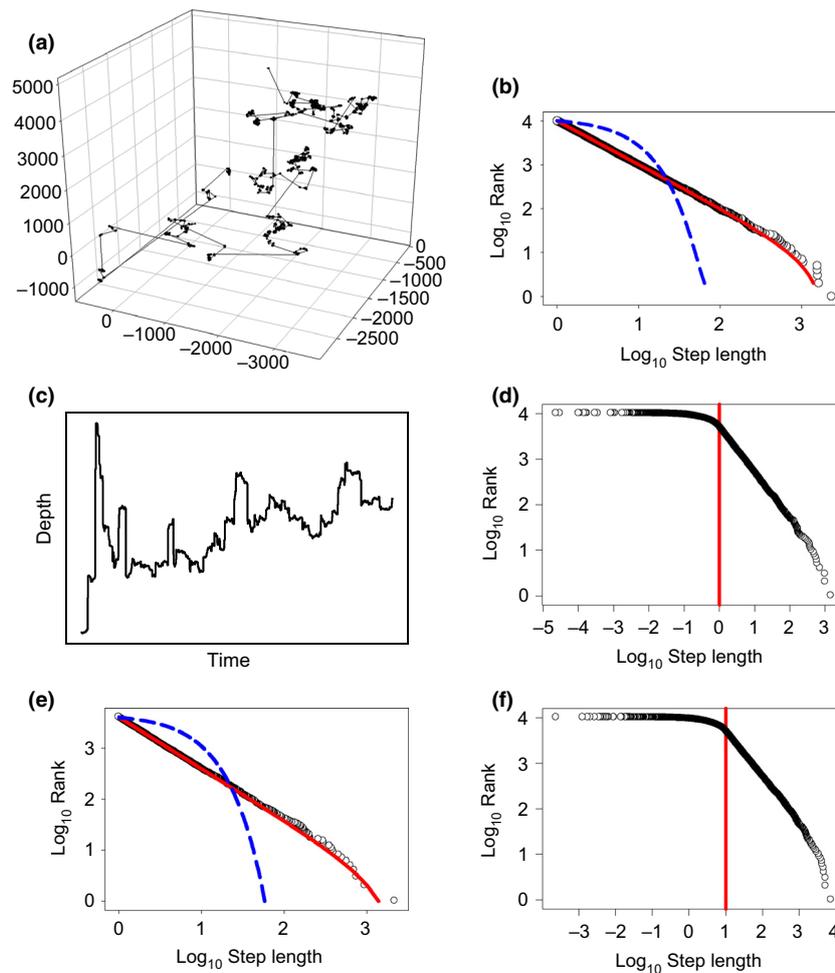

Fig. 1. Three-dimensional and 1D analysis of a 3D Lévy flight. (a) The 3D plot; (b) maximum likelihood estimation (MLE) analysis in 3D showing a good fit with $\mu = 1.996$, very close to the value of 2·0 used to generate the data; (c) vertical displacements from the z axis; (d) rank step-length plot of vertical displacements showing two clear domains, red line indicates x_{min} at a value of 1·0; (e) MLE analysis of step-lengths $>x_{min}$ showing a good fit to truncated Pareto (TP) distribution with $\mu = 2.01$, very close to the original 3D track; black circles are observations, red line is fitted TP, blue dashed line is competing exponential. (f) Rank step-length plot of 1 dimension of a simulated 3D Lévy path with $x_{min} = 10$ and $x_{max} = 10000$, vertical red reference line indicates x_{min}, the plot is visually almost indistinguishable from that shown in (d).

3D to confirm the accuracy of the simulated data (Fig. 1b). A 1D dataset of step-lengths was then computed using just the z axis to give a series of vertical displacements (Fig. 1c). A initial plot of this dataset, however, failed to confirm the expected symmetry with the plot shown in Fig. 1d, being quite unlike the plot shown in Fig. 1b. However, it was noted by Sims *et al.* (2008; Supplementary Methods and Results 2, p. 8) that projection from 3D to 1D was expected to produce many step-lengths $< x_{min}$ which do not follow a power-law distribution. Closer inspection of the plot confirmed that the inflection point of the plot separating the two domains occurred at 1·0, the x_{min} value of the original 3D dataset. While points below x_{min} clearly do not fit a power-law distribution, those above x_{min} do, as expected. MLE analysis of the step-lengths above x_{min} showed a good fit to a truncated Pareto-Lévy power-law (TP) distribution with $\mu = 2.01$ (Fig. 1e), which was very close to the value of $\mu = 2.0$ used to generate the original 3D data set. Therefore, once data points below x_{min} were removed, the symmetry of the Lévy flight was evident. The symmetry was confirmed by repeating the 1D analysis using the x and y dimensions and with the x, y and z dimensions of two further datasets with $\mu = 1.5$ and $\mu = 2.5$, which gave almost identical results once values below x_{min} were ignored (Table 1). Differences in the estimated exponents were <1·0%, and therefore, the exponent values were conserved as predicted. Differences in the x_{max} values were expected given that with a power-law distribution long steps are much rarer than short steps, and therefore, these long displacements are effectively under-sampled. With the values closer to x_{min}, there are very many more steps, so the displacements in each dimension are more thoroughly sampled leading to the conservation of the x_{min} value along each axis. Analysis of a 3D Lévy flight dataset with $x_{min} = 10$ demonstrates that the inflection point again corresponds to the x_{min} value used to generate the original dataset (Fig. 1f), confirming this to be a general principle.

With step-lengths drawn from an exponential distribution, representing simple Brownian movement, the overall pattern was also conserved in the 1D analysis, but not with the fidelity found for the Lévy distribution; the exponent differed by more than 57% (Table S5, Appendix S1, section 11) and the overall fit was not as good (Fig. 2). However, the fit was still much better than the competing TP distribution, and this result was supported by Akaike weights, which suggests that 3D exponential movements cannot easily be mistaken for Lévy movements (and *vice versa*) when reduced to one dimension.

Composite Brownian (CB or CCRW) random walks have recently been proposed as alternative models to Lévy walks (Jansen, Mashanova & Petrovskii 2012; Reynolds 2012). Therefore, a simulated CB dataset was generated, based on a fit to empirical data (see Empirical analysis below) and was examined for symmetry in the same way as the other simulated datasets (Appendix S1, section 7). This dataset was also found to project with sufficient symmetry for clear identification using AIC; indeed, the plots of the individual x, y and z dimensions are almost indistinguishable from the original 3D plot (Appendix S1, section 12, Figs S11 and S12).

ESTIMATING THE X_{MIN} PARAMETER

In the simulated data, the x_{min} parameter was already known. With empirical datasets, however, the x_{min} value cannot be known *a priori,* and therefore, an objective method of estimating this value is required. Clauset, Shalizi & Newman (2009) suggest an iterative search of all possible values in the dataset as potential values for x_{min}, using a Kolmogorov–Smirnov GOF test to determine the best fitting value. Following detailed investigations (described in full in Appendix S1, section 4), a modified version of this scheme was adopted, whereby the GOF result was modified according to the extent of the fit, with fits to a reduced data range being penalised; the purpose of which was to reduce the likelihood of fitting to a very small extent of the data. This method was found to perform well in estimating the true x_{min} value in simulated data and was therefore used when analysing both the simulated empirical measurement error data, and when re-analysing the wandering albatross GPS-tracked movement data.

EMPIRICAL MEASUREMENT ERRORS

To investigate whether the observed symmetry of a Lévy flight would be conserved in empirical data, four sources of potential measurement error were simulated: (i) low spatial resolution, whereby the tag records in multiples of 0·5 or 1·0; (ii)

Table 1. Symmetry of Lévy analysis in three dimensions

μ	Dimension	x_{min}	μ	x_{max}	% Error in μ	wAIC	Alt wAIC	*P*-value
1·5	X	1·0055	1·5095	1680·55	−0·63	1·00	0·00	0·7760
1·5	Y	1·0006	1·5150	1408·71	−1·00	1·00	0·00	0·8264
1·5	Z	1·0004	1·5145	1099·32	−0·97	1·00	0·00	0·1504
2·0	X	1·0010	1·9855	613·42	0·72	1·00	0·00	0·8420
2·0	Y	1·0003	1·9919	808·47	0·40	1·00	0·00	0·4960
2·0	Z	1·0032	2·0099	2170·03	−0·50	1·00	0·00	0·3992
2·5	X	1·0001	2·4858	216·71	0·57	1·00	0·00	0·7656
2·5	Y	1·0012	2·4882	113·06	0·47	1·00	0·00	0·7720
2·5	Z	1·0014	2·4805	130·00	0·78	1·00	0·00	0·9256

Analysing each dimension of the 3D tracks separately shows that both the exponent and the fit to the truncated Pareto distribution are conserved. Note that the *P*-values shown here should be interpreted as significant if >0·1.
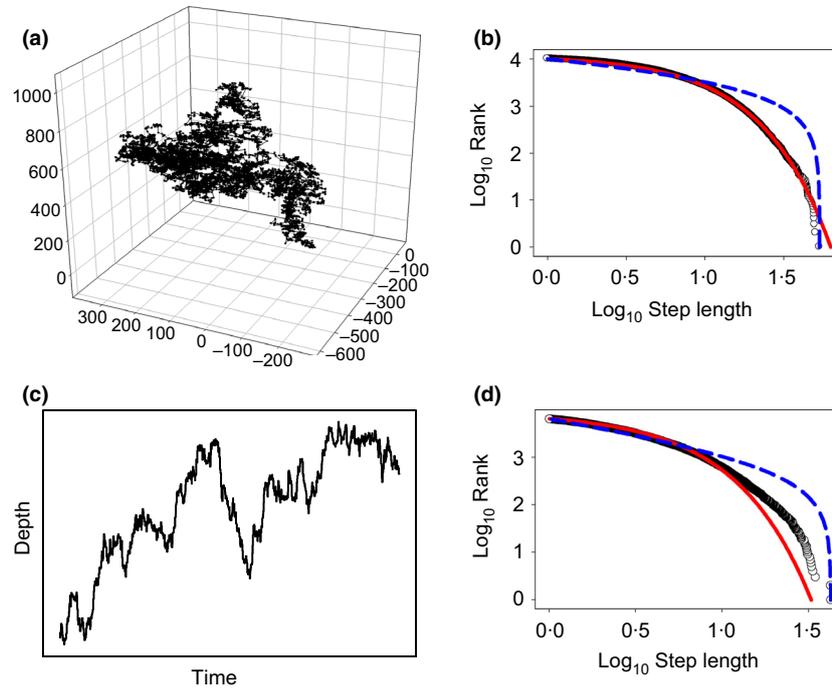
Fig. 2. Analysis of a 3D exponential track. (a) The 3D exponential track, note the smaller scale compared with the Lévy track shown in Fig. 1a. (b) maximum likelihood estimation (MLE) analysis of the 3D track, where black circles are observations, red line is fitted exponential, blue dashed line is competing truncated Pareto (TP). (c) Vertical displacements from the 3D track. These look very different from the Lévy displacements shown in Fig. 1c. (d) MLE analysis of vertical displacements for values $>x_{min}$ (1·0) showing that while the exponential fit (red line) is clearly better that the competing TP (blue dashed line) the symmetry is not conserved as well as with a TP dataset.

under-sampling, whereby the animal performs more turns than are recorded by the tag; (iii) over-sampling, whereby the tag records multiple locations between turning points, and (iv) track gaps, where random gaps appear in the data resulting in runs of data points followed by a gap, as might be expected in GPS datasets. Full details of these investigations are given in Appendix S1 (section 5). Despite simulated errors being severe in some cases, all the truncated power-law datasets were correctly identified as being derived from a TP distribution. Similarly, the estimation of the exponent was in all cases accurate enough not to affect any interpretations or conclusions about behaviour patterns relevant to testing the LFF hypothesis. With both over- and under-sampled data, the fitted x_{min} values were predictably high, leading to a power-law fit to less of the dataset, a feature that would therefore be expected in empirical data.

A NEW ANALYSIS METHOD FOR 2 AND 3D DATA

The results described above show clearly that 3D Lévy movement datasets have a dimensional symmetry in which the overall pattern and exponent are conserved when reduced to 1 dimension. The symmetry in Lévy flight has been shown to be robust to potential measurement errors in low spatial or temporal resolution data, supporting the contention that the 1D datasets analysed in previous studies (Sims *et al.* 2008; Humphries *et al.* 2010) are very likely to have been derived from a 3D movement pattern consistent with that of a biological Lévy flight.

The corollary of this symmetry is that a Lévy distributed 1D dataset is likely to be strongly representative of the 2D or 3D dataset from which it was originally derived; likewise, a 1D exponentially distributed dataset will most likely have been derived from a 2D or 3D exponential dataset. The symmetry can be exploited to allow the straightforward and accurate determination of step-lengths in both 2D and 3D empirical data by analysing movements in a single dimension, as all dimensions will have characteristics representative of the whole. While it is possible that the horizontal and vertical components of a trajectory might differ, as is the case with wind-borne seeds (Reynolds 2013), differences are less likely between the axes of a horizontal movement path.

While exponential datasets do not project into 1D with the same fidelity as a Lévy walk, they do so sufficiently well not to be easily mistaken for a Lévy pattern or *vice versa,* making the method valid for any 2D or 3D empirical data. Taking a single dimension solves the problems associated with identifying turning points, thus making the computation of step-lengths in complex movement datasets straightforward and objective.

AN EMPIRICAL DEMONSTRATION OF THE NEW METHOD

To demonstrate the utility of our proposed new methodology, we re-analysed 27 wandering albatross (*D. exulans*) datasets, previously analysed by Humphries *et al.* (2012), where landings on the water were identified and used as turning points for the Lévy analysis. In this study, step-lengths were calculated as displacements in one dimension from the 2D GPS

track of each bird. The datasets were recorded at minimum intervals of either 10 s or 1 min, and therefore, for consistency, track gaps exceeding 1 min were ignored in all cases. The only other processing required was the correction of sampling artefacts through the coalescing of steps that formed part of a continuous movement, as described previously in Humphries *et al.* (2010).

The simulated datasets used previously comprised 10^4 data points providing sufficient data to sample the distribution fully in all dimensions, resulting in equivalence in the estimated exponent for any dimension. With the albatross movement data, however, the datasets had far fewer data points once steps were coalesced and points below x_{min} were ignored, hence, it was possible that a power-law distribution may not have been sufficiently sampled in all dimensions for congruence in the exponent between either dimension (x or y). Therefore, both dimensions from each dataset were analysed separately, and the results from each compared before conclusions were drawn about whether a Lévy or exponential pattern was present.

Following the MLE analysis, model selection was performed, as described in Appendix S1, section 9, to determine whether a dataset was best fit by either a TP or exponential distribution (or neither). The best fitting model was therefore selected based on Akaike weights, the GOF (Kolmogorov–Smirnov D statistic) and further, in the case of the TP, an exponent in the Lévy range and spanning at least 1·5 orders of magnitude of the data.

Of the 27 *D. exulans* analysed, 20 birds (74%) were best fit by a TP distribution in both dimensions, 6 (22%) were best fit by TP in only one dimension, and a single bird was classified as being a 'mixed' model (i.e. fitting neither distribution) in either

dimension. None were best fit by the exponential distribution in either dimension. The majority of fits were to a subset of the original data; however, this was expected from the simulated data analysis. An average of *c.* 69% of data points were 'lost' through the coalescing of move steps and the fitting of x_{min}, which tended to be conservative with the best fit often being well beyond the inflection point of the curve in the rank step-length plot (Fig. 3a). Furthermore, in most cases, the inflection point was, as expected, less well defined than with the simulated data which tended to increase the fitted x_{min} value (Fig. 3b). It should be remembered that taking a single dimension results in a large number of points below the best fit x_{min} value and while this tends to make the fit appear poorer, these points are artefacts and need to be ignored. While the average x_{max} value was 69% of the maximum step-length, 15 of the 40 datasets (i.e. the separate x and y dimensions, 37·5%) had x_{max} values equal to the maximum step. Of the 40 datasets, 21 were found to have a best fit power-law model that spanned more than two orders of magnitude; the mean for all 40 datasets was 2·23 with values ranging from 1·51 to 3·79. For the 20 best fitting datasets, the mean span was 2·66 orders of magnitude. Results are summarised in Appendix S1, section 11, Tables S11–13. The MLE results in the form of ranked step-length plots for all birds are shown in Appendix S1, section 12, Fig. S10. A further requirement for a good fit to a Lévy walk is suggested to be uniform turn-angle distribution. Analysis provided in Appendix S1 (section 6) shows that this requirement is also fulfilled by the albatross data.

To confirm further the TP distribution as the best fit, we fitted the empirical data to CB distributions as described by Jansen, Mashanova & Petrovskii (2012). The results are
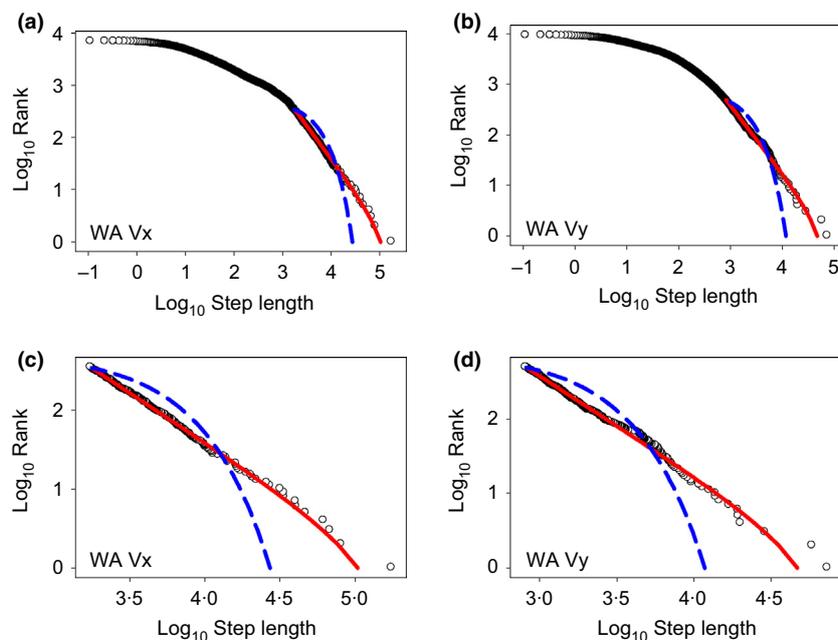

Fig. 3. Maximum likelihood estimation (MLE) analysis of *Diomedea exulans* bird V. (a) and (b) show the MLE analysis of the x and y dimensions, respectively, with all data points included to illustrate the extent of the fit. (c, d) The same plots but with the data points below x_{min} removed to illustrate that above x_{min} the fit to a truncated Pareto (TP) distribution is very good. Black circles are observations, red line is the fitted TP distribution and blue dashed line is the competing exponential.

described in full in Appendix S1 (section 9) where it is shown that only four of the 20 datasets were best fit by a CB distribution.

Given that the empirical data available for analysis comprised far fewer data points than the simulated data used previously, our result showing close equivalence in the estimated exponent (μ) values was perhaps unexpected. For the 20 birds that were best fit by a TP distribution, the difference in the estimated value of μ between the two dimensions (expressed as the difference divided by the mean) ranged from 1·42% to 63%. However, in seven birds, the μ values of the two dimensions were within 10%, and for a further six birds were within 20% of each other; therefore, the equivalence was somewhat higher than expected.

Discussion

We have demonstrated that a range of move step-length distributions typically found in empirical datasets project into 1D with sufficient fidelity, even with common empirical measurement errors, to be clearly identified in a subsequent MLE analysis. Using this finding, we propose a method for the identification of turns and step-lengths in high-resolution 2D or 3D datasets where previous methods have been found to be unsatisfactory.

The new method was illustrated using high-resolution GPS data from wandering albatross (*Diomedea exulans*). We found Lévy movement patterns were prevalent, occurring in both dimensions for 20 of the 27 birds analysed. The majority of fits were found to be very good, with significant *P*-values computed for 23 individual dimension datasets and with five birds having significant *P*-values for both dimensions. In a previous study, where the distribution of landing locations was analysed (Humphries *et al.* 2012), only four of the *D. exulans* datasets were best fit by a TP distribution. Because *D. exulans* landed relatively infrequently during foraging trips, the analysis of the previous study resulted in very few data points which was shown to reduce the likelihood of a TP fit. Consequently, the study by Humphries *et al.* (2012) detected fewer examples of Lévy flight behaviour, compared with the black browed albatross (*Thalassarche melanophrys*) datasets for which far more data points were available. In the current study however, with significantly more data to analyse, we found very good support for the presence of Lévy flight movement patterns for the majority of wandering albatrosses, improving the rate of detection of Lévy flight behaviour from 15% to 74% of individual birds. Given the significant increase in the detection of Lévy patterns with the new method, it seems likely that previous studies purporting to demonstrate biological Lévy flight, or questioning its existence, might have been strengthened (e.g. Viswanathan *et al.* 1996) or have drawn quite different conclusions (e.g. Edwards *et al.* 2007; Edwards 2011), had this new methodology been employed. Furthermore, the movements analysed here represent characteristics of the actual flight path of the birds, rather than the distribution of the landings, which might correspond to the fractal nature of the prey distribution (Miramontes, Boyer & Bartumeus 2012). The movements analysed here therefore better reflect the complex paths taken during animal foraging/searching behaviour.

In the previous study by Humphries *et al.* (2012), the Lévy exponents were found to be lower than the theoretical optimum value of 2·0 (mean 1·19). Here, however, the mean value of 1·75 (SD 0·31) is closer to the optimum. Exponents <2·0 have been shown theoretically to be optimum values where targets (i.e. prey) are nonrevisitable (i.e. single prey items as opposed to patches; Viswanathan *et al.* 1999), and it was proposed by Humphries *et al.* (2012) that this was the most likely scenario for wandering albatrosses foraging in the open ocean. Eight datasets analysed here have a value slightly larger than 2·0, (mean 2·26, SD 0·16) suggesting more abundant prey. The results presented here therefore suggest a broader range of behaviours and of foraging environments than previously concluded. That not all datasets were found to fit a Lévy distribution is unsurprising because albatrosses are known to use olfactory clues (Nevitt, Losekoot & Weimerskirch 2008) and will on those occasions be performing directed, rather than random searches, and will not be expected to fit a Lévy pattern.

Given that Lévy movement patterns have been shown to optimise random searches for sparse targets (Viswanathan *et al.* 1999, 2002, 2011), our finding that Lévy movement patterns are prevalent in wandering albatrosses engaged in foraging trips in the open ocean, where prey patches are sparsely and unpredictably distributed, provides further evidence that adaptations for stochastic search movements described by Lévy flights may have naturally evolved (Humphries *et al.* 2012; Sims *et al.* 2012).

APPLICABILITY TO EMPIRICAL DATASETS

In principle, the method we have outlined here can be applied to almost any 2D or 3D movement dataset. It should be emphasised that the method is intended to identify turns and step-lengths in movement data suitable for subsequent analysis (such as MLE), but does not in itself provide direct evidence of the process that might have generated the observed step-length distribution, be it a correlated random walk, a Lévy walk or some other process, such as a continuous time random walk (Reynolds 2010).

Furthermore, very low-resolution datasets, such as those produced via Argos satellites, where there are few locations per day, will not capture sufficient fine-scale behaviour for robust conclusions to be drawn about the precise spatial form of the movement pattern (Bradshaw, Sims & Hays 2007). As was found with the original analysis of the *D. exulans* landings data (Humphries *et al.* 2012), there are sometimes too few data points to sample the distribution sufficiently for a power law to be discernible. Turchin (1998) comments that there is no generally acceptable solution to deal with over-sampled data, however, with 1D data, over-sampling is preferable to under-sampling. With over-sampled 1D data, it is straightforward to coalesce steps that have been artificially divided by the sampling interval and therefore to recover accurately the correct turning points. With under-sampled data, certainly at the further extremes, too much of the original movement is lost

and cannot be recovered. Therefore, high-resolution datasets, such as those obtained using GPS, are expected to give much better results.

FURTHER RESEARCH

The method presented here would be well suited to other GPS datasets, for example, golden eagles (*Aquila chrysaetos*; Lanzone *et al.* 2012) or griffon vultures (*Gyps fulvus*; Nathan *et al.* 2012), both of which perform extensive foraging flights and might be expected to exhibit Lévy flight patterns. Terrestrial GPS studies of predators such as wolves (*Canis lupus*; Gurarie *et al.* 2011), lynx (*Lynx Canadensis*; Olson *et al.* 2011) or cougar (*Puma concolor*; Knopff *et al.* 2010) could also make use of this methodology for testing the possibility of scale independence in animal movement or for identifying the times/ locations where optimal search strategies may be employed. The method may also benefit studies of the movements of nematodes (Ohkubo *et al.* 2010) or even individual immune cells (Harris *et al.* 2012).

It would also be interesting to apply this method to studies that have led to debate, such as that by de Jager *et al.* (2011), where the movements of mussels (*Mytilus edulis*) were found to follow a Lévy-like walk pattern but which was challenged by Jansen, Mashanova & Petrovskii (2012). The method presented here is simpler to implement than the methods employed in that study and requires no sensitivity testing to determine the best parameters.

The simplicity of the method, together with the now very abundant, high-resolution, 2D data available for analysis from a very broad range of studies, should allow a more thorough test of the LFF hypothesis, as well as the provision of a useful tool for the analysis of movement in diverse organisms. To encourage research in this area, the software we developed to perform the MLE analysis is freely available for download with this study from the Sims Lab web site (www.mba.ac.uk/simslab/).

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Details of supporting simulations and analyses, supporting tables and figures.