Variation in individual walking behavior creates the impression of a Lévy flight

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Many animal paths have an intricate statistical pattern that manifests itself as a power law-like tail in the distribution of movement lengths. Such distributions occur if individuals move according to a Lévy flight (a mode of dispersal in which the distance moved follows a power law), or if there is variation between individuals such that some individuals move much farther than others. Distinguishing between these two mechanisms requires large quantities of data, which are not available for most species studied. Here, we analyze paths of black bean aphids (*Aphis fabae* Scopoli) and show that individual animals move in a predominantly diffusive manner, but that, because of variation at population level, they collectively appear to display superdiffusive characteristics, often interpreted as being characteristic for a Lévy flight.

animal movement | diffusion | random walk | statistical inference | movement ecology

Following the suggestion by Mandelbrot (1) that animal movement shows scale invariance and fractal properties, the study of animal movement has attracted much attention (2–9). Several studies have reported movement length distributions with a fat tail, corresponding to a power law, which could be indicative of a fractal movement pattern known as a Lévy flight (2). The agreement between a power law distribution and the data are sometimes very good (e.g., see the top right panel of figure 4 in ref. 4); however, often the rate of decay in bout duration frequency is best described by a power law with an exponential cutoff, i.e., a power law-type rate of decay for intermediate bout durations, and an exponential rate of decay for long bouts (5, 7, 9–12).

There are two potential explanations for such distributions. One possibility is that the long movements are overrepresented for all individuals, for instance, because all tracks have Lévy flight characteristics (13). Alternatively, there is variation between individuals, such that some individuals move much longer and farther than others, and the population aggregate appears to show a fat tail, but individual's bout distributions do not (14–16). One can distinguish between these mechanisms by rescaling the trajectories, such that the mean bout length is the same for all trajectories. If one then aggregates these rescaled distributions and the resulting aggregate is fat tailed, the "fat-tailedness" is a property of the individual trajectories. If, on the contrary, the population distribution loses its fat tail after rescaling, the fat tail is caused by variation between trajectories (Fig. 1).

We used this idea to analyze walking tracks of apterous black bean aphids. Aphids are small insects that feed on plants and walk to locate suitable feeding places and to reposition themselves on the plants on which they live. They are convenient to study walking behavior because they are small, easy to rear, and walk over small distances, which makes it easy to gather and analyze data. Moreover, they walk through alternating bouts of directed, fast movement, with periods of slow, undirected movement, and the length distribution of these bouts of directed movement is fat-tailed and best described by a power law with exponential cutoff (Fig. 2A) (9).

Individual Variation Between Individuals

We will first demonstrate that there is substantial variation between individuals. For this, we used a bootstrapping procedure for which we constructed tracks in which the bouts were randomly drawn from the observed aggregate distribution of bouts in the population. We then rescaled the artificial tracks and the original tracks as described in *Materials and Methods* and in *SI Appendix, Statistical Analysis of Data*. This showed that the original scaled tracks differ significantly from a population in which the bouts are all drawn from the same distribution. Next, we constructed tracks from exponential distributions with a parameter equal to that estimated from the original track. After scaling, the aggregates showed no significant difference from the original scaled tracks (*SI Appendix, Bootstrapping Procedure to Test Whether Bouts Within Tracks Are Exponentially Distributed*). This suggests that movement lengths within tracks are exponentially distributed, but differ in the parameter of this exponential distribution, and that the power law with exponential cutoff in the population data results from a superposition of these exponential distributions. We confirmed this by plotting the rescaled bout distribution, which agrees with an exponential distribution (Fig. 2B). We also estimated the parameter of the exponential distribution for all individual tracks (*SI Appendix, Theoretical Prediction of ψ(λ) and Scaled Bout Distribution*), and this demonstrates there is considerable variation (Fig. 2C). Because the scaled individual bout durations have no indication of a fat tail, but the distribution of parameters has substantial variation, this gives further support to the statement that the approximate power law in the bout distributions originates from the differences between individuals.

Movement of Nonidentical Individuals

To interpret this finding, we applied the tools of statistical mechanics. A bout of a given duration can be obtained by many different combinations of steps of various lengths, and which of all these possible realizations actually happens is not known. However, in a statistical equilibrium the probability density that a random sampling of the system will return a bout of length τ is given by the Boltzmann distribution (17):

$$\phi(\tau, \lambda) \propto \exp(-\lambda\tau), \tag{1}$$

where λ is the parameter quantifying the given equilibrium. This is a fundamental law of statistical mechanics (*SI Appendix, Movement of Non-Identical Individuals: Model Derivation Using Statistical Mechanics*).
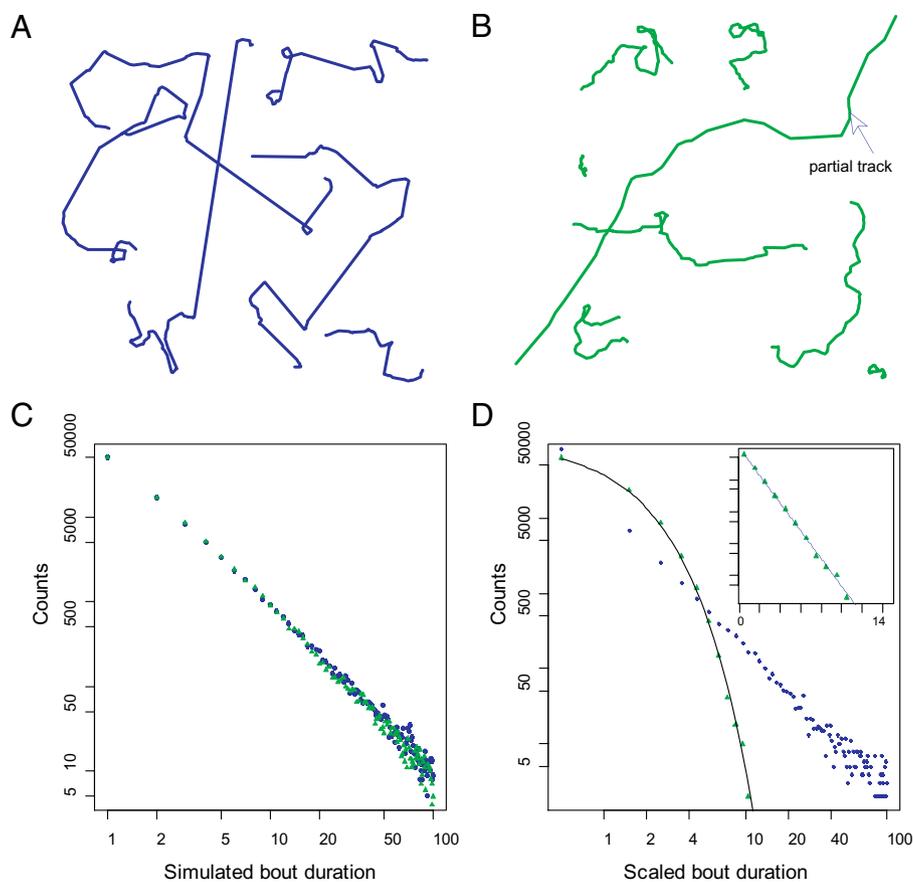
Fig. 1. Two possible explanations for fat-tailed movement data: (*A*) All tracks are similar in that they have bout durations drawn from the same fat-tailed distribution (blue tracks) or (*B*) all tracks are diffusive and have movement lengths drawn from exponential distributions, but individuals differ in that some move much more than others (green tracks). The difference between individuals is chosen such that the aggregated distributions of movement lengths (*C*) is identical (over a larger range) and has power-law characteristics, which show as a straight line on a double log plot (blue circles and green triangles represent the blue and the green tracks). One can distinguish between these two cases by scaling the tracks (here, dividing each value by the track mean bout duration) so that they have the same typical length and aggregate the scaled data (*D*). For the blue tracks, the scaling does not affect the fat tail, whereas for the green tracks, scaling reveals the exponential nature of the individual bout distributions as a straight line on a semi-log plot (see *Inset*). The lines show a unit exponential distribution.

The results in Fig. 2*B* justify the assumption that there exists an ideal distribution of the bout duration, $\phi(\tau,\lambda)$, given by the exponential distribution. The parameter of this distribution, λ, is likely to depend on properties that may affect individual motion, e.g., body mass, leg or wing length, metabolic rate, motivational state. If these traits vary among individuals, different individuals will have different values of λ, and this will make the bout distribution in the population different from the ideal distribution. In the population, λ is described by a probability distribution $\psi(\lambda)$ (Fig. 2*C*) rather than a single-valued parameter (16), and the observed aggregate probability distribution function $\Phi(\tau)$, of bout duration is:

$$\Phi(\tau) = \int_{\lambda_{min}}^{\lambda_{max}} \lambda \exp(-\lambda\tau)\psi(\lambda)d\lambda, \qquad [2]$$

where λ is distributed over a finite, positive domain. It can be shown that, for small bout durations, this leads to near linear behavior, whereas for large bout durations, we find an exponentially decaying distribution (*SI Appendix, Movement of Non-Identical Individuals*, and *SI Appendix*, Fig. S2). This observation explains why power laws are ubiquitous in the movement of a population of nonidentical individuals, as the crossover of these two asymptotic behaviors creates the appearance of a power law with cutoff.

This also suggests a procedure to differentiate between the two possible explanations for fat tailed distributions: either each and every individual generates bouts from the same distribution Φ and these bouts are uncorrelated within tracks, or each individual generates exponentially distributed bouts, but with different parameters for the exponential and the same aggregate distribution Φ, which we assume has a truncated fat tail. To distinguish between these two explanations, we will select the one which is most likely, given the data (*Materials and Methods*). This procedure is more conservative than the methods applied earlier and tends to be biased toward the first explanation for shorter tracks. However, if we used the tracks with five or more bouts, this method selected the second explanation, from which we infer that the tracks are structured according to the Boltzmann distribution.

Discussion

Here we have provided conclusive evidence that, for a population that has a bout distribution that is fat-tailed, an exponential, Boltzmann-like distribution of movement bouts can describe the movement of individual aphids. As a result of variation between individuals, the population as a whole appears to display a non-diffusive type of movement.

Distributions of bouts often can be described by a power law (4) for part of the domain, but also can be fitted reasonably well by an exponential-type distribution in other parts (10–12), sug-
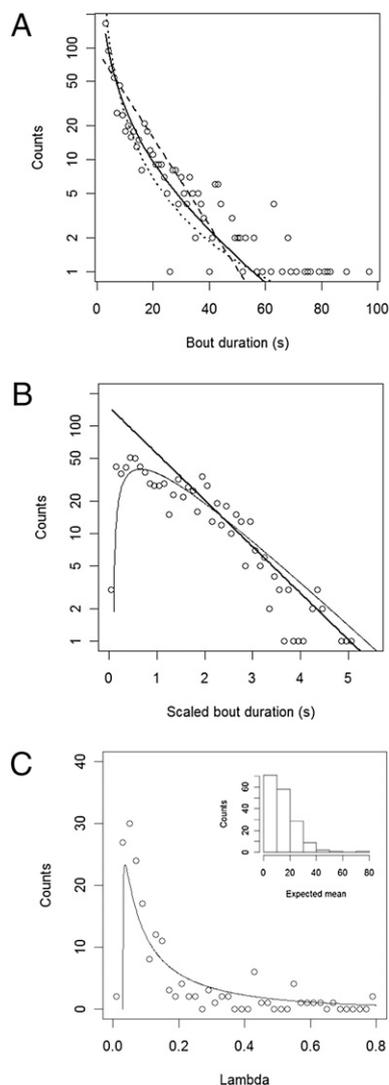
Fig. 2. The data of aphid tracks with at least three bouts per track (*A*) Distribution of the bout durations fitted with distributions based on the exponential (dashed line), power law (dotted line), and power law with exponential cutoff (solid line) functions by using maximum likelihoods. The power law with exponential cutoff provides the best fit: the maximum log likelihoods are −2,708, −2,672, and −2,623, respectively, giving the power law with exponential cutoff ($\sim \tau^{-1.19} e^{-0.03\tau}$) an Akaike weight of 1.0. (*B*) Bout durations scaled as described in *Materials and Methods*. Because bouts are at least 3 s, the scaled bout duration underrepresents short-scaled bouts. The straight line is a unit exponential, scaled to account for the bouts shorter than 3 s. The curve is a theoretical prediction (*SI Appendix, Theoretical Prediction of ψ(λ) and Scaled Bout Distribution*) of the scaled bout duration distribution based on the best fit distribution used in *A*. (*C*) Frequency of the exponential parameter λ: the curve is the theoretical prediction (*SI Appendix*) of the exponential parameter based on the best fit distribution portrayed in *A*. *Inset*: Distribution of the predicted mean bout lengths ($\tilde{\lambda}^{-1}$) for the tracks.

gesting a power law with exponential cutoff. It has been argued that such a cutoff should always be present as a result of the effects of finite space (e.g., animal territory) or at smaller scales by environmental factors such as distribution of food items (18), which truncates paths.

Here we have shown that in a population in which the movement characteristics appear to have a fat tail the appearance of a fat tail is caused by variation between individuals. This shows that population aggregates of movement data can be very different

from the corresponding data at the individual level. The power law with a cutoff that we found was not the result of a truncation or interruption of paths of all individual, for instance, through encountering the edge of the arena, or because the predator encounters a prey item, but came from the differences between individuals.

If a power law is encountered in aggregated data, it need not mean that individual paths have the same power law signature. For instance, in Fig. 1, the aggregated bouts obey a shifted power law resulting from a population of individuals whose bouts come from an exponential distribution. This shows that one ought to be cautious in attributing properties of the population aggregate to the individual. For instance, it has been argued that, if movement data are distributed according to a power law (with or without cutoff), the location of prey items under certain conditions is optimized (3, 18, 19). Therefore, this does not necessarily mean that, if the population aggregate shows a power law (with or without cutoff), individuals in this population are optimized with respect to the location of prey.

Fat-tailed distributions are a fingerprint of a non-Brownian, superdiffusive motion (a spread faster than through diffusion) (20, 21). Our results suggest that, at the time scale at which we made our observations, individual movement has diffusive characteristics, yet at population level, the movement characteristics appear to have superdiffusive properties. A similar result was presented for the movement of humans, traced by their mobile phones' position (22); however, human individual movement could be characterized by a Lévy flight up to a certain scale. Although it is no surprise that mobile phone movement is different from that of insects, it is interesting to observe that superdiffusive movement in both cases could be explained by population-level variation. This is also supported by a number of other studies in which considerable variation in movement parameters between individuals was observed, with distributions that resemble power laws with cutoffs, even though it was not always established whether individuals move diffusively (23–27). These observations, combined with our finding that individual movement has diffusive characteristics, raise the question in how far the behavior of other animals truly has fractal properties, or whether this is a result of the pooling of data across individuals together with individual variation (14, 15).

This observation has important consequences for movement and spread of populations of organisms. For instance, if certain individuals move more than others, and thus make more contacts, this would provide a mechanistic underpinning for the existence of "superspreaders," which can enhance the spread of disease. It has also been suggested that superdiffusive movement has evolved to the extent that it optimizes search efficiency (3, 19). If it is indeed the case that not the individual trajectories, but rather the population aggregate, is optimal, it is feasible that there is selection for individual movement characteristics of a scale that complements that of the population ensemble. This would open the way to formulate a mechanistic framework to explain animal searching behavior and generate novel hypotheses about its evolution.

Materials and Methods

Black bean aphids (*Aphis fabae* Scopoli) were reared on bean plants (*Vicia faba* L.) as described previously (28). Aphids were taken from the plant and placed in 9-cm Petri dishes on filter paper in groups of 10 and 20 and video-recorded using a Watec 902 camera with HF9HA-1B Fujinon lens (ALRAD). Paths were calculated from the records with GMimPro software (http://www.nimr.mrc.ac.uk/gmimpro/) (29). Paths consisted of alternated intervals of high and low speed. A walking bout was defined as a movement of at least 3 s in which the speed exceeded 0.3 mm/s at every second (9). We analyzed 171 paths consisting of three or more bouts, and a total of 800 bouts over all paths.

To rescale the tracks and to estimate the exponential parameter from the data, we had to take into account the discretisation and minimal length of the data. To rescale the bout length τ we used the following formula:

$$\tau' = 1 + \tilde{\lambda} z \left(\tau_i + \frac{1}{1 - e^{-\tilde{\lambda}}} \right) \qquad [3]$$

where $\tilde{\lambda} = \frac{n-1}{n} \ln\left(1 + \frac{n}{s - 3n + n^{-2}}\right)$, n is the number of bouts in the track, and s is the sum of all bout lengths in the track (*SI Appendix, Statistical Analysis of Data*, describes justification and derivation).

To establish the likelihoods of the hypotheses (first, that the tracks are unstructured, and second, that the tracks are structured according to the Boltzmann distribution), the following procedure was implemented. Let the likelihood of hypothesis i given the data in track j, T_j, be given by $\Phi_i^{tr}(T_j)$, then the likelihood is $\Pi_{j=1}^{M} \Phi_i^{tr}(T_j)$, with M the number of tracks. The calcu-

lation of the track likelihood under the first explanation follows from the fact that all bouts are uncorrelated and drawn from the aggregate distribution Φ. For the calculations, we assumed that Φ followed a discretized power law with exponential cutoff (9). The likelihood to find the bouts in the track under the second explanation follows from the assumption that they are all drawn from the same exponential distribution. Details of the calculation are explained in *SI Appendix, Inferring the Structure Within Tracks*.

1. Mandelbrot B (1977) *The Fractal Geometry of Nature* (Freeman, New York).
2. Viswanathan GM, et al. (1996) Levy flight search patterns of wandering albatrosses. *Nature* 381:413–415.
3. Viswanathan GM, et al. (1999) Optimizing the success of random searches. *Nature* 401:911–914.
4. Bartumeus F, Peters F, Pueyo S, Marrasé C, Catalan J (2003) Helical Lévy walks: adjusting searching statistics to resource availability in microzooplankton. *Proc Natl Acad Sci USA* 100:12771–12775.
5. Edwards AM, et al. (2007) Revisiting Lévy flight search patterns of wandering albatrosses, bumblebees and deer. *Nature* 449:1044–1048.
6. Reynolds AM, Smith AD, Reynolds DR, Carreck NL, Osborne JL (2007) Honeybees perform optimal scale-free searching flights when attempting to locate a food source. *J Exp Biol* 210:3763–3770.
7. Sims DW, et al. (2008) Scaling laws of marine predator search behaviour. *Nature* 451:1098–1102.
8. Codling EA, Plank MJ, Benhamou S (2008) Random walk models in biology. *J R Soc Interface* 5:813–834.
9. Mashanova A, Oliver TH, Jansen VAA (2010) Evidence for intermittency and a truncated power law from highly resolved aphid movement data. *J R Soc Interface* 7:199–208.
10. Newman MEJ (2005) Power laws, Pareto distributions and Zipf's law. *Contemp Phys* 46:323–351.
11. Clauset A, Shalizi CR, Newman MEJ (2009) Power-law distributions in empirical data. *SIAM Review* 51:661–703.
12. Barthelemy P, Bertolotti J, Wiersma DS (2008) A Lévy flight for light. *Nature* 453:495–498.
13. Brockmann D, Hufnagel L, Geisel T (2006) The scaling laws of human travel. *Nature* 439:462–465.
14. Turchin P (1996) Fractal analyses of animal movement: A critique. *Ecology* 77:2086–2090.
15. Benhamou S (2007) How many animals really do the Lévy walk? *Ecology* 88:1962–1969.

16. Petrovskii SV, Morozov AY (2009) Dispersal in a statistically structured population: Fat tails revisited. *Am Nat* 173:278–289.
17. Balescu R (1975) *Equilibrium and Nonequilibrium Statistical Mechanics* (John Wiley, New York).
18. Viswanathan GM, Raposo EP, da Luz MGE (2008) Levy flights and superdiffusion in the context of biological encounters and random searches. *Phys Life Rev* 5:133–150.
19. Bartumeus F, Catalan J, Fulco UL, Lyra ML, Viswanathan GM (2002) Optimizing the encounter rate in biological interactions: Lévy versus Brownian strategies. *Phys Rev Lett*, 10.1103/PhysRevLett.88.097901.
20. Shlesinger MF, Zaslavsky GM, Klafter J (1993) Strange kinetics. *Nature* 363:31–37.
21. Klafter J, Sokolov IM (2005) Anomalous diffusion spreads its wings. *Phys World* 18:29–32.
22. González MC, Hidalgo CA, Barabási A-L (2008) Understanding individual human mobility patterns. *Nature* 453:779–782.
23. Tufto J, Ringsby TH, Dhondt AA, Adriaensen F, Matthysen E (2005) A parametric model for estimation of dispersal patterns applied to five passerine spatially structured populations. *Am Nat* 165:E13–E26.
24. Hapca S, Crawford JW, Young IM (2009) Anomalous diffusion of heterogeneous populations characterized by normal diffusion at the individual level. *J R Soc Interface* 6:111–122.
25. Yamamura K (2002) Dispersal distance of heterogeneous populations. *Popul Ecol* 44:93–101.
26. Clark JS, Silman M, Kern R, Macklin E, HilleRisLambers J (1999) Seed dispersal near and far: Patterns across temperate and tropical forests. *Ecology* 80:1475–1494.
27. Humphries NE, et al. (2010) Environmental context explains Lévy and Brownian movement patterns of marine predators. *Nature* 465:1066–1069.
28. Oliver TH, Mashanova A, Leather SR, Cook JM, Jansen VAA (2007) Ant semiochemicals limit apterous aphid dispersal. *Proc Biol Sci* 274:3127–3131.
29. Mashanov GI, Molloy JE (2007) Automatic detection of single fluorophores in live cells. *Biophys J* 92:2199–2211.

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