Evidence for intermittency and a truncated power law from highly resolved aphid movement data

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Power laws are increasingly used to describe animal movement. Despite this, the use of power laws has been criticized on both empirical and theoretical grounds, and alternative models based on extensions of conventional random walk theory (Brownian motion) have been suggested. In this paper, we analyse a large volume of data of aphid walking behaviour (65 068 data points), which provides a highly resolved dataset to investigate the pattern of movement. We show that aphid movement is intermittent—with alternations of a slow movement with frequent change of direction and a fast, relatively directed movement—and that the fast movement consists of two phases—a strongly directed phase that gradually changes into an uncorrelated random walk. By measuring the mean-squared displacement and the duration of non-stop movement episodes we found that both spatial and temporal aspects of aphid movement are best described using a truncated power law approach. We suggest that the observed spatial pattern arises from the duration of non-stop movement phases rather than from correlations in turning angles. We discuss the implications of these findings for interpreting movement data, such as distinguishing between movement and non-movement, and the effect of the range of data used in the analysis on the conclusions.

Keywords: intermittency; Lévy walk; power law; scale-free distribution; super-diffusion

1. INTRODUCTION

Power laws arise from processes in which the variable measured has no characteristic scale, i.e. both short and long values occur, with no scale being dominant (most frequent). An important consequence of the scale-free properties is that animals with this type of movement can be super-diffusive, which means that the displacement from the starting point increases faster than predicted by a simple (uncorrelated) random walk approach (Klafter & Sokolov 2005). In relation to movement, two terms related to power laws are used—a Lévy flight and a Lévy walk. Both types approximate non-diffusive movement in which the step lengths l come from a power-law distribution $P(l) \propto l^{-\mu}$ with $1 < \mu < 3$ (Shlesinger *et al.* 1993). For such values of μ, the sum of step lengths (the displacement after n steps) is dominated by rare large values and, for a large number of steps, the average step length tends to infinity. While in a Lévy flight step length is the main concept, in a Lévy walk time to complete a step is taken into account. A longer step normally requires more time than a shorter step. Hence, in Lévy walks, in spite of the average step length being infinite, the average displacement R after time t is finite and defined as $R(t) \propto t^{\gamma}$, where the values of $\gamma = 1/2$ corresponds to a simple diffusion and $\gamma = 1$ corresponds to ballistic motion (movement in a straight line) (Shlesinger *et al.* 1993).

Power laws with exponent values indicative of Lévy patterns have been found in the distribution of flight times (the duration of non-stop movement) of albatrosses, bumble-bees and deer (Viswanathan *et al.* 1996, 1999; for a contrasting view, see Edwards *et al.* 2007), and in microzooplankton (Bartumeus *et al.* 2003); in the duration of the inactive phase in *Drosophila* (Cole 1995; Martin 2004) and spider monkeys (Ramos-Fernandes *et al.* 2004); and in the distributions of move-step-lengths (the distance travelled between consecutive time intervals) in grey seals (Austin *et al.* 2004; for a contrasting view, see Sims *et al.* 2007 and Edwards 2008) and other marine predators (Sims *et al.* 2008). Other examples can be found in Edwards *et al.* (2007) and Sims *et al.* (2008). Even human hunter gatherers (Brown *et al.* 2007) and the distance travelled by bank notes (Brockmann *et al.* 2006) show power law behaviour.

However, the use of Lévy walks to describe animal movement patterns is not generally accepted. For instance, only 30 per cent of grey seals' movement fits Lévy statistics (Austin *et al.* 2004), and the movement pattern of reindeer changes with the season (Mårell *et al.* 2002). Edwards *et al.* (2007) showed that other models were better suited to describe some of the movement patterns previously classified as Lévy walks. Gonzalez *et al.* (2008) showed that, unlike the movement of bank notes, which follows a power law (Brockmann *et al.* 2006), movement of individuals can only be approximated as a Lévy walk within a certain region (home range), but not on a global scale.

Patterns qualitatively similar to power laws within a certain time range can also be obtained by modifying simple random walk models. Turchin (1996) argued that such patterns could often be described by a correlated random walk (a random walk in which the direction of the move depends on the direction of the previous move), and Benhamou (2007) suggested using a combination of simple random walks to generate power law-like distributions (also see Reynolds 2008). Some other alternatives include introduction of waiting times and combining simple diffusion with directed (ballistic) movement (Turchin 1998; Codling *et al.* 2008).

Intermittent movement behaviour, in which episodes of high activity are interspersed with episodes of inactivity, became a recent addition to the list of how power laws can arise. Intermittent movement is widely observed in animals (Kramer & McLaughlin 2001). Cole (1995) was the first to find power law in the duration of the inactive phase in *Drosophila*. Benichou *et al.* (2005) showed that move durations and pause durations reported by Kramer & McLaughlin (2001) had a power law relationship. While theoretical studies have shown that intermittent behaviour is an efficient searching strategy on its own (Benichou *et al.* 2005, 2006) or in combination with the power law relocation phase (Lomholt *et al.* 2008), detailed experimental studies on intermittency are scarce (for a contrasting view, see Martin 2004; Reynolds & Frye 2007).

The debate in the recent literature about whether or not animal movement is best described as a Lévy walk can be partly explained by difficulties in fitting power laws. Sims *et al.* (2007) and White *et al.* (2008) have shown that different methods of fitting give different values for the exponent that affects the final conclusion. The reliability of the analysis can be increased by increasing the amount of data available. Collecting animal movement data through tagging animals and following them is time-consuming and costly. For this reason, there is ambiguity about the nature of the distributions of the step lengths or moving times, in particular, in the tail of the distributions where observations are infrequent, and where it is difficult to get sufficient resolution. Recent advances in video-tracking techniques have simplified the process of obtaining detailed movement data (Martin 2004; Oliver *et al.* 2007; Reynolds & Frye 2007), thus providing an opportunity to identify the exact form of the distribution.

One of the peculiar and distinctive properties of a power law distribution is that long moves are expected to be more frequent than with a Gaussian or an exponential distribution, which are used in simple random walks. Evidently, for any animal the duration of moves or the distance moved in one 'step' is limited owing to physical constraints. This suggests that the power law characteristics hold true only in a limited range, and that a truncated power law should provide a more generic description (Newman 2005; Clauset *et al.* 2007). This limitation has been taken into account in some theoretical studies (Viswanathan *et al.* 1999), but, typically, an asymptotic (unlimited) power law has been considered in empirical studies of animal movement.

The truncated power law can also be identified by measuring the mean-squared displacement (MSD). In diffusive processes, the MSD grows linearly with time (a power function with exponent 1) while in a power law process it grows over-linearly (exponent between 1 and 2, with the value of 2 corresponding to movement in a straight line) (Bartumeus *et al.* 2005). If a super-diffusive behaviour develops into a diffusive behaviour, the exponent of the MSD decreases to 1 with the transition time being proportional to the maximum step length (Barthelemy *et al.* 2008). Qualitatively, this pattern is similar to a correlated random walk (random walk in which a direction of the move depends on the direction of the previous step) (Codling *et al.* 2008). Another way to detect long-range correlations in the movement is to measure the root-mean square fluctuations of the displacement,

$$F(t) = \sqrt{\langle (\Delta y(t))^2 \rangle - \langle \Delta y(t) \rangle^2},$$

where $\Delta y(t) = y\ (t_0 + t) - y\ (t_0)$ (e.g. Viswanathan *et al.* 1996). In uncorrelated processes, $F(t) \propto t^\alpha$ with $\alpha = \frac{1}{2}$ while other values of α indicate the presence of long-range correlations with no characteristic scale (Viswanathan *et al.* 1996; Atkinson *et al.* 2002).

In this study, we have generated and analysed a dataset obtained through video-tracking the walking behaviour of black bean aphids *Aphis fabae* Scopoli (Hemiptera: Aphididae). *A. fabae* is a major pest on beans and sugar beet, which can spread fast on an epidemic scale (Williams *et al.* 1999 and references therein) suggesting possible super-diffusive movement. The spread of aphid pests involves some flying dispersal by winged individuals (alates), but a significant proportion of local movement is achieved by non-winged individuals (apterae), which move across the ground between plants (Hodgson 1991; Furuta & Aloo 1994).

On a practical side, aphids are small and easy to rear, and their movements cover a relatively small area. This allowed us to obtain a large collection of highly time-resolved data. Moreover, we found that aphid walking behaviour has intermittent characteristics, allowing us to distinguish movement from non-movement, which facilitated the analysis. We will show that the truncated power law is indeed a more universal model for the description of the walking behaviour of the black bean aphid in space and time, and discuss the implications of these findings.
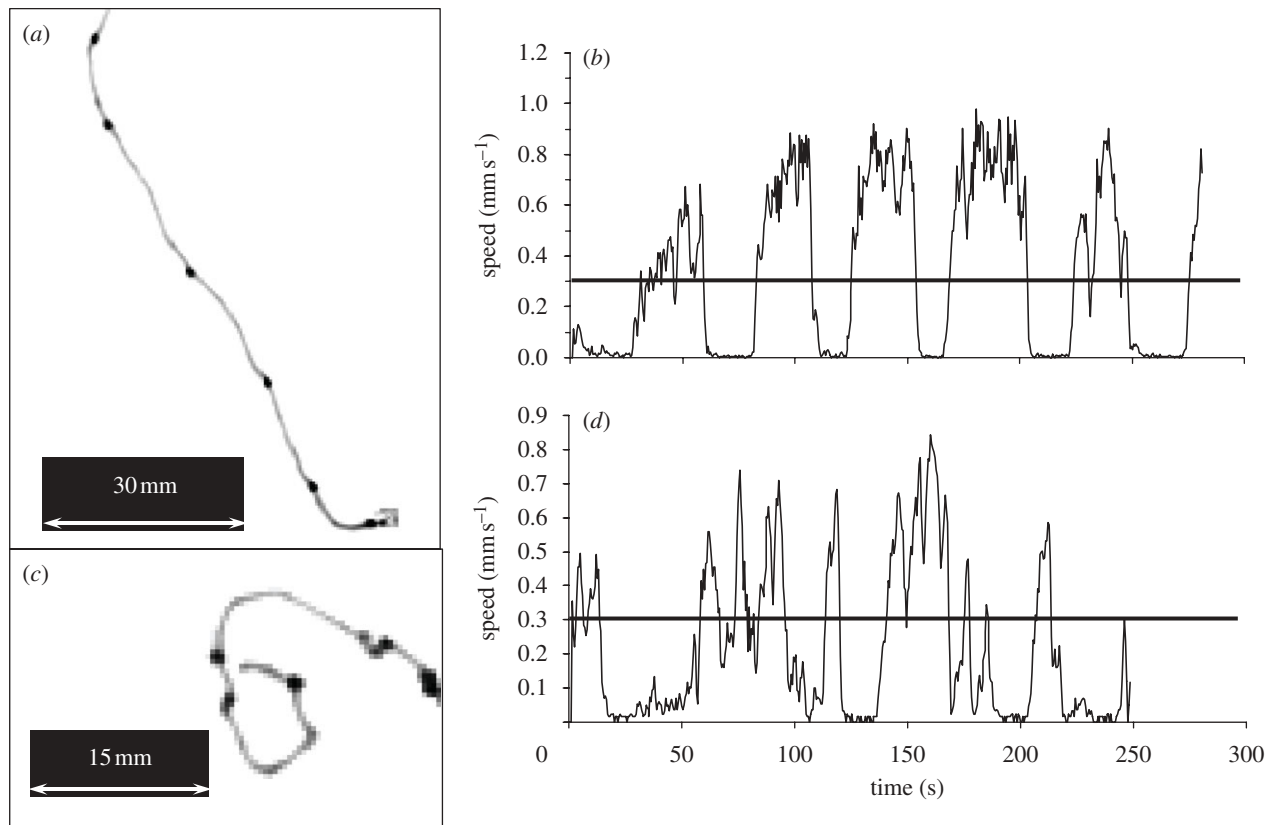
Figure 1. Two examples of aphid paths. (*a,c*) Two-dimensional image of tracks showing temporal variance of pixel intensity during the record. The longer an aphid stayed in the same place the darker the colour is. It can be seen that fast movement (grey lines) is often interrupted by slowing down (black patches). These images were obtained using GMIMPRO software. (*b,d*) Corresponding speed variation in time. The horizontal lines indicate the threshold between movement and non-movement which we employed.

2. MATERIAL AND METHODS

2.1. Experimental data

Black bean aphids, *A. fabae* Scopoli, were collected from Silwood Park, UK, and kept in culture for 2 years. Aphids were taken from plants (*Vicia faba* L.), placed on clean filter paper in 9 cm (diameter) Petri dishes with 10 or 20 aphids per dish (12 replica each), left for 10–20 min to settle and then video-recorded for 5 min with frames taken at 0.5 s time interval (see Oliver *et al.* 2007 for the details of the setup and software used). Three hundred and sixty aphids were used in this study.

2.2. Data analysis

Movement paths of aphids were calculated using the automatic single particle-tracking module from the free image analysis package GMIMPRO (www.nimr.mrc.ac.uk/ GMimPro). We used measurements taken at 1 s intervals for further analysis (65 068 data points) because it reduced the number of data points by a factor of 2 while still capturing all relevant features of aphid movement that we discuss in this paper. A sample video illustrating aphid movement and tracking procedure can be found in the electronic supplementary material (S1).

MSD was calculated by averaging squared distances between the points separated by increasing the time interval t starting with the first point and moving along the path using all possible pairs (using non-overlapping pairs gives very similar results; the all possible pairs method was chosen solely for presentational purpose as it smoothes the line). The term MSD is used as an equivalent to squared net displacement (e.g. Turchin 1998).

Aphid paths consisted of alternating intervals of high and low speed (figure 1). Visual inspection readily reveals that high speed was correlated with directed movement (the corresponding turning angles close to 0), while, at low speed, the distribution of the turning angles was much broader and became uniform for the speed values inferior to approximately 0.3 mm s^{-1} (figure 2). This observation shows that we can classify the movement as either slow and undirected, or fast and directed. This motivated the use of a speed of 0.3 mm s^{-1} as a threshold separating movement (in a sense of 'dislocation' as opposed to turning on a spot, swinging, etc.) from non-movement. Different threshold levels did not qualitatively affect the results (table S2 in the electronic supplementary material). Note that the chosen value was much higher than the noise of the system (the noise level was measured by recording dead aphids and there were no speed values higher than 0.05 mm s^{-1}) and corresponded to approximately $\frac{1}{2}$ pixel (for comparison, the average size of aphids was 1–1.5 mm). A high temporal resolution of the data is essential to observe such dichotomy in turning angles—e.g. it completely disappeared when we
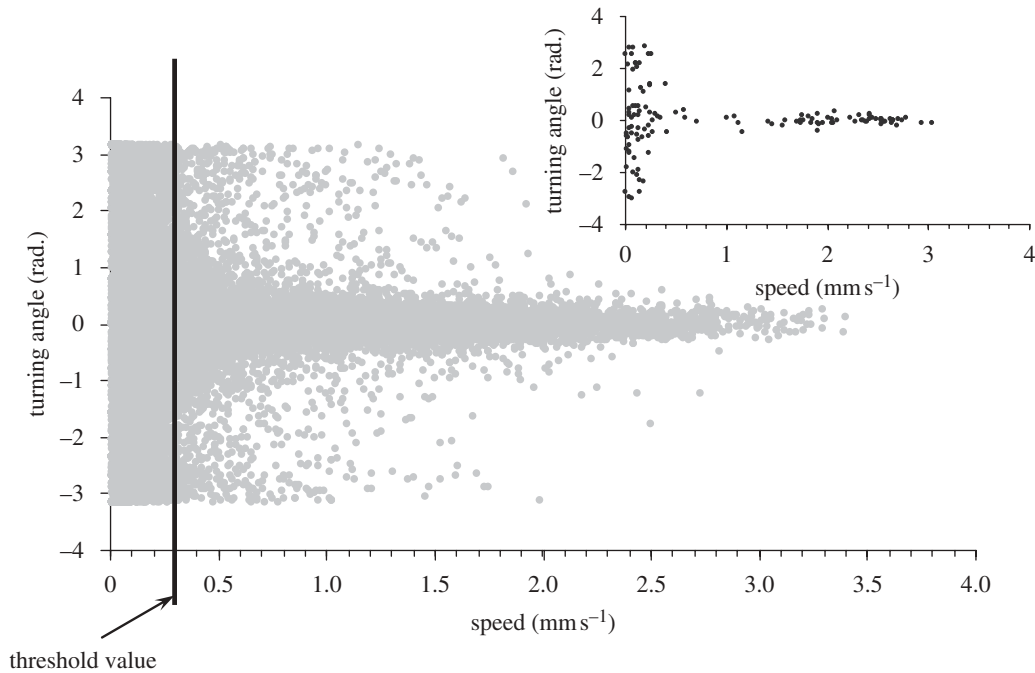
Figure 2. Speed versus turning angle relationship measured from aphid tracks at 1 s intervals. It can be seen that for low speed the corresponding turning angle varied greatly while when the speed was high the turning angle was close to zero indicating directed movement. The threshold value of 0.3 mm s^{-1} was used to distinguish moves from non-moves. Other values for the threshold did not change the results qualitatively. The inset shows the same relationship for a single track.

reconstructed figure 2 using measurements taken at 4 s intervals.

In principle, a correlation between turning angle and speed can arise as an artefact of discrete sampling: if an animal moves at a fixed rate and is sampled at discrete intervals, the distance covered between samples will be negatively correlated with the curvature of the path (Bovet & Benhamou 1988; Codling & Hill 2005). Analysis of artificial tracks with a fixed speed revealed that the pattern in figure 2 cannot be generated by such artefacts under the sampling rate used in this study (figure S3 in the electronic supplementary material).

By applying this threshold we separated paths into subsequent bouts of movement so that a bout started when the speed was ≥ 0.3 mm s^{-1} and ended when the speed was < 0.3 mm s^{-1}. For example, the path shown in figure 1*a* is interpreted as three long bouts in the middle of the path and a few shorter ones at the beginning and the end of the path. The distribution of the bouts' duration was used for model fitting (as in Viswanathan *et al.* 1996; Edwards *et al.* 2007). We chose the duration of the bouts, rather than displacement between start and end points, since aphids were restricted to Petri dishes. We pooled the bout durations of aphid records from dishes with 10 and 20 aphids per dish as we did not detect any significant difference between the two ($\chi^2 = 89.1$, $P = 0.28$, d.f. = 84).

2.3. Model fitting

Three models were fitted to the distribution of the bout durations—a power law (expected for Levy flight), an exponential distribution (expected if change from movement to non-movement was a random Poisson process), and a truncated power law. For the truncated power

law, we chose an exponential decay for the longest bouts as reported by Edwards *et al.* (2007). In this way, our truncated power law model captures the transition from super-diffusive to diffusive processes. We fitted the models using a maximum likelihood method (e.g. Hilborn & Mangel 1997), which has been advocated as the most accurate for fitting the power law models by White *et al.* (2008).

Log-likelihood functions were derived for the range starting with $x_{\min}$ and proceeding to infinity (assuming that values higher than the recorded ones were possible). We did not consider an upper cut-off because (i) the longest bouts lasted less than half of the record duration, and (ii) the duration of bouts was not affected by the size of Petri dishes: there were examples of aphids moving along the boundaries. Since the data were binned with 1 s bin width, the continuous distributions were converted to the discrete ones so that the value for the bin j was obtained by integrating over $j - 0.5$ to $j + 0.5$. The details of the derivation of the log-likelihood functions are given in the appendix.

The log-likelihood function for the power law model $f(x) = Cx^{-\mu}$ is

$$l(\mu|\text{data}) = \sum_{j=1}^{x_{\max}} d_j \log \left[\frac{(j - 0.5)^{1-\mu} - (j + 0.5)^{1-\mu}}{x_{\min}^{1-\mu}} \right],$$

(2.1)

where $\mu > 1$ (required for the power law to converge) is the parameter of the power law distribution, d_j is the number of data points of value j, $x_{\min}$ is the smallest value of x used for fitting and $x_{\max}$ is the largest bin. The best value of μ is the one that maximizes the log-likelihood function.

For the exponential distribution $f(x) = Ce^{-\lambda x}$ with the parameter λ the log-likelihood function is

$$l(\lambda|\text{data}) = \sum_{j=1}^{x_{\max}} d_j \log\left[\frac{e^{-\lambda(j-0.5)} - e^{-\lambda(j+0.5)}}{e^{-\lambda x_{\min}}}\right], \quad (2.2)$$

and for the truncated power law $f(x) = Cx^{-\mu} e^{-\lambda x}$ with parameters μ and λ

$$l(\mu, \lambda|\text{data})$$

$$= \sum_{j=1}^{x_{\max}} d_j \log\frac{\Gamma(1-\mu, \lambda(j-0.5)) - \Gamma(1-\mu, \lambda(j+0.5))}{\Gamma(1-\mu, \lambda x_{\min})},$$

$$(2.3)$$

where $\Gamma(1-\mu, \lambda j)$ is the incomplete gamma function.

The performance of the models was compared using Akaike weights (Burnham & Anderson 2002),

$$w_i = \frac{e^{-\Delta_i/2}}{\sum_J e^{-\Delta_j/2}},$$

where J is the number of models compared and $\Delta_I = \text{AIC}_i - \text{AIC}_{\min}$ is calculated using the Akaike information criterion, $\text{AIC}_i = -2l_i + 2K_i$ with l_i being the maximum log-likelihood and K_i being the number of parameters in the model i. The best model has the smallest AIC ($\text{AIC}_{\min}$) and contributes most to the denominator; as a result its weight is close to 1.

The 95 per cent confidence intervals were calculated using the profile likelihood-ratio test (Hilborn & Mangel 1997; Edwards *et al.* 2007). All calculations were made using MATHEMATICA 5.2.

3. RESULTS

We found that the movement of aphids was intermittent—fast movement alternated with slow movement phases (figure 1). This pattern suggests that movement and non-movement can be distinguished by applying some threshold value. Until recently, this threshold was dictated by the technical restrictions such as the frequency at which it is feasible to record the data (Cole 1995; Viswanathan *et al.* 1996; Atkinson *et al.* 2002) or GPS accuracy (Austin *et al.* 2004). Modern video-recording techniques allow us to collect data at a very high resolution and the threshold has to be defined intentionally. For example, Martin (2004), who studied *Drosophila* movement from video records, chose the threshold by trying a range of values. Kane *et al.* (2004) defined a fish as moving if the fish moved approximately half of its length per second. Arbitrary choice of the threshold value inevitably introduces an element of subjectivity in the analysis. We found that speed was not the only parameter indicating whether an animal was moving. Changes of direction occurred much more often at low speed than at high speed (figure 2). This allows us to introduce a natural dichotomy between movement and non-movement based on the characteristics of the movement behaviour.

We measured two characteristics of movement—the MSD and the distribution of bout durations. We measured MSD (equivalent to net-squared displacement) because it is a convenient parameter to quantify dispersal (Kareiva & Shigesada 1983; Turchin 1998) and is not affected by any assumptions (e.g. distinguishing between movement and movement). In simple diffusion, MSD depends linearly (power function with the exponent value of 1) on the time intervals at which it is measured. In the case of long-distance correlations that are characterized by power laws, the MSD grows faster, and the exponent value can be estimated as a slope of the MSD on a double-log scale (e.g. Ramos-Fernandes *et al.* 2004). In black bean aphids, a power law relationship between MSD and time was found for the time intervals up to about 20 s, which is indicated by a straight line when plotted on the double-log scales (figure 3*a*). The exponent value is close to 2, meaning that movement in this time interval is nearly directed. For longer intervals the power law is truncated—the line curves. We also measured the root mean-square fluctuation of the displacement (RMSFD), which is often used as an indicator of long-range correlations with no characteristic scale (Viswanathan *et al.* 1996; Atkinson *et al.* 2002; Reynolds *et al.* 2007). RMSFD shows the same pattern with the exponent value of 0.95 for the first 20 s and of 0.59 (which is close to the 0.5 value indicative of uncorrelated random walk) for 20–60 s (figure 3*b*). For larger time intervals, the power law is not a good fit, which might be related to the size of the Petri dish.

Further, we analysed the distribution of bout durations to see whether a truncated power law in displacement is accompanied by a similar temporal pattern. Figure 4*a* shows a linear part of the distribution plotted on the double-log scale suggesting a power law distribution. However, for long moves, the distribution departs from a power law, which becomes even more evident if the short moves are excluded from the analysis (figure 4*b*,*c*). This change is captured by a truncated power law model which is favoured overwhelmingly over both power law and exponential models for the cases when short moves (up to 10 s) were included in the analysis (table 1). When only the moves lasting 10 s or more were included, the truncated power law reduced to the exponential (the exponent μ was close to 0). Both models had a similar maximum log-likelihood, but the exponential was slightly favoured because it had fewer parameters.

To test whether the change of walking behaviour from directed movement for the time interval up to 20 s to movement similar to an uncorrelated random walk for the intervals between 20 and 60 s were affected by boundaries, we compared distribution of duration of the bouts lasting between 20 and 60 s (278 bouts) with the duration of the bouts within the same time interval from four records of walking aphids (from the same stock) moving in 25×25 cm dish, 10 aphids per dish (23 bouts in total). We found no significant difference in these two distributions ($\chi^2 = 34.7$, $P = 0.53$, d.f. $= 36$), although the area of the large dish was about 10 times bigger than the area of 9 cm Petri dishes.

We have thus found truncated power law behaviour in both space (MSD) and time (distribution of bout durations). In both cases strong correlations were found within a 20 s interval. This was also supported
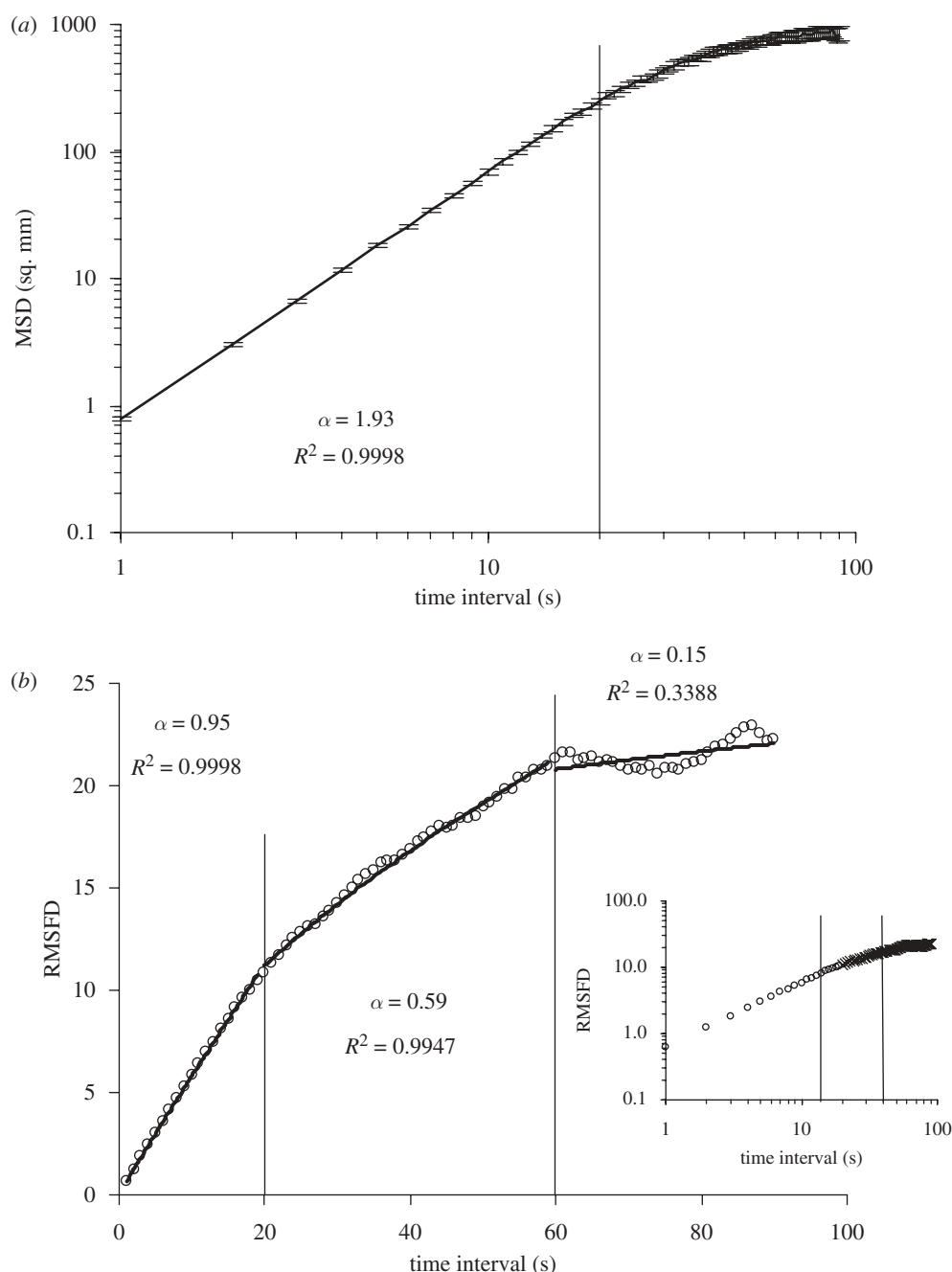
Figure 3. (*a*) Mean-squared displacement (MSD) ± SE measured from the tracks of aphids. The tracks recorded at 10 and 20 aphids per dish (12 replicas each, 360 aphids altogether) were pooled. If plotted separately, the two lines are very similar with the SEs being closely overlapping. MSD starts as a straight line on double-log scales indicating a power law relationship and then gradually slows down. For the first 20 s, the equation fitted with the least sum of squares method is $y = 0.8x^{1.93}$, $R^2 = 0.9998$. The exponent value of 1.93 indicates the directed movement. (*b*) Root mean-squared fluctuation of the displacement (RMSFD). The exponent of the power law fitted to the first 20 s is 0.95 (indicating the presence of correlations), and to the 21–60 s is 0.59 (which is not very different from the 0.5 expected for an uncorrelated process). The exponent values were found by the least sum of squares method. The inset shows the same graph on the log–log scales.

by RMSFD results, for which the correlation weakened for large time intervals. This pattern can suggest that the truncated power law in MSD in aphids is driven by a truncated power law in movement duration. When aphids start to move, they tend to walk for at least 20 s, after which they continue to move for an approximately exponentially distributed time interval.

Given that the approximate speed of aphids in this experiment was about 0.5 mm s^{-1} (Oliver *et al.* 2007), aphids would have travelled about 1 cm during this

time interval. This distance is very small when compared with the size of a bean leaf, but could be an optimal distance if searching for a different feeding place within the leaf.

Interestingly, the estimated exponent of the power law for all three cases was close to 2, which has been suggested as an optimal value when searching for renewable sparsely distributed targets (Viswanathan *et al.* 1999). For the truncated power law, the exponent decreased (and even fell below 1) when the short moves
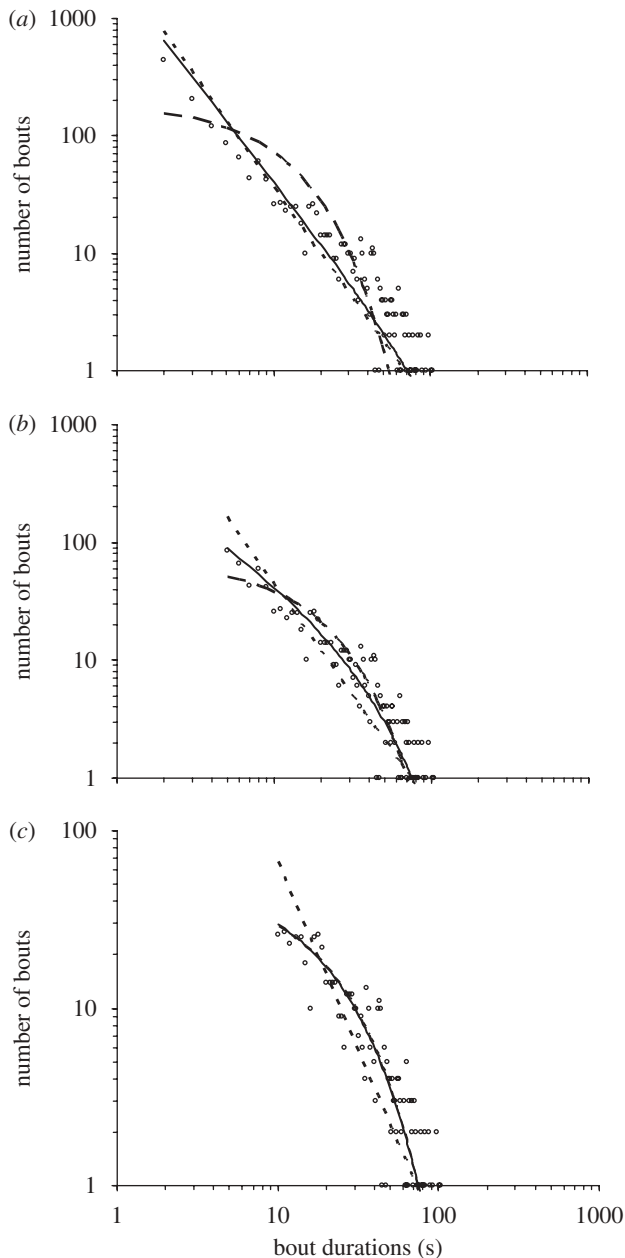
Figure 4. Double-log plots of the distributions of the bout durations (symbols) together with the best-fit exponential (dashed line), power law (dotted line) and truncated power law (solid line) distributions fitted for the datasets with the minimal move duration of 2 s (*a*), 5 s (*b*) and 10 s (*c*). The best-fit parameters were found by fitting the unbounded distributions to the data while the plotted values were calculated for the bounded distribution to retain $\sum_{j=x_{min}}^{x_{max}} p(j) = 1$ (the formulae are given in the appendix).

were excluded. Note that the requirement for the exponent of a power law distribution to be more than 1 comes from the fact that for the lower values the distribution does not converge. However, for the truncated power law this restriction is lifted since the convergence is ensured by the exponential component.

4. DISCUSSION

There is an ongoing debate whether a Lévy pattern, characterized by the presence of power laws, is an

appropriate model to describe animal movement. While some authors strongly support the Lévy walk approach (for the latest see Buchanan 2008; Sims *et al.* 2008), others show that at least in some cases non-heavy-tail distributions such as exponentials are a better fit to the datasets that were originally shown to fit a Lévy walk (Edwards *et al.* 2007). Our results show that if we would only have measured the value of the exponent of the power law distribution (which is a principal method for detecting Lévy patterns (Sims *et al.* 2007; White *et al.* 2008)) we would have concluded that any data range convincingly confirmed Lévy behaviour. However, applying more than one model allowed us to get a better understanding of the aphid walking pattern: we have shown that the short moves were power law distributed, but the long moves were exponentially distributed. Therefore, the conclusion whether an exponential or a power law is a good fit to the dataset depends heavily on how the data were collected.

Given that the observed distribution was a mixture of a power law and an exponential, it was not surprising that a truncated power law was the best fit to the data. We found a truncated power law in both MSD and distribution of bout durations of black bean aphids. This indicates the presence of correlations in both space and time within a limited time interval. We are not aware of studies where both MSD and duration of bouts (active periods) were measured at the same time. Our finding suggests that correlations in time lead to correlations in space and provides evidence for an assumption that the duration of a move can be used as a measure of the move length made in some previous studies (Viswanathan *et al.* 1996, 1999).

In both space and time, strong correlations were found for about 20 s, which suggests that within 20 s aphids kept moving and this movement was directional. After 20 s the MSD and bout durations were truncated. This might suggest that truncation in the MSD was driven by truncation in bout durations. In this sense, the observed shape of the MSD should not be interpreted as a correlated random walk since it does not emerge from the correlations in the turning angles but from another truncated power law process.

The observed truncation in the distribution of the bout durations could potentially arise for various reasons—the two obvious ones being encountering boundaries of the arena and encountering other aphids. Since the two density treatments did not differ, encountering other aphids was not likely to cause the truncation. Boundaries were not likely to cause truncation either since we found no difference in distribution of bout durations in the region where truncation occurred (between 20 and 60 s) between aphids moving in small Petri dishes (9 cm in diameter) and large square dishes (25 × 25 cm). The second change in behaviour at 60 s is more likely to be related to the boundaries because, with the mean speed being about 0.5 mm s^{-1} (Oliver *et al.* 2007), on average an aphid would move a distance of 30 mm, which is one-third of the Petri dish diameter. These results suggest that the truncation might be an intrinsic property of aphid movement rather than simply an artefact of the

Table 1. The best-fit parameters (with 95% confidence intervals), maximum log-likelihood and Akaike weights for the models fitted to the different parts of the dataset.

model	best-fit parameters	maximum log-likelihood	Akaike weights
fitting to the whole dataset (starting from 2 s moves)			
power law	$\mu = 1.869\ (1.827-1.912)$	-4858.02	0
exponential	$\lambda = 0.097\ (0.092-0.102)$	-5405.30	0
truncated power law	$\mu = 1.667\ (1.584-1.734)$	-4828.27	1
	$\lambda = 0.007\ (0.005-0.010)$		
fitting to part of the dataset (starting from 5 s moves)			
power law	$\mu = 1.890\ (1.831-1.952)$	-3258.22	0
exponential	$\lambda = 0.061\ (0.057-0.066)$	-3206.61	0
truncated power law	$\mu = 0.903\ (0.697-1.085)$	-3172.53	1
	$\lambda = 0.029\ (0.023-0.036)$		
fitting to part of the dataset (starting from 10 s moves)			
power law	$\mu = 2.115\ (2.024-2.212)$	-2245.63	0
exponential	$\lambda = 0.052\ (0.048-0.057)$	-2170.88	0.7
truncated power law	$\mu = 0.080\ (0-0.511)$	-2170.78	0.3
	$\lambda = 0.050\ (0.038-0.560)$		

experimental design. Our observations differ from the observations of Reynolds and Frye (2007), who found only one change in root mean-square fluctuations of displacement in *Drosophila*, which they related to the space restrictions.

Our data have demonstrated two distinct modes in the movement of aphids—fast and directed or slow with random change of direction. This intermittency can be interpreted in two ways: (i) the slow phase can be interpreted as non-movement, and then plotting the turning angles against the speed allows us to introduce a natural dichotomy between movement and non-movement based on the characteristics of the movement behaviour; (ii) the slow phase can be interpreted as an intensive (foraging) phase as opposed to a fast extensive (relocation) phase. Intermittent locomotion in which movements are interspersed with pauses has been reported for at least 21 species (Kramer & McLaughlin 2001). Few explanations for these pauses have been suggested such as recovering from fatigue, reducing detection by predators, stabilizing the perceptual field and others. Our study shows that in aphids such pauses are not complete stops, but small moves with a recordable change of the position and, therefore, they are best interpreted as a short-range (intensive) search. Such intermittency has been reported earlier in Bewick swans (Nolet & Mooij 2002) and in *Drosophila* (Reynolds & Frye 2007).

Intermittency on its own or combined with power laws has been shown to be beneficial when searching for sparse targets (Benichou *et al.* 2005, 2006; Reynolds 2006; Lomholt *et al.* 2008). Typically, aphids feed on leaves and young shoots. Although a leaf surface does not look like a collection of sparsely distributed food parcels, aphids choose particular sites where they can reach phloem vessels with their stylets, and the vessels are not evenly distributed within the leaf. Aphid movement is similar to the movement of *Drosophila*, where intermittency was combined with power law-distributed long moves (Reynolds & Frye 2007), apart from the truncation of the power law. Such truncation might facilitate a search within a restricted area, thus keeping an aphid within a leaf.

To summarize, we have shown that in aphid movement intermittency is combined with a relocation phase consisting of directed and diffusive parts, which are best described as a truncated power law. A truncated power law was found in both space and time suggesting that an individual's decisions to start and to stop movement lead to a corresponding pattern in the MSD. This approach, along with the consideration that data resolution can affect the interpretation of movement patterns, provides a universal model for movement patterns, and can serve as a useful building block to integrate movement in models that describe the population biology and ecology of moving animals.

APPENDIX A. DERIVATION OF THE LOG-LIKELIHOOD FUNCTIONS

A.1. Log-likelihood function for the exponential distribution

The *pdf* of the exponential model is

$$f(x) = Ce^{-\lambda x}, \quad x \in [x_{\min}, \infty],$$

where C is the normalization constant,

$$C = \frac{\lambda}{e^{-\lambda x_{\min}}},$$

as obtained by solving $\int_{x_{\min}}^{\infty} f(x)\mathrm{d}x = 1$. Then, the probability of x being j

$$P(x = j|\lambda) = \int_{j-0.5}^{j+0.5} f(x)\mathrm{d}x$$

$$= -\frac{C}{\lambda}\left[e^{-\lambda x}\right]_{j-0.5}^{j+0.5} = \frac{e^{-\lambda(j-0.5)} - e^{-\lambda(j+0.5)}}{e^{-\lambda x_{\min}}},$$

and the log-likelihood function is

$$l(\lambda|\text{data}) = \sum_{j=1}^{x_{\max}} d_j \log\left[\frac{\mathrm{e}^{-\lambda(j-0.5)} - \mathrm{e}^{-\lambda(j+0.5)}}{\mathrm{e}^{-\lambda x_{\min}}}\right],$$

where d_j is the number of data points of the value j. The summation can be carried out up to any value larger than $x_{\max}$ but for all those values $d_j = 0$ and therefore they have no effect on the results.

Over the bounded range $x \in [x_{\min}, x_{\max}]$,

$$C = \frac{\lambda}{\mathrm{e}^{-\lambda x_{\min}} - \mathrm{e}^{-\lambda x_{\max}}},$$

and the probability mass function is

$$P(x = j|\lambda) = \frac{\mathrm{e}^{-\lambda(j-0.5)} - \mathrm{e}^{-\lambda(j+0.5)}}{\mathrm{e}^{-\lambda x_{\min}} - \mathrm{e}^{-\lambda x_{\max}}}.$$

A.2. Log-likelihood function for the power law distribution

Similar to the exponential distribution, the *pdf* of the power law model is $f(x) = Cx^{-\mu}$, $x \in [x_{\min}, \infty]$, where $C = \mu - 1/x_{\min}^{1-\mu}$ for $\mu > 1$ (for smaller μ the distribution cannot be scaled). Then, the probability of x being j is

$$P(x = j|\mu) = \int_{j-0.5}^{j+0.5} f(x)\mathrm{d}x = \frac{C}{1-\mu}\left[x^{1-\mu}\right]_{j-0.5}^{j+0.5}$$

$$= \frac{(j-0.5)^{1-\mu} - (j+0.5)^{1-\mu}}{x_{\min}^{1-\mu}},$$

and the log-likelihood function is

$$l(\mu|\text{data}) = \sum_{j=1}^{x_{\max}} d_j \log\left[\frac{(j-0.5)^{1-\mu} - (j+0.5)^{1-\mu}}{x_{\min}^{1-\mu}}\right].$$

Over the bounded range $x \in [x_{\min}, x_{\max}]$,

$$C = \frac{\mu - 1}{x_{\min}^{1-\mu} - x_{\max}^{1-\mu}},$$

and the probability mass function is

$$P(x = j|\mu) = \frac{(j-0.5)^{1-\mu} - (j+0.5)^{1-\mu}}{x_{\min}^{1-\mu} - x_{\max}^{1-\mu}}.$$

A.3. Log-likelihood function for the truncated power law distribution

The *pdf* of the truncated power law is

$$f(x) = Cx^{-\mu}\,\mathrm{e}^{-\lambda x}, \quad x \in [x_{\min}, \infty],$$

where

$$C = 1/\lambda^{\mu-1}\Gamma(1 - \mu, \lambda x_{\min})$$

for the positive values of x with $\Gamma()$ being the incomplete gamma function. Then, the probability of x

being j is

$$P(x = j|\lambda, \mu)$$

$$= \int_{j-0.5}^{j+0.5} f(x)\mathrm{d}x = -C\lambda^{\mu-1}[\Gamma(1-\mu, \lambda x]_{j-0.5}^{j+0.5}$$

$$= \frac{\Gamma(1 - \mu, \lambda(j-0.5)) - \Gamma(1 - \mu, \lambda(j+0.5))}{\Gamma(1 - \mu, \lambda x_{\min})},$$

and the log-likelihood function is

$$l(\lambda, \mu|\text{data})$$

$$= \sum_{j=1}^{x_{\max}} d_j \log\frac{\Gamma(1 - \mu, \lambda(j-0.5)) - \Gamma(1 - \mu, \lambda(j+0.5))}{\Gamma(1 - \mu, \lambda x_{\min})}.$$

Over the bounded range $x \in [x_{\min}, x_{\max}]$,

$$C = \frac{1}{\lambda^{\mu-1}(\Gamma(1 - \mu, \lambda x_{\min}) - \Gamma(1 - \mu, \lambda x_{\max}))},$$

and the probability mass function is

$$P(x = j|\lambda, \mu)$$

$$= \frac{\Gamma(1 - \mu, \lambda(j-0.5)) - \Gamma(1 - \mu, \lambda(j+0.5))}{\Gamma(1 - \mu, \lambda x_{\min}) - \Gamma(1 - \mu, \lambda x_{\max})}.$$

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