This pdf consists of four parts. **First**, the original paper (including an erratum) by Monique de Jager and colleagues:

Lévy Walks Evolve Through Interaction Between Movement and Environmental Complexity
Monique de Jager, *et al.*
Science **332**, 1551 (2011);
DOI: 10.1126/science.1201187

Second, the associated supporting online material:

Supporting Online Material

Third, a comment on the paper by Vincent Jansen and colleagues:

Comment on "Lévy Walks Evolve Through Interaction Between Movement and Environmental Complexity"
Vincent A. A. Jansen, *et al.*
Science **335**, 918 (2012);
DOI: 10.1126/science.1215747

And **fourth**, the response of Monique de Jager and colleagues to these comments:

Response to Comment on "Lévy Walks Evolve Through Interaction Between Movement and Environmental Complexity"
Monique de Jager, *et al.*
Science **335**, 918 (2012);
DOI: 10.1126/science.1215903

4. V. B. Polyakov, R. N. Clayton, J. Horita, S. D. Mineev, *Geochim. Cosmochim. Acta* **71**, 3833 (2007).
5. I. B. Butler, C. Archer, D. Vance, A. Oldroyd, D. Rickard, *Earth Planet. Sci. Lett.* **236**, 430 (2005).
6. Y. Duan *et al.*, *Earth Planet. Sci. Lett.* **290**, 244 (2010).
7. C. M. Johnson, B. L. Beard, E. E. Roden, *Annu. Rev. Earth Planet. Sci.* **36**, 457 (2008).
8. C. Archer, D. Vance, *Geology* **34**, 153 (2006).
9. R. Raiswell, D. E. Canfield, *Am. J. Sci.* **298**, 219 (1998).
10. J. L. Skulan, B. L. Beard, C. M. Johnson, *Geochim. Cosmochim. Acta* **66**, 2995 (2002).
11. A. D. Anbar, O. Rouxel, *Annu. Rev. Earth Planet. Sci.* **35**, 717 (2007).
12. Materials and methods and detailed results are available as supporting material on *Science* Online.
13. D. Rickard, G. W. Luther III, *Geochim. Cosmochim. Acta* **61**, 135 (1997).
14. G. W. Luther III, D. Rickard, *J. Nanopart. Res.* **7**, 389 (2005).
15. D. Rickard, G. W. Luther 3rd, *Chem. Rev.* **107**, 514 (2007).
16. E. A. Schauble, *Rev. Mineral. Geochem.* **55**, 65 (2004).
17. A. D. Anbar, J. E. Roe, J. Barling, K. H. Nealson, *Science* **288**, 126 (2000).
18. I. B. Butler, M. E. Bottcher, D. Rickard, A. Oldroyd, *Earth Planet. Sci. Lett.* **228**, 495 (2004).
19. A. E. Isley, *J. Geol.* **103**, 169 (1995).
20. K. E. Yamaguchi, C. M. Johnson, B. L. Beard, H. Ohmoto, *Chem. Geol.* **218**, 135 (2005).
21. R. Guilbaud, I. B. Butler, R. M. Ellam, D. Rickard, A. Oldroyd, *Geochim. Cosmochim. Acta* **75**, 2721 (2011).
22. A. D. Czaja *et al.*, *Earth Planet. Sci. Lett.* **292**, 170 (2010).
23. D. E. Canfield, *Annu. Rev. Earth Planet. Sci.* **33**, 1 (2005).
24. S. W. Poulton, P. W. Fralick, D. E. Canfield, *Nat. Geosci.* **3**, 486 (2010).
25. D. E. Canfield, *Nature* **396**, 450 (1998).
26. C. Li *et al.*, *Science* **328**, 80 (2010); 10.1126/science.1182369.
27. A. McAnena, S. Severmann, S. W. Poulton, *Geochim. Cosmochim. Acta* **73**, A854 (2009).
28. C. M. Johnson, E. E. Roden, S. A. Welch, B. L. Beard, *Geochim. Cosmochim. Acta* **69**, 963 (2005).
29. S. Severmann, T. W. Lyons, A. Anbar, J. McManus, G. Gordon, *Geology* **36**, 487 (2008).
30. O. J. Rouxel, M. Auro, *Geostand. Geoanal. Res.* **34**, 135 (2010).

Acknowledgments: This work was funded by an ECOSSE Ph.D. studentship to R.G. and Natural Environment Research Council research grant NE/E003958/1 to I.B.B. We are thankful to K. Keefe, V. Gallagher, N. Odling, B. D. Roach, S. Mowbray, and C. Fricke for technical support and B. Ngwenya, A. Matthews, D. Rickard, A. McAnena, and M. Pękala for constructive discussions.

Supporting Online Material

www.sciencemag.org/cgi/content/full/332/6037/1548/DC1
Materials and Methods
Fig. S1
Table S1
References (*31*–*41*)

17 January 2011; accepted 17 May 2011
10.1126/science.1202924

Lévy Walks Evolve Through Interaction Between Movement and Environmental Complexity

Monique de Jager,[1]* Franz J. Weissing,[2] Peter M. J. Herman,[1] Bart A. Nolet,[3,4] Johan van de Koppel[1,4]

Ecological theory predicts that animal movement is shaped by its efficiency of resource acquisition. Focusing solely on efficiency, however, ignores the fact that animal activity can affect resource availability and distribution. Here, we show that feedback between individual behavior and environmental complexity can explain movement strategies in mussels. Specifically, experiments show that mussels use a Lévy walk during the formation of spatially patterned beds, and models reveal that this Lévy movement accelerates pattern formation. The emergent patterning in mussel beds, in turn, improves individual fitness. These results suggest that Lévy walks evolved as a result of the selective advantage conferred by autonomously generated, emergent spatial patterns in mussel beds. Our results emphasize that an interaction between individual selection and habitat complexity shapes animal movement in natural systems.

Animals must face the daunting complexity of the natural world when searching for food, shelter, and other resources crucial for survival. To cope with the challenge to maximize the probability of resource encounters, many organisms adopt specialized search strategies (*1*, *2*) that can be described by random walks. Brownian and Lévy walks are prominent examples of random walk strategies where both the direction and step length of the constituent moves are drawn from a probability distribution (*1*–*4*). These movement patterns differ in the distribution of step lengths, which are derived from an exponential distribution in the case of Brownian motion, but follow a power-law distribution in case of Lévy motion (*4*–*7*), where many short steps are occasionally alternated with a long step. Model simulations have shown that a Lévy walk provides faster dispersal (*2*, *3*), more newly visited sites (*1*, *2*), and less intraspecific competition than Brownian walks (*4*); it is therefore considered the most efficient random search strategy in resource-limited environments where food occurs patchily at locations unknown to the searcher (*1*–*3*) and, most importantly, where the resource distribution is largely unaffected by the activities of the searching animal (*8*, *9*). Although shown to be optimal for only these specific conditions, Lévy walks are broadly found in nature (*1*, *10*–*12*), suggesting that they are adaptive over a wider range of conditions. To explain this wide occurrence, we hypothesize that organisms themselves affect the availability and spatial distribution of the resources upon which they depend (*13*). Consequently, the movement strategies of organisms can shape the environment.

On intertidal flats, the distribution of regularly spaced clumps of mussels (*Mytilus edulis*) results from the interaction between local mussel density and the crawling movement of young mussels (*5*, *14*, *15*). In particular, pattern formation in mussel beds is attributable to two opposing mechanisms: cooperation and competition (*16*). By moving into cooperative aggregations, mussels increase their local density, which decreases wave stress and predation risk. Conversely, competition for algae, which occurs on a larger spatial scale than facilitation, prevents the formation of larger clumps by limiting the number of mussels within a long range. The interaction of local facilitation and long-range competition results in the emergence of a patchy distribution of individuals, which simultaneously reduces risk and minimizes competition for algae (*15*). Hence, in this system, the distribution of suitable settling locations, an important resource for mussels, is determined by the existing distribution of mussels, which develops in response to the movement of its comprising individuals. Here, we investigate

Table 1. Goodness-of-fit (G), AIC weights, adjusted R^2, and Lévy exponents for three classes of movement strategies. The observed step length distribution is best explained by a Lévy walk or a truncated Lévy walk, with Lévy exponents close to 2.

	G	AIC weights	Adjusted R^2	Lévy exponent
Truncated Lévy walk	22.45	0.443	0.997	2.01
Lévy walk	47.22	0.428	0.997	2.06
Brownian walk	–190.09	0.129	0.837	–

---

[1] Spatial Ecology Department, Netherlands Institute of Ecology (NIOO-KNAW), Post Office Box 140, 4400 AC Yerseke, Netherlands. [2] Theoretical Biology Group, Centre for Ecological and Evolutionary Studies, University of Groningen, Nijenborgh 7, 9747 AG Groningen, Netherlands. [3] Department of Animal Ecology, Netherlands Institute of Ecology (NIOO-KNAW), Post Office Box 50, 6700 AB Wageningen, Netherlands. [4] Project Group Movement Ecology, Netherlands Institute of Ecology (NIOO-KNAW), Post Office Box 50, 6700 AB Wageningen, Netherlands.

*To whom correspondence should be addressed. E-mail: m.dejager@nioo.knaw.nl

whether the interplay between movement strategy and habitat complexity results in the emergence of Lévy walks in these self-organizing mussel beds.

We first tested the hypothesis that mussel movement is described by a Lévy walk (or a truncated Lévy walk) against alternative models reported in the literature, namely, a Brownian walk and a composite Brownian walk (*17*–*19*). We observed the movements of 50 mussels during the process of pattern formation and of 12 mussels in solitary experiments in mesocosm tanks. Step lengths were estimated by the distance between two subsequent reorientation events (*5*). The resulting step length distribution was compared with the family of power-law distributions, $P(l) = Cl^{-\mu}$, where $P(l)$ is the probability of a step of length l and C is a constant ensuring that the total probability equals 1. The exponent μ defines the shape of the distribution and therefore determines the resulting movement strategy. If $1 < \mu < 3$, the movement pattern corresponds to a Lévy walk. When μ approaches 1, the movement is approximately ballistic, while it is approximately Brownian when μ approaches 3 (and for $\mu > 3$) (*2*, *5*, *20*) (fig. S2.2). The Lévy walks found in nature typically have an exponent μ of ~2 (*1*, *10*–*12*).

Our results show that mussels use a Lévy walk during the process of pattern formation. On the basis of maximum-likelihood estimation and the derived goodness-of-fit (G), Akaike information criterion (AIC), and the fraction of variance explained by the model (R^2), we found that Lévy walk and truncated Lévy walk distributions, both with $\mu \approx 2$, provided the best fit to the data over a range of at least two orders of magnitude (*5*) (Table 1, Fig. 1, and table S3.1). A possible alternative explanation is that mussel movement follows a composite Brownian walk, where movement speeds are adjusted to local environmental conditions (*17*–*21*). Such a strategy can have a step length distribution similar to that of a Lévy walk and is therefore often overlooked. However, when mussel movements were grouped by local mussel density (the density of mussels within a radius of 3.3 cm) and long-range density (the density of mussels within a radius of 22.5 cm), step length distributions did not differ between the density categories, and mussels were found to perform a Lévy walk with $\mu \approx 2$, irrespective of the local and long-range density (*5*) (table S3.2). Hence, we reject the hypotheses of Brownian walk and composite Brownian walk and conclude that mussel movement is best described by a Lévy walk.

To examine why mussels adopt a Lévy walk, we investigated the effect of movement strategy on the rate of pattern formation by designing an individual-based model (*5*). In this model, patterns arise by the mussels' decisions to stay at a location or move away from it. We used experimental data from a previous study to estimate the parameters of this stop-or-move behavior (*5*, *15*) (fig. S2.2). Although step length distributions are unaffected by mussel density, we found that the probability that a mussel moves decreases with short-range density (the density of mussels within a radius of 3.3 cm) and increases with long-range density (the density of mussels within a radius of 22.5 cm). On the basis of these parameters, simulated mussels stay in places where they can aggregate with direct neighbors, but move away from crowded locations where food becomes limiting. If a simulated mussel moves, the movement distance is randomly drawn from the power-law distribution that corresponds to its movement strategy. For a range of movement strategies ($1 < \mu \leq 3$), we observed the distance traveled until a pattern has formed. Operationally, we say that a pattern has formed when the density of simulated mussels within 3.3-cm distance is on average 1.5 times as large as the density of mussels within 22.5-cm distance of an individual. Assuming that the movement speed is constant, the rate of pattern formation for each movement strategy is proportional to the inverse of the average distance traversed by the mussels until a pattern has formed (*5*).

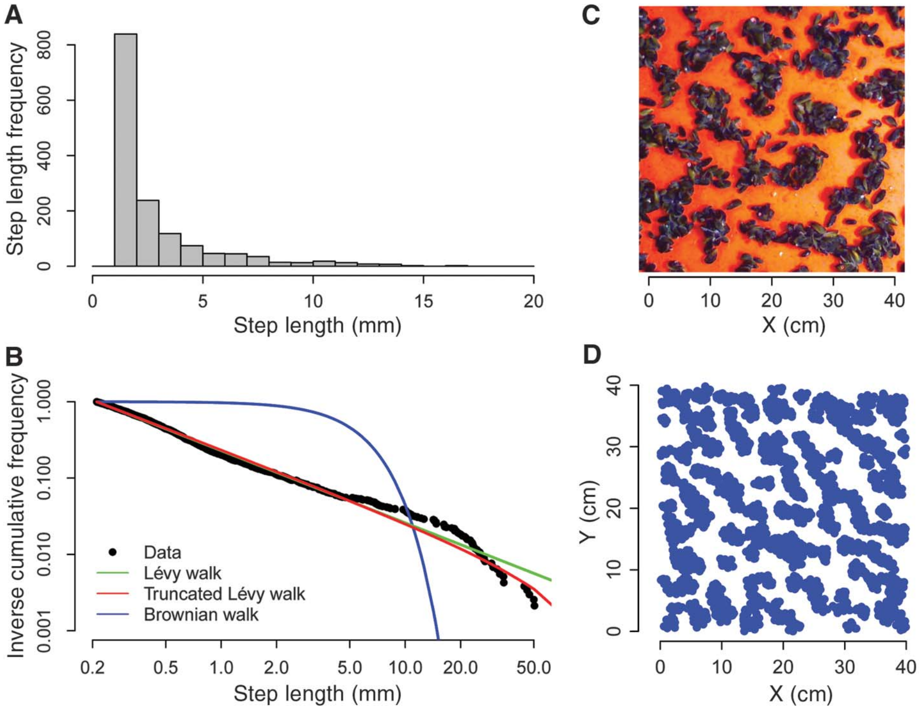


Fig. 1. Experimental and model results showing that mussel movement, which is best described by a Lévy walk, generates patterns in mussel beds. (**A**) Frequency distribution of step lengths of all solitary mussels (12 mussels, 12,401 steps). (**B**) Inverse cumulative frequency distribution of the step lengths. (**C**) Pattern formation in an experimental mussel bed. (**D**) Pattern generated with our individual-based model.

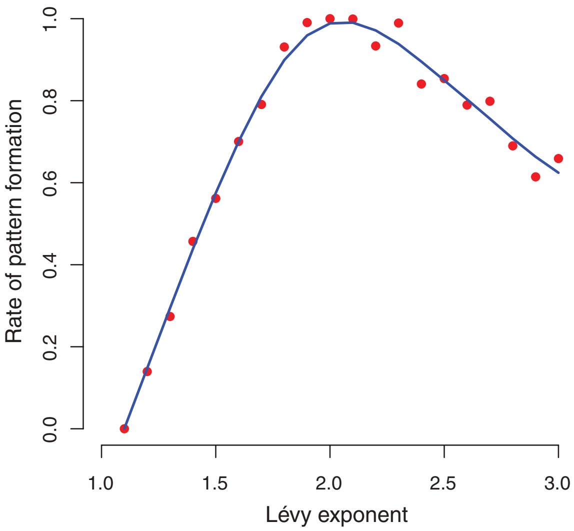


Fig. 2. The rate of pattern formation for various movement strategies. Because we assume that movement speed is constant, we can calculate the rate of patterning as the normalized inverse of the distance traversed until a pattern is formed. A Lévy walk with exponent $\mu \approx 2$ minimizes the time needed to form a pattern.

Simulations reveal that movement strategies differ strongly in terms of the rate at which they create patterns (Fig. 2). A Lévy walk with exponent $\mu \approx 2$ generated a spatially heterogeneous pattern more rapidly than did either ballistic movement ($\mu \rightarrow 1$) or a Brownian walk ($\mu \rightarrow 3$). Specifically, the large steps associated with a small value of μ prevented quick formation of tight clusters, whereas a larger value of μ required many small steps to create clustering. A Lévy walk with $\mu \approx 2$ seems to be the optimal trade-off between finding dispersed conspecifics and maintaining high local densities, thereby maximizing the rate of pattern development. Hence, our simulation results suggest that a Lévy strategy with $\mu \approx 2$ is optimal for pattern formation.

Because pattern formation both improves mussel survival and decreases competition between mussels (*14*), the movement strategy of individual mussels is likely to be an important determinant of fitness. However, strategies that lead to a desirable outcome at the population level are often not evolutionarily stable, as they can be exploited by free-riding strategies (*22*). To determine the long-term outcome of selection acting on mussels differing in movement strategy (i.e., their exponent μ), we created a pairwise invasibility plot (PIP, Fig. 3) by performing an evolutionary invasibility analysis (*5*, *23*, *24*). The values along the *x* axis of the PIP represent a broad range of hypothetical resident populations, each with a particular movement strategy characterized by an exponent μ_{res}. The *y* axis represents the exponents μ_{mut} of potential mutant strategies. The colors indicate whether a mutant strategy μ_{mut} can successfully invade a resident strategy μ_{res}—i.e., whether mutant individuals have a higher fitness than resident individuals in the environment created by the resident population. Intersections between the lines separating the colored areas indicate the presence of an evolutionary attractor, thus predicting the outcome of selection on mussel movement strategies. Fitness was given by the product of mussel survival (which is proportional to short-range mussel density) and fecundity (which is inversely proportional to long-range mussel density and the energy invested in movement) (*5*).

The PIP reveals that a Lévy walk with $\mu \approx 2$ is the unique evolutionary attractor of the system (Fig. 3) (*23, 24*). Specifically, a succession of invasion events will lead to the establishment of a resident population with $\mu \approx 2$, and a resident population with $\mu \approx 2$ cannot be invaded by any other movement strategy. We conclude that the Lévy walk strategy observed in our experiments (Fig. 1) not only has a high patterning efficiency (Fig. 2) but is also an evolutionarily stable strategy (Fig. 3).

Our study demonstrates an evolutionary feedback between individual movement behavior and higher-level complexity and could explain the evolution of Lévy walks in mussel beds. Rather than being a direct adaptation to an externally determined environment, Lévy movement in our study was found to result from feedback between animal behavior and mussel-generated environmental complexity. In essence, a Lévy walk with $\mu \approx 2$ creates a spatial environment in which just this movement strategy can flourish.

Although our study addresses a specific system, the assumption that search strategies can evolve through feedback between animal movement and environmental heterogeneity may be broadly applicable. Such feedbacks may exist not only in the search for conspecifics (as seen here in mussels) but also in the search for resources shared with conspecifics, because resource patterns reflect the movement patterns of their consumers. This applies, for instance, to the interaction between herbivores and vegetation, which shapes grasslands globally (*25*). Additionally, feedback between movement strategy and habitat complexity may arise when the spatial distribution of a particular species depends on interactions with a searching organism [as in predator-prey relationships or animal-mediated seed dispersal (*26*)]. We conclude that the interaction between animal movement and habitat complexity is a key component in understanding the evolution of animal movement strategies.

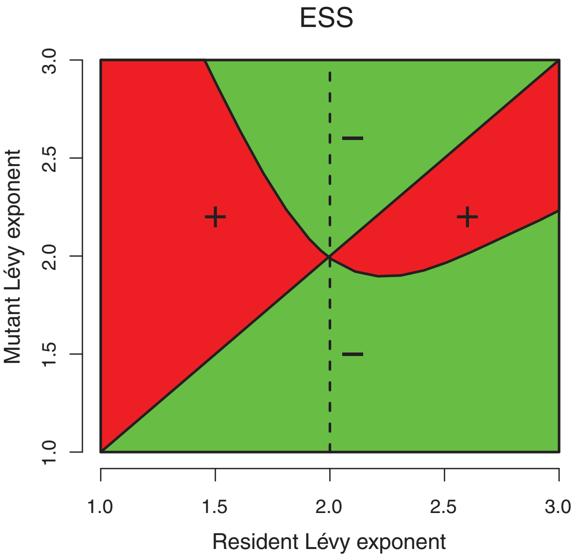


Fig. 3. Pairwise invasibility plot (PIP) indicating that the movement strategy evolves toward a Lévy walk with $\mu \approx 2$. For a range of resident (*x* axis) and mutant (*y* axis) movement strategies, the PIP indicates whether a mutant has a higher (red) or a lower (green) fitness than the resident and, hence, whether a mutant can invade the resident population (*23*). Here, the PIP shows that a Lévy walk with $\mu \approx 2$ is the sole evolutionarily stable strategy (ESS).

References and Notes

1. D. W. Sims *et al.*, *Nature* **451**, 1098 (2008).
2. F. Bartumeus, M. G. E. Da Luz, G. M. Viswanathan, J. Catalan, *Ecology* **86**, 3078 (2005).
3. F. Bartumeus, *Oikos* **118**, 488 (2009).
4. G. M. Viswanathan *et al.*, *Physica A* **282**, 1 (2000).
5. Materials and methods are available as supporting material on *Science* Online.
6. G. M. Viswanathan, *Nature* **465**, 1018 (2010).
7. E. A. Codling, M. J. Plank, S. Benhamou, *J. R. Soc. Interface* **5**, 813 (2008).
8. G. M. Viswanathan *et al.*, *Nature* **401**, 911 (1999).
9. A. M. Reynolds, F. Bartumeus, *J. Theor. Biol.* **260**, 98 (2009).
10. G. Ramos-Fernández *et al.*, *Behav. Ecol. Sociobiol.* **55**, 223 (2004).
11. A. M. Reynolds *et al.*, *Ecology* **88**, 1955 (2007).
12. N. E. Humphries *et al.*, *Nature* **465**, 1066 (2010).
13. C. G. Jones, J. H. Lawton, M. Shachak, *Oikos* **69**, 373 (1994).
14. R. A. Maas Geesteranus, *Arch. Neerl. Zool.* **6**, 283 (1942).
15. J. van de Koppel *et al.*, *Science* **322**, 739 (2008).
16. J. van de Koppel, M. Rietkerk, N. Dankers, P. M. Herman, *Am. Nat.* **165**, E66 (2005).
17. S. Benhamou, *Ecology* **88**, 1962 (2007).
18. A. Reynolds, *Ecology* **89**, 2347, discussion 2351 (2008).
19. S. Benhamou, *Ecology* **89**, 2351 (2008).
20. A. M. Reynolds, C. J. Rhodes, *Ecology* **90**, 877 (2009).
21. B. A. Nolet, W. M. Mooij, *J. Anim. Ecol.* **71**, 451 (2002).
22. C. Hauert, *Adv. Complex Syst.* **9**, 315 (2006).
23. S. A. H. Geritz, E. Kisdi, G. Meszena, J. A. J. Metz, *Evol. Ecol.* **12**, 35 (1998).
24. F. Dercole, S. Rinaldi, *Analysis of Evolutionary Processes: The Adaptive Dynamics Approach and Its Applications* (Princeton Univ. Press, Princeton, NJ, 2008)
25. P. Adler, D. Raff, W. Lauenroth, *Oecologia* **128**, 465 (2001).
26. D. Boyer, O. Lopez-Corona, *J. Phys. A* **42**, 434014 (2009).

Acknowledgments: For assistance, we thank S. Benhamou, A. Kölzsch, J. Powell, G. Theraulaz, W. Mooij, A. van den Berg, and J. van Soelen. We thank S. Kéfi, F. Bartumeus, B. Silliman, and M. Rietkerk for comments on manuscript drafts. M.d.J. and J.v.d.K. designed the study. Experimental data were collected by M.d.J. and J.v.d.K. B.A.N. introduced the topic of Lévy walks, and F.J.W. suggested the evolutionary invasion analysis. All analyses and modeling were done by M.d.J., assisted by J.v.d.K., P.M.J.H., and F.J.W. The paper was written by M.d.J. and J.v.d.K., and all authors contributed to the subsequent drafts. The authors declare no competing financial interests. M.d.J. is supported by a grant from the Netherlands Organization of Scientific Research–Earth and Life Sciences (NWO-ALW), and Project Group Movement Ecology by the KNAW Strategic Fund. This is publication 5033 of the Netherlands Institute of Ecology (NIOO-KNAW).

Supporting Online Material

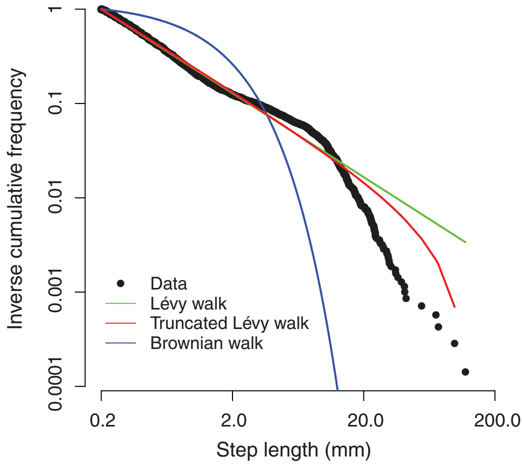
www.sciencemag.org/cgi/content/full/332/6037/1551/DC1
Materials and Methods
Figs. S2.1 to S2.3
Tables S3.1 and S3.2
References and Notes
Movie S1
Matlab code for individual-based model of mussel movement (The MathWorks, Inc.)

2 December 2010; accepted 16 May 2011
10.1126/science.1201187

ERRATUM

Post date 23 December 2011

Reports: "Lévy walks evolve through interaction between movement and environmental complexity" by M. de Jager *et al.* (24 June, p. 1551). The statistical analysis of the mussel movement contained errors, which were pointed out by V. Jansen. First, the data that was used contained duplicates of a number of individuals, while other individuals had accidentally been omitted. Second, the parameter λ of the exponential distribution (which describes the Brownian walk strategy) was mistakenly estimated without considering the lower boundary of the data. Third, the AIC was estimated incorrectly, by using a least-squares rather than a maximum-likelihood calculation. Additionally, the weighed AIC was calculated incorrectly. These mistakes have been corrected using the methods of Edwards *et al.* [A. M. Edwards *et al.*, *Nature* **449**, 1044 (2007)]; the results of the new analysis are plotted in a new Fig. 1B shown here. In Fig. 1B of the original Report, a Rayleigh distribution was accidentally plotted instead of an exponential distribution to describe the Brownian walk. In the statistical analysis, however, an exponential distribution was used to describe a Brownian walk. Furthermore, the movement patterns of mussels in different density treatments were reanalyzed after the comments of F. van Langevelde. The former results were found to be erroneous due to an error in the script; the scaling exponent of the movement strategy does not stay constant when mussel density increases. Although some corrections were made to the data and movement analysis, the overall conclusion of the paper that mussels adopt a Lévy walk, especially when alone, remains unchanged. We thank V. Jansen and F. van Langevelde for bringing these issues to our attention.



www.sciencemag.org/cgi/content/full/332/6037/1551/DC1

Supporting Online Material for

Lévy Walks Evolve Through Interaction Between Movement and Environmental Complexity

Monique de Jager,* Franz J. Weissing, Peter M. J. Herman, Bart A. Nolet, Johan van de Koppel

*To whom correspondence should be addressed. E-mail: m.dejager@nioo.knaw.nl

Published 24 June 2011, *Science* **332**, 1551 (2011)
DOI: 10.1126/science.1201187

This PDF file includes:

Materials and Methods
Figs. S2.1 to S2.3
Tables S3.1 and S3.2
References and Notes
Caption for Movie S1

Other Supporting Online Material for this manuscript includes the following:
(available at www.sciencemag.org/cgi/content/full/332/6037/1551/DC1)

Movie S1
Matlab code for individual-based model of mussel movement (The MathWorks, Inc.)

Supporting Online Material for

Lévy walks evolve through interaction between movement and environmental complexity

Monique de Jager*, Franz J. Weissing, Peter M.J. Herman, Bart A. Nolet, Johan van de Koppel

*To whom correspondence should be addressed. Email: M.deJager@nioo.knaw.nl;

This PDF file includes

Materials and Methods

Figures S2.1 to S2.3

Tables S3.1 and S3.2

References

Other Supporting Online Material for this manuscript includes the following:
(available at www.sciencemag.org/cgi/content/full/...)

Movie S1

Matlab code (written for Matlab version 7.9.0 (R2009b © The MathWorks, Inc.))

Supporting Online Material

S1 Materials and Methods

S1.1 Characteristics of mussel movement

Although mussel movement becomes limited with increasing shell size, young mussels are good crawlers for many months after their metamorphosis (*S1*). During this period, mussels are able to search for conspecifics and aggregate. Once arrived at a good quality location, with respect to the number of neighbors and food availability, a mussel stops moving and attaches itself to the bed. When conditions become less suitable, a young mussel can still detach itself and search for a better location. This movement and attachment behavior at individual level directly affects the habitat quality for others, thereby leading to spatial patterning in mussel beds.

S1.2 Extraction of mussel movement data

Step lengths of young blue mussels (*Mytilus edulis*, 1.5-3 cm long) were obtained from experimental data of Van de Koppel *et al.* (2008, *S2*). The blue mussels used in these experiments were obtained from wooden wave-breaker poles near Vlissingen, the Netherlands. Experiments were performed in a 120x80x8 cm containers filled with unfiltered seawater. Mussels were placed on a 60x80 cm red PVC sheet. To record mussel movement, a Logitech QuickCam 9000 Pro webcam, which was positioned about 60 cm above the water surface and attached to a computer, photographed the mussels at 1 minute intervals for several hours. In total, 62 mussels were used for the experiments, resulting in 19,401 steps. Tracks of twelve of these mussels (12,401 steps) were obtained from isolation experiments, preventing the mussels from finding conspecifics and creating clusters. To investigate density-dependence, the tracks of the other 50 mussels (7,000 steps) were obtained from pattern formation experiments (see Fig. 1b). In pattern formation experiments, mussels are initially evenly distributed over the red PVC sheet, after which the mussels start to move and create patterns.

The first method that we used for the extraction of step lengths was to simply calculate the distance between two subsequent points using a 60 seconds interval. This time interval was chosen since our observations revealed that time intervals between 40 and 80 seconds are most adequate for monitoring mussel movements in our experiments.

In addition, we extracted step length distributions by applying two step length extraction methods suggested by Turchin (1998, *S3*). In the ‘error radius method’ (illustrated in Fig. S2.1a), the movements performed in *n* time intervals are aggregated into a single ‘step’ if the *n*-1 intermediate spatial positions are no more than a predefined distance *x* away from the line connecting the beginning of the movement to the end of it. When applying this method, the value of x was chosen by starting with a small value and then incrementing it iteratively until oversampling was minimized, i.e., until autocorrelation in the turning angle vanished. Autocorrelation was calculated with the acf function in R (R version 2.10.0 © 2009 The R Foundation for Statistical Computing). When the autocorrelation of *n* data points exceeded the confidence interval derived with the acf function, the distance *x* was increased by 0.01 cm.

Turchin's 'angle method' (illustrated in Fig. S2.1b) concerns the angle between movements. The movements performed in *n* time intervals are aggregated into a single step if the angle between the starting position and the end position is smaller than a predefined value $\beta_{max.}$. When this value is exceeded after the *n*th movement, the corresponding point becomes the starting point for the next step. The threshold value β_{max} was also chosen iteratively, starting with a small angle and gradually increasing it until the autocorrelation in turning angles vanished.

As shown in Table S3.1, the method used for estimating step lengths does not affect our conclusions: in all cases, the data are best explained by a Lévy walk, where the pure Lévy walk model performs almost as well as a truncated Lévy walk. In all cases, R^2–values of the best-fitting models exceed 0.995.

S1.3 Fitting movement types to step length data

The step length data of the mussel movements were used to create a step length frequency distribution (Fig. 1a). When plotted on a log-log scale, a power-law probability distribution $P(l) = Cl^{-\mu}$ results in a straight line with slope $-\mu$. However, drawing conclusions from this kind of presentation can be deceptive (*S4-S6*). We therefore used a more robust method (*S5*) and first determined the inverse cumulative frequency distribution of our data, which for each step length l gives the fraction of steps with lengths larger or equal to l. This cumulative distribution is plotted in Fig. 1b on a log-log scale. We compared this distribution with the cumulative probability distribution of three random movement strategies: Brownian walk, Lévy walk, and truncated Lévy walk.

Brownian walk

Brownian walk is a random movement strategy that corresponds to normal diffusion. The step length distribution can be derived from an exponential distribution with $\lambda > 0$:

$$f(l) = \lambda e^{-\lambda l}. \tag{1}$$

Lévy walk

The frequency distribution of step lengths that characterizes a Lévy walk has a heavy tail and is scale-free, i.e. the characteristic exponent of the distribution is independent of scale. To fit a Lévy walk to the data, a Pareto distribution (*S7*) was used:

$$f(l) = C_{\mu} l^{-\mu}. \tag{2}$$

The shape parameter μ (which has to exceed 1) is known as the Lévy exponent or scaling exponent and determines the movement strategy (see Fig. S2.2). When μ is close to 1, the resulting movement strategy resembles ballistic, straight-line motion, as the probability to move a very large distance is equal to the chance of making a small displacement. A movement strategy is called a Lévy walk when the scaling exponent is between 1 and 3. When μ approaches 1, the movement is approximately ballistic, while it is approximately Brownian when μ approaches 3 (and for $\mu > 3$). The Lévy walks found in nature typically have an exponent μ of approximately 2 (S*4, S8-S10*). C_μ is a normalization constant ensuring that the distribution $f(l)$ has a total mass equal to 1, i.e. that all values of $f(l)$ sum up to 1. If we impose the additional criterion that steps must have a minimum length $l_{min}(0 < l_{min} < l)$, this constant is given by

$$C_\mu = (\mu - 1) l_{min}^{\mu-1} \,. \tag{3}$$

When fitting our data to a Lévy walk, we used the value of l_{min} that provided the best fit of the step length distributions to the actual data.

Truncated Lévy walk

A truncated Lévy walk differs from a standard Lévy walk in the tail section of the frequency distribution; a truncated Lévy walk has a maximum step size and, as a consequence, loses its infinite variance and scale-free character at large step sizes. The truncated Lévy walk was represented by the truncated Pareto distribution, which can be described by the same function $f(l)$ as a standard Pareto distribution, but with different constant C_μ:

$$C_\mu = \frac{\mu - 1}{l_{min}^{1-\mu} - l_{max}^{1-\mu}} \,. \tag{4}$$

In a truncated Lévy walk, step lengths are constrained to the interval $l_{min} < l < l_{max}$. When fitting our data to a truncated Lévy walk, we used those values of l_{min} and l_{max} that yielded the best fit of the movement models to the data (l_{min} = 0.42 cm and l_{max} = 58.84 cm).

Goodness-of-fit and model selection

For the frequency distributions mentioned above, the fit to the step length data of solitary mussels was calculated using Maximum Likelihood estimation by fitting the inverse cumulative frequency distribution to that of the experimental data. By comparing the inverse cumulative distributions to that of the data, Goodness-of-fit (G) and the Akaike Information Criterion (AIC) were calculated as well as the variance explained by the fitted model (R^2). The Goodness-of-fit method measures how well the experimental data follows the frequency distributions of the movement strategies; the fit is best when the G-value is closest to zero. The Goodness-of-fit value is calculated as

$$G = 2 \sum O_i \ln\left(\frac{O_i}{E_i}\right), \tag{5}$$

where O is the inverse cumulative distribution of the experimental data and E is that of the fitted movement strategies. We used the inverse cumulative distribution as this is the most robust method to compare the observed and expected distributions (*S5*). The highest AIC weight, which is calculated by comparing the AIC values, and the highest R^2 correspond to the movement type best fitting the actual data (*S11*). This method was used for the analysis of the movement strategies of the 12 solitary mussels, both individually and as a whole, using the step lengths obtained per minute as well as those derived with the two methods of Turchin (see Fig. S2.1). Additionally, step lengths obtained from pattern formation experiments were grouped for different combinations of local density (within a radius of 3.3 cm) and long-range density (within a radius of 22.5 cm). These groups of step lengths were used for determining the Lévy exponent at different densities, in order to observe whether a composite Brownian walk exists in mussel movement (see Table S3.2).

S1.4 Computer Simulations

Individual based model

We developed an individual based model that describes pattern formation in mussels by relating the chance of movement to the short- and long-range densities of mussels, following Van de Koppel *et al.* (2008, *S2*). Whereas they modeled pattern formation in mussel beds by adjusting the movement speed to the short- and long-range densities (*S2*), we extracted the stop and move behavior of the mussels from the experimental data. In our model, 2500 'mussels' (with a radius of 1.5 cm each) are initially spread homogeneously within a 150 cm by 150 cm arena. Each time step, the short-range (D_1) and long-range (D_2) densities are determined for each individual, based on mussel densities within a radius of 3.3 cm and 22.5 cm, respectively. These radii correspond to the ranges in which we found significant correlations with the probability of moving in a multi-variate regression analysis of our experimental data ($F = 77.17$, $p << 0.001$, $R^2 = 0.622$, $df = 136$). The probability P_{move} that a mussel moves is negatively related to the short-range density D_1 and positively related to the long-range density D_2 (see Fig. S2.3), which causes mussels to stay in places where they can aggregate with direct neighbors, but move away from crowded locations where food becomes limiting. In the model, we used a linear relationship between P_{move} and the two densities:

$$P_{move} = a - bD_1 + cD_2, \tag{6}$$

which was obtained by applying linear regression to our experimental data ($a = 0.63$, $b = 1.26$, and $c = 1.05$). If a mussel decided to move in our model, its step length l was chosen at random from a power law distribution (*S12*) with a given Lévy exponent $\mu > 1$:

$$l = l_{min}(1 - x)^{-\frac{1}{\mu - 1}}, \tag{7}$$

where x is a random variable that is uniformly distributed over the unit interval ($0 \leq x \leq 1$), and l_{min} is the minimum distance traveled when moving (*S7*), which we have set at 0.3 cm. Each simulation step, mussels move instantaneously from one location to another, though step lengths were truncated when a movement path was obstructed by another mussel. This truncation was calculated by determining the free movement path until collision, using a band width of 3 cm (the size of a mussel) around the line segment connecting the mussels' original location to its intended destination. When a conspecific was located within this band, the mussel stopped in front of this conspecific, thereby truncating its movement path. All movements occurred simultaneously and all individuals in a simulation used the same movement strategy.

As differences occur in the average distance covered per simulation step between the movement strategies (ballistic individuals move a larger distance per simulation step than Lévy or Brownian walkers) and assuming that movement speed is constant, more time is needed for a ballistic step than for a Brownian step. To avoid having Brownian movers switch more frequently between moving and stopping than ballistic movers, we updated the state of either moving or stopping not after each simulation step but after an average distance moved.

A simulation was finished when the average short-range density exceeded 1.5 times the mean long-range density. At that moment, the total distance travelled was recorded. As we assume that the movement speed is constant, the rate of patterning is proportional to the normalized inverse of the distance traversed until a pattern is formed. Simulations were run for a range of Lévy exponents ($1 < \mu \leq 3$), and for each value the rate of pattern formation was plotted as a function of μ. The model was implemented in Matlab version 7.9 (©1984-2009. The MathWorks, Inc.).

Evolutionary model

Evolutionary change was studied in a monomorphic resident population by investigating whether the fitness of rare mutants is higher than that of the residents, implying that the mutants can increase in frequency (*S13,* S14). After the mussels moved an equal distance, we recorded the short-range density, the long-range density, and the fraction of mussels that was still moving, for both the residents and the mutants. In a population with non-overlapping generations, fitness is given by the product of survival probability and fecundity. We assumed that survival probability is proportional to the local mussel density D_1 and that fecundity is inversely proportional to the long-range density D_2 (as this density affects food supply) and to the time *X* spent on moving (as energy spent on moving cannot be invested in offspring production). Dividing the fitness measures thus obtained for a mutant and a resident results in a measure for the relative fitness of the mutant strategy:

$$F_{mut} = \frac{D_{1,mut}}{D_{1,res}} * \frac{D_{2,res}}{D_{2,mut}} * \frac{X_{res}}{X_{mut}}\,. \tag{8}$$

Mutant strategies with a relative fitness value larger than one will invade and potentially take over the resident population. For any combination of resident and mutant movement strategy, the relative fitness of the mutants is depicted in a pairwise invasibility plot (*S14*, see Fig. 3). In this plot, the color red indicates that the mutant has a higher fitness than the resident ($F_{mut} > 1$), while the color green indicates that the mutant cannot invade the resident population ($F_{mut} < 1$). The intersection of the line separating these two scenarios ($F_{mut} = 1$) with the main diagonal of the pairwise invasibility plot corresponds to an evolutionarily singular strategy (*S13, S14*).

S2 Supporting Online Figures

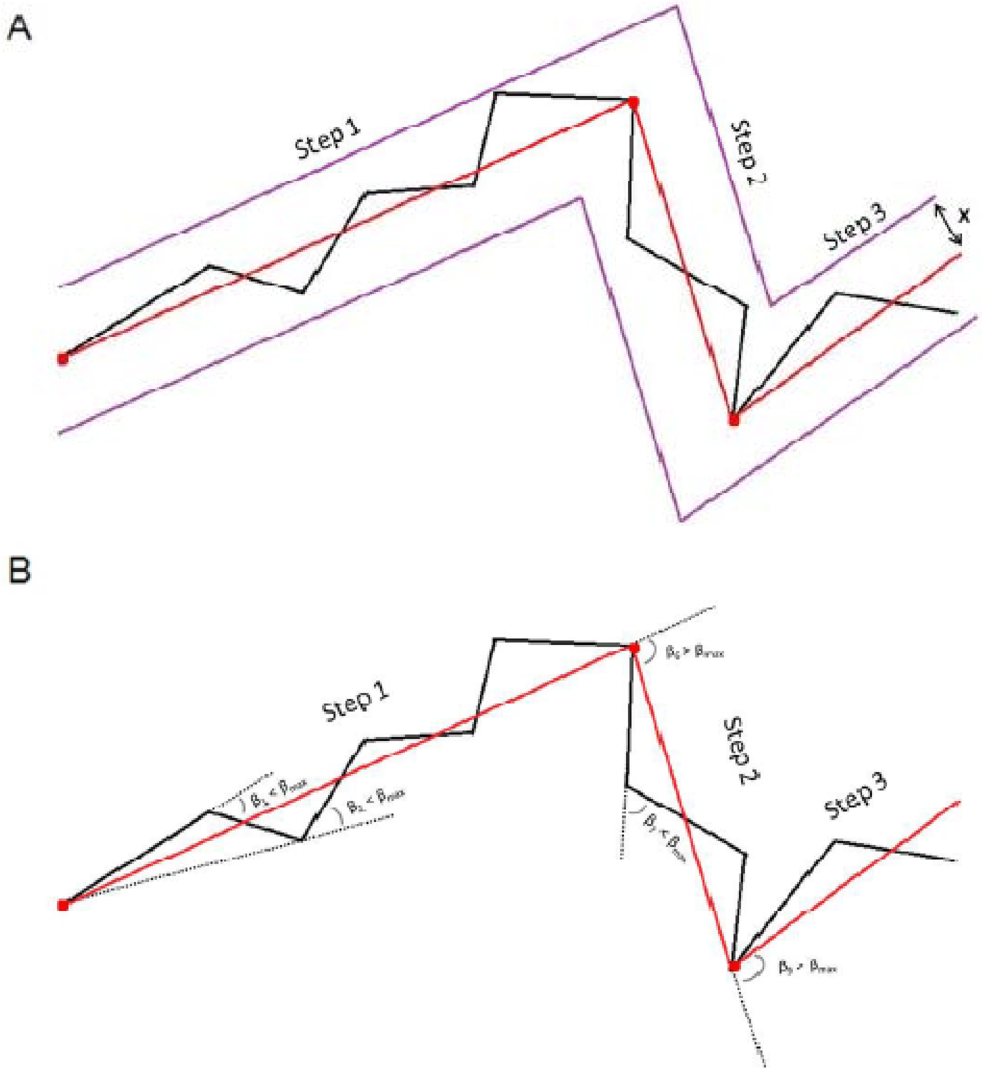


Fig. S2.1. Step length calculation using the 'error radius method' (A) and the 'angle method' (B). In the first method **(A)**, *n* steps are aggregated into one move if the *n*-1 intermediate spatial positions are no more than *x* units away from the line connecting the beginning of the step to the end of it. The second method **(B)** is based on reorientation events; when the angle β (between the dotted black line and the solid black line) exceeds a certain threshold value, the corresponding point is the next new point (after Turchin, 1998; *S3*).

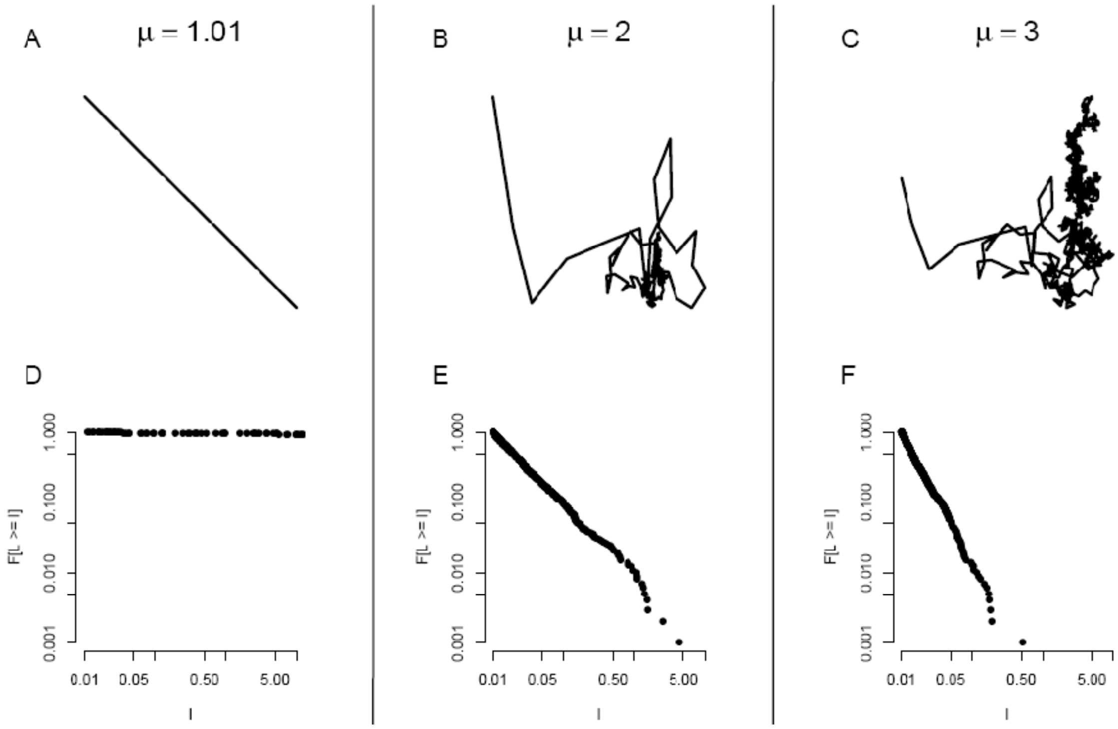


Fig. S2.2. The Lévy exponent μ determines the shape of the step length distribution and thus the movement strategy. When μ is close to 1, the movement strategy resembles ballistic, straight-line motion (**A, D**), whereas the step length distribution is similar to that of a Brownian walk when μ approaches 3 (**C, F**). The movement strategy is referred to as a Lévy walk when $1 < \mu < 3$ (**B, E**). **A**, **B**, and **C** show movement trajectories obtained with μ = 1.01, 2, and 3, respectively. The inverse cumulative step length frequency distributions (i.e. the fraction of steps that is larger than or equal to the displacement length (l) that is given on the x-axis) are given by **D**, **E**, and **F** for μ = 1.01, 2, and 3, respectively.

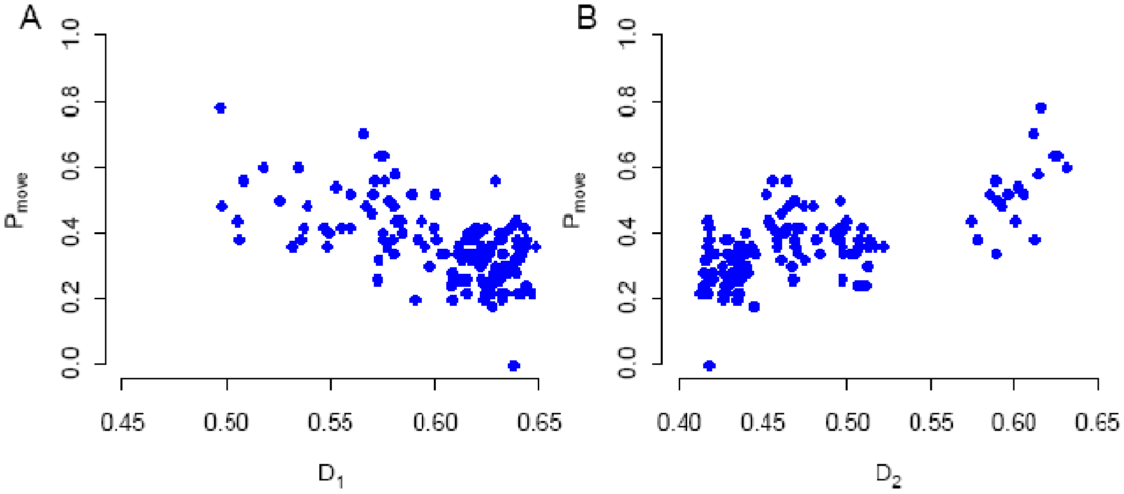


Fig. S2.3. Experimental data shows that the probability of moving depends on short-range and long-range mussel densities. (A) Local mussel density decreases the probability of moving; mussels tend to stay in denser clumps. **(B)** The probability of moving positively correlates with long-range density; mussels move away from areas where competition is high.

S3 Supporting Online Tables

Table S3.1. Summary of the model fits to the step length data. Goodness-of-fit (G), AIC weights and % variance explained of each movement strategy fitted to the mussel data (R^2) for all three methods that were used to obtain the step lengths. Truncated Lévy walk (TLW) corresponds best to the raw data and the data obtained using the error radius method. Data acquired with the angle method was best described by a Lévy walk (LW). Lévy exponents ranged from 1.930 to 2.174, with a mean μ of 2.032.

Method	Model	G	AIC weights	Adjusted R^2	Lévy exponent
Step per minute	Truncated Lévy walk	33.60	0.446	0.999	2.127
	Lévy walk	64.54	0.431	0.999	2.174
	Brownian walk	-119.43	0.123	0.878	-
Error radius method	Truncated Lévy walk	-2.69	0.437	0.997	1.967
	Lévy walk	3.93	0.401	0.995	2.045
	Brownian walk	-344.85	0.163	0.898	-
Angle method	Truncated Lévy walk	36.43	0.445	0.995	1.930
	Lévy walk	73.20	0.453	0.996	1.946
	Brownian walk	-106.00	0.103	0.734	-

Table S3.2. Lévy exponent during pattern formation. Lévy exponents for step lengths in different local and long-range density groups, for all three methods that were used to obtain the step lengths. Low/Low = both low local and long-range densities; Low/High = low local and high long-range density; High/Low = high local and low long-range density; High/High = both high local and long-range densities. Pattern formation in mussel beds produces an environment with high local densities and low long-range densities. There is no significant correlation between Lévy exponent and the degree of patterning, as well as any other relationship between the exponent and mussel density; we can therefore reject the hypothesis of a composite Brownian walk, where movement speeds are adjusted to local environmental conditions (*S15-S18*).

Method	Low/Low	Low/High	High/Low	High/High
Step per minute	2.05	2.05	2.06	2.05
Error radius method	2.00	2.07	2.05	2.05
Angle method	2.00	2.00	2.00	2.00

S4 Supporting Online References

S1. R. A. Maas Geesteranus, *Arch Neerl Zool* **6**, 283 (1942).

S2. J. van de Koppel *et al.*, *Science* **322**, 739 (2008).

S3. P. Turchin, *Quantitative Analysis of Movement*. (Sinauer Associates, 1998).

S4. D. W. Sims, D. Righton, J. W. Pitchford, *J. Anim. Ecol.* **76**, 222 (2007).

S5. A. M. Edwards *et al.*, *Nature* **449**, 1044 (2007).

S6. E. P. White, *Ecology* **89**, 2971 (2008).

S7. A. Clauset, C. R. Shalizi, M. E. J. Newman, *SIAM Rev*. **51**, 661 (2009).

10. G. Ramos-Fernandez et al., Behav. Ecol. Sociobiol. 55, 223 (2004).

11. A. M. Reynolds et al., Ecology 88, 1955 (2007).

12. N. E. Humphries et al., Nature 465, 1066 (2010).

S11. K. P. Burnham, D. R. Anderson, *Model selection and multimodel inference: A practical information-theoretic approach* (Springer-Verlag, 2002).

S12. M.E.J. Newman, *Contemp. Phys.* **46**, 323 (2005).

S13. S. A. H. Geritz, E. Kisdi, G. Meszena, J. A. J. Metz, *Evol. Ecol.* **12**, 35 (1998).

S14. F. Dercole, S. Rinaldi, *Analysis of evolutionary processes: the adaptive dynamics approach and its applications* (Princeton University Press, 2008)

S15. S. Benhamou, *Ecology* **88**, 1962 (2007).

S16. A. Reynolds, *Ecology* **89**, 2347 (2008).

S17. S. Benhamou, *Ecology* **89**, 2351 (2008).

S18. B. A. Nolet, W. M. Mooij, *J. Anim. Ecol.* **71**, 451 (2002).

Movie S1

1201187S1.mov: Time-laps movie showing the movement behavior of a single mussel, with the corresponding movement track plotted as the mussel is moving. The video covers nearly a two hour time period (QuickTime movie, 11 MB), with images taken every 10 seconds. We acknowledge Aniek van den Berg for running this movement experiment.

Matlab code:

IBM1201187S1.m: Individual Based model of mussels moving into a self-organized pattern. The code was written for Matlab version 7.9.0 (R2009b © The Mathworks, Inc.) and shows the distribution of mussels after each simulation step.

Comment on "Lévy Walks Evolve Through Interaction Between Movement and Environmental Complexity"

Vincent A. A. Jansen,[1]* Alla Mashanova,[1] Sergei Petrovskii[2]

de Jager *et al*. (Reports, 24 June 2011, p. 1551) concluded that mussels Lévy walk. We confronted a larger model set with these data and found that mussels do not Lévy walk: Their movement is best described by a composite Brownian walk. This shows how model selection based on an impoverished set of candidate models can lead to incorrect inferences.

A Lévy walk is a form of movement in which small steps are interspersed with very long ones, in such a manner that the step length distribution follows a power law. Movement characterized by a Lévy walk has no characteristic scale, and dispersal is superdiffusive so that individuals can cover distance much quicker than in standard diffusion models. de Jager *et al*. (*1*) studied the movements of individual mussels and concluded that mussels move according to a Lévy walk.

The argument of (*1*) is based on model selection, a statistical methodology that compares a number of models—in this case, different step length distributions—and selects the model that describes the data best as the most likely model to explain the data (*2*). This methodology is used to infer types of movements of animals (*3*) and has led to a number of studies that claim Lévy walks are often encountered in the movement of animals. The methodology in (*1*) contrasts a power-law distribution, which is indicative of a Lévy walk, with an exponential distribution, which indicates a simple random walk. If one has to choose between these alternatives, the power-law distribution gives the best description. However, if a wider set of alternatives is considered, this conclusion does not follow.

Heterogeneity in individual movement behavior can create the impression of a power law (*4*–*6*). Mussels' movement is heterogeneous as they switch between moving very little or not at all, and moving much farther (*1*, *7*). If mussels switch between different modes, and in each mode display Brownian motion, this suggests the use of a composite Brownian walk, which describes the movement as a sum of weighted exponential distributions. We confronted this plausible model with the mussel movement data (*8*).

Visual inspection of the data shows that the cumulative distribution of step lengths has a humped pattern that is indicative of a sum of exponentials (Fig. 1A). We applied a model selection procedure based on the Akaike information criterion (AIC) (*2*, *3*). We compared six different step length distributions: an exponential distribution, a power law, a truncated power law, and three hyperexponential distributions (a sum of two, three, or four exponentials to describe composite Brownian walks). We did this for the data truncated as in (*1*) (Fig. 1A) as well as all the full, untruncated data set (Fig. 1B). In both cases, we found that the composite Brownian walk consisting of the sum of three exponentials was the best model (Fig. 1 and Table 1). This convincingly shows that the mussels described in (*1*) do not do a Lévy walk. Only when we did not take the composite Brownian walk models into account did the truncated power law model perform best and could we reproduce the result in (*1*).

Mussel movement is best described by a composite Brownian walk with three modes of movement with different characteristic scales between which the mussels switch. The mean movement in these modes is robust to truncation of the data set, in contrast to the parameters of the power law, which were sensitive to truncation [Table 1;

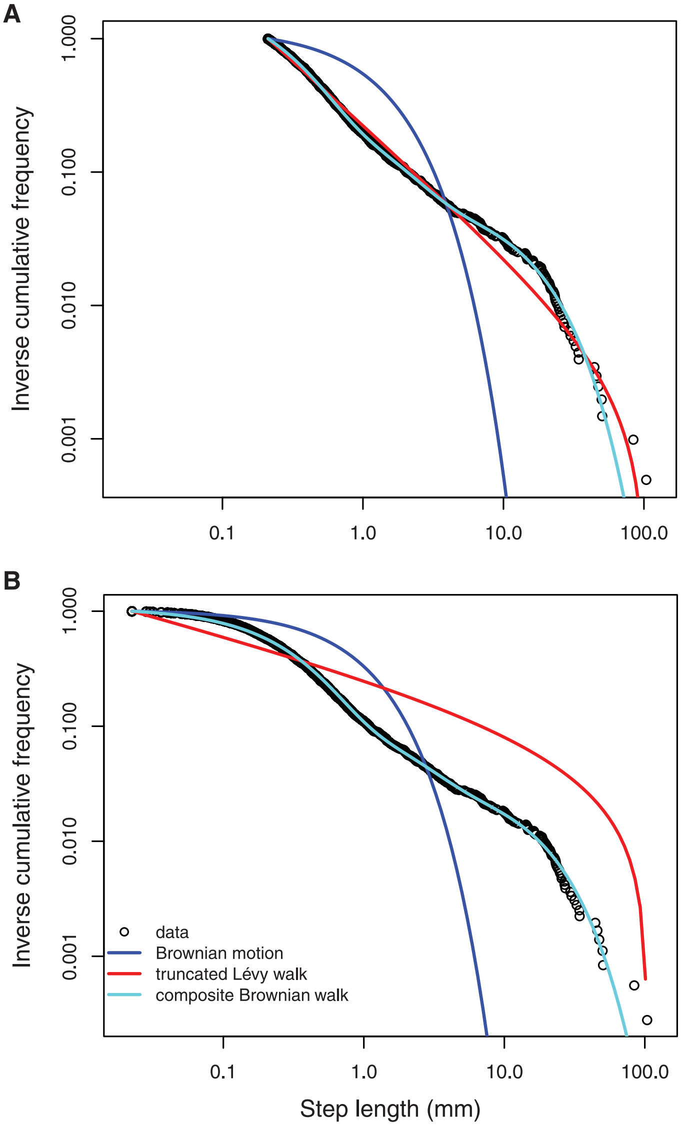


Fig. 1. The step length distribution for mussel movement [as in (*10*)] and curves depicting some of the models. The circles represent the inverse cumulative frequency of step lengths, The curves represent Brownian motion (blue), a truncated power law (red), and a composite Brownian walk consisting of a mixture of three exponentials (blue-green). (**A**) Data as truncated in Fig. 1 in (*1*, *10*) (2029 steps). (**B**) The full untruncated data set (3584 steps).

---

[1]School of Biological Sciences, Royal Holloway, University of London, Surrey TW20 0EX, UK. [2]Department of Mathematics, University of Leicester, Leicester LE1 7RH, UK.

*To whom correspondence should be addressed. E-mail: vincent.jansen@rhul.ac.uk

Table 1. Model parameters and Akaike weights. The maximum likelihood parameter estimates, log maximum likelihoods (ML), AIC values, and Akaike weights are calculated (for details, see SOM) for the data shown in Fig. 1, A and B. The Akaike weights without the composite Brownian walks are given in brackets. We analyzed the full data set (*) with $x_{min} = 0.02236$ mm, and the data set truncated as in (*1*) (†) with $x_{min} = 0.21095$ mm. For x_{max}, the longest observed step length (103.9mm) was used. The mix of four exponentials is not the best model according to the AIC weights. It gives a marginally, but not significantly, better fit and is overfitted.

Models	Formula	Parameters*	Parameters†	ML	AIC	Weight
Exponential (Brownian motion)	$P(X=x)=\lambda e^{-\lambda(x-x_{min})}$	$\lambda = 1.133$	$\lambda = 0.770$	–3136.89* –2558.67†	6275.78* 5119.37†	0 (0)* 0 (0)†
Power law (Lévy walk)	$P(X=x)=\frac{\mu-1}{x_{min}^{1-\mu}}x^{-\mu}$	$\mu = 1.397$	$\mu = 1.975$	–2290.10* –1002.32†	4582.20* 2006.64†	0 (0) * 0 (0.006)†
Truncated power law (Lévy walk)	$P(X=x)=\frac{\mu-1}{x_{min}^{1-\mu}-x_{max}^{1-\mu}}x^{-\mu}$	$\mu = 1.320$	$\mu = 1.960$	–2119.55* –997.29†	4241.10* 1996.58†	0 (1) * 0 (0.994)†
Mix of two exponentials (Composite Brownian walk)	$P(X=x)=\sum_{i=1}^{2} p_i\lambda_i e^{-\lambda i(x-x_{min})}$ with $\sum_{i=1}^{2} p_i = 1$	$p = 0.073$, $\lambda_1 = 0.122$, $\lambda_2 = 3.238$	$p = 0.127$, $\lambda_1 = 0.123$, $\lambda_2 = 3.275$	–906.15* –1022.44†	1818.31* 2050.87†	0* 0†
Mix of three exponentials (Composite Brownian walk)	$P(X=x)=\sum_{i=1}^{3} p_i\lambda_i e^{-\lambda i(x-x_{min})}$ with $\sum_{i=1}^{3} p_i = 1$	$p_1 = 0.034$, $p_2 = 0.099$, $\lambda_1 = 0.069$, $\lambda_2 = 0.652$, $\lambda_3 = 3.613$	$p_1 = 0.063$, $p_2 = 0.210$, $\lambda_1 = 0.072$, $\lambda_2 = 0.832$, $\lambda_3 = 4.309$	–861.55* –966.70†	1733.11* 1943.40 †	0.881* 0.873†
Mix of four exponentials (Composite Brownian walk)	$P(X=x)=\sum_{i=1}^{4} p_i\lambda_i e^{-\lambda i(x-x_{min})}$ with $\sum_{i=1}^{4} p_i = 1$	$p_1 = 0.014$, $p_2 =0.034$, $p_3 = 0.085$, $\lambda_1 = 0.656$, $\lambda_2 = 0.069$, $\lambda_3 = 0.652$ $\lambda_4 = 3.613$	$p_1 = 0.017$, $p_2 = 0.060$, $p_3 = 0.202$, $\lambda_1 = 0.377$, $\lambda_2 = 0.070$, $\lambda_3 = 0.902$, $\lambda_4 = 4.345$	–861.55* –966.63†	1737.11* 1947.26†	0.119* 0.127†

also see supporting online material (SOM)]. This analysis does not tell us what these modes are, but we speculate that it relates to the stop-move behavior that mussels show, even in homogeneous environments (*1*). We speculate that the mode with the smallest average movement (~0.4 mm) is related to nonmovement, combined with observational error. The next mode (average movement ~1.5 mm) is related to mussels moving their shells but not displacing, and the mode with the largest movements (on average 14 mm, about the size of a small mussel) is related to actual displacement. This suggests that in a homogeneous environment, mussels are mostly stationary, and if they move, they either wobble or move about randomly. Indeed, if we remove movements smaller than half the size of a small mussel (7.5 mm), the remaining data points are best described by Brownian motion. This shows that mussel movement is not scale invariant and not superdiffusive.

de Jager *et al.*'s analysis (*1*) does show that mussels do not perform a simple random walk and that they intersperse relatively long displacements with virtually no displacement. However, one should not infer from that analysis that the movement distribution therefore follows a power law or that mussels move according to a Lévy walk, and there is no need to suggest that mussels must possess some form of memory to produce a power law–like distribution (*9*). Having included the option of a composite Brownian walk, which was discussed in (*1*) but not included in the set of models tested, one finds that this describes mussels' movement extremely well.

Our analysis illustrates why one has to be cautious with inferring that animals move according to a Lévy walk based on too narrow a set of candidate models: If one has to choose between a power law and Brownian motion, often the power law is best, but this could simply reflect the absence of a better model. To make defensible inferences about animal movement, model selection should start with a set of carefully chosen models based on biologically relevant alternatives (*2*). Heterogeneous random movement often provides such an alternative and has the additional advantage that it can suggest a simple mechanism for the observed behavior.

References and Notes

1. M. de Jager, F. J. Weissing, P. M. J. Herman, B. A. Nolet, J. van de Koppel, *Science* **332**, 1551 (2011).
2. K. P. Burnham, D. R. Anderson, *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach* (Springer-Verlag, New York, ed. 2, 2002).
3. A. M. Edwards *et al.*, *Nature* **449**, 1044 (2007).
4. S. Benhamou, *Ecology* **88**, 1962 (2007).
5. S. V. Petrovskii, A. Y. Morozov, *Am. Nat.* **173**, 278 (2009).
6. S. Petrovskii, A. Mashanova, V. A. A. Jansen, *Proc. Natl. Acad. Sci. U.S.A.* **108**, 8704 (2011).
7. J. van de Koppel *et al.*, *Science* **322**, 739 (2008).
8. We found that the results published in (*1*) were based on a corrupted data set and that there were errors in the statistical analysis. [For details, see our SOM and the correction to the de Jager paper (*10*).] Here, we analyzed a corrected and untruncated data set provided to us by M. de Jager on 20 October 2011. This data set has 3584 data points, of which 2029 remain after truncation. Since doing our analysis, an amended figure has been published (*10*), which appears to be based on ~7000 data points after truncation.
9. D. Grünbaum, *Science* **332**, 1514 (2011).
10. M. de Jager, F. J. Weissing, P. M. J. Herman, B. A. Nolet, J. van de Koppel *Science* **334**, 1641 (2011).

Acknowledgments: We thank M. de Jager for supplying the data to do this analysis and the authors of (*1*) for their constructive comments. This work was funded by Biotechnology and Biological Sciences Research Council Grant BB/G007934/1 (to V.A.A.J.) and Leverhulme Trust Grant F/00 568/X (to S.P.).

Supporting Online Material

www.sciencemag.org/cgi/content/full/335/6071/918-c/DC1
Materials and Methods
SOM Text
References

25 October 2011; accepted 13 January 2012
10.1126/science.1215747

Response to Comment on "Lévy Walks Evolve Through Interaction Between Movement and Environmental Complexity"

Monique de Jager,[1]* Franz J. Weissing,[2] Peter M. J. Herman,[1]
Bart A. Nolet,[3,4] Johan van de Koppel[1,2,4]

We agree with Jansen *et al*. that a composite movement model provides a better statistical description of mussel movement than any simple movement strategy. This does not undermine the take-home message of our paper, which addresses the feedback between individual movement patterns and spatial complexity. Simple movement strategies provide more insight in the eco-evolutionary analysis and are therefore our model of choice.

The purpose of our paper (*1*, *2*) was to demonstrate that movement strategies are shaped by the interaction between individual selection and the formation of spatial complexity on the population level. We showed that in a family of movement models ranging from ballistic motion, to Lévy walk, to Brownian motion, a Lévy walk with exponent $\mu \approx 2$ is the optimal strategy for mussels involved in pattern formation. Within this family of models, a single parameter (the scaling exponent μ) distinguishes between the different movement strategies. We intentionally chose a one-dimensional strategy space that can easily be used in pairwise invasibility analyses and the subsequent pairwise invasibility plots. It also keeps focus on the main differences in movement strategy, contrasting ballistic movement, Brownian diffusion, and long-tailed step length distributions, as in Lévy walks. As is often the case, the better fit of the complex model (i.e., composite Brownian walk) trades off with the elegance and clarity of the simpler model.

Nevertheless, it might be interesting to examine the mechanisms behind the composite Brownian walk that was observed in our mussel movement data by Jansen *et al*. (*3*). Below, we investigate three possible causes of the observed movement pattern: (i) mussels switch between multiple movement modes because of changes in environmental conditions; (ii) the (collective) composite Brownian walk might be an ensemble of different individual Brownian walks; or (iii) internal switches between movement modes exist, with which mussels try to approximate a Lévy walk.

The first possible mechanism behind a composite Brownian walk is that mussels switch between movement modes in response to changes in environmental conditions. For example, a composite Brownian walk will result if animals switch between local Brownian search within a resource patch and straight-lined ballistic search between patches (*4*–*6*). Because the solitary mussels in our experiment were situated in a bare, homogeneous environment, repeated switches between movement strategies induced by changing environmental conditions do not provide a plausible explanation for the observed composite walk.

A second possible explanation for the observed composite Brownian walk could be that variation in individual movement behavior can explain the improved fit by the composite Brownian model (*7*)—for example, multiple different Brownian walks together make up the observed composite walk. To investigate this, we examined the individual movement tracks of the 12 mussels in our experiment. We indeed found a large variety of movement trajectories (Fig. 1); some mussels moved a large distance, whereas others stayed approximately at the original location. We fitted a Brownian walk, a Lévy walk, a truncated Lévy walk, and two composite Brownian walks to these individual movement trajectories, using the corrected data set and the analysis suggested by Jansen *et al.* (*2*, *3*). The analysis (Table 1 and Fig. 2) reveals that, in most cases, a Brownian walk fitted very poorly to the data. A truncated Lévy walk provided large improvement over a Brownian walk, whereas a composite Brownian walk provided only small further improvement in fit, indicating that even at the individual level, composite behavior might underlie a long-tailed movement pattern.

A third possibility to mechanistically underpin the improved fit by a composite Brownian walk is that mussels use an internal switching rule to alternate between movement modes, independent from external triggers. Our study (*1*, *2*) shows that a long-tailed step length distribution is a rewarding strategy for mussels living in, and contributing to, a spatially complex system. It is not obvious, however, how an animal should achieve such a step length distribution in prac-

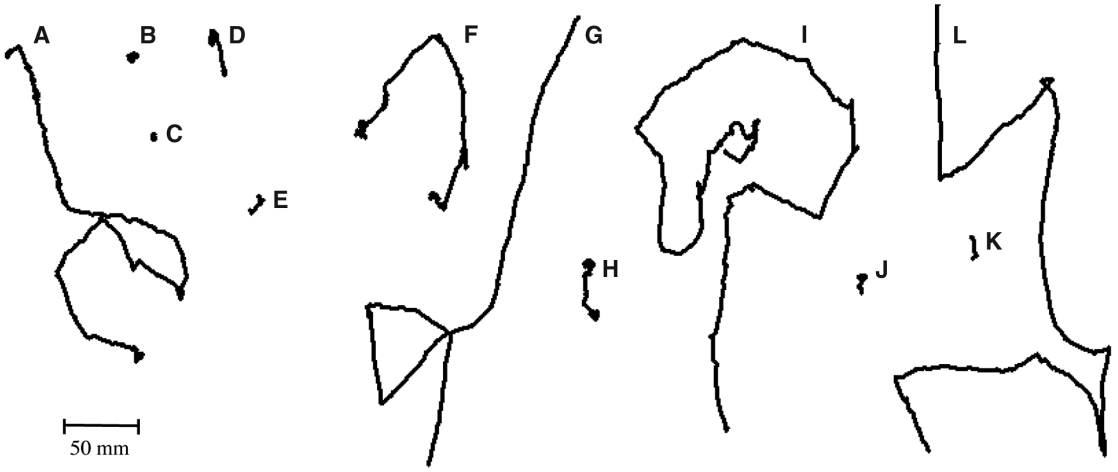


Fig. 1. Movement trajectories of the 12 mussels on which we based the model fitting in (*1*, *4*).

---

[1]Spatial Ecology Department, Royal Netherlands Institute for Sea Research (NIOZ), Post Office Box 140, 4400 AC Yerseke, Netherlands. [2]Theoretical Biology Group, Centre for Ecological and Evolutionary Studies, University of Groningen, Nijenborgh 7, 9747 AG Groningen, Netherlands. [3]Department of Animal Ecology, Netherlands Institute of Ecology (NIOO-KNAW), Post Office Box 50, 6700 AB Wageningen, Netherlands. [4]Project Group Movement Ecology, Netherlands Institute of Ecology (NIOO-KNAW), Post Office Box 50, 6700 AB Wageningen, Netherlands.

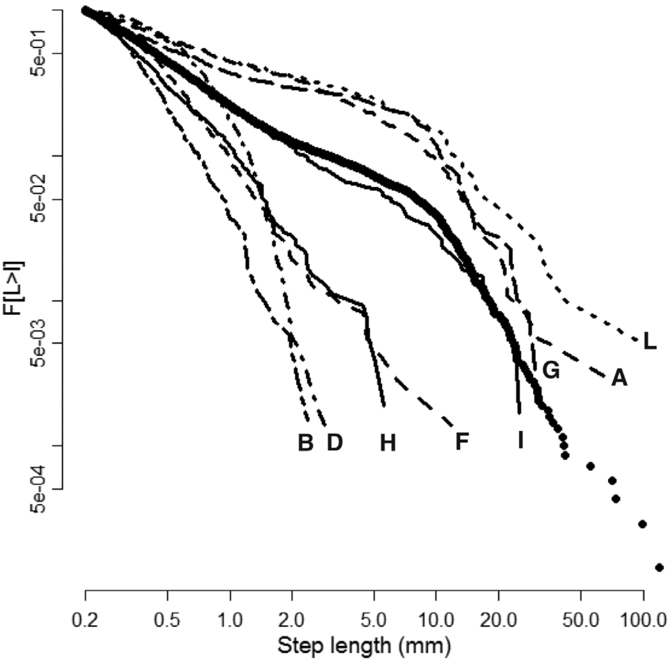
*To whom correspondence should be addressed. E-mail: m.dejager@nioo.knaw.nl

tice. It is possible that animals approximate a Lévy walk by adopting an intrinsic composite movement strategy with different modes (which do not necessarily need to be Brownian). The observation by Jansen *et al.* (*3*) that a composite walk yields a better fit to the observations thus suggests an interesting solution for this problem, which is worth further investigation. However, we think it most advisable to examine this switching behavior by means of temporal and spatial correlations of movement steps within animal tracks rather than fitting multimodal models to step size distributions. In our opinion, the observation by Jansen *et al.* (*3*) does not change the overall conclusion of our paper (*1*), but it may contribute to a better understanding of the behavioral mechanisms by which animals achieve their optimal movement strategy.

Table 1. Comparison of five movement models (Brownian walk, BW; Lévy walk, LW; truncated Lévy walk, TLW; composite Brownian walk with two movement modes, CBW2; composite Brownian walk with three movement modes, CBW3) for the eight mussels for which sufficient data ($n > 50$) were available. For each mussel, the table presents the Akaike information criterion (AIC) and the Akaike weights (wAIC) for the five movement models. The minimal AIC value (corresponding to the best model) is shown in bold. The Akaike weights correspond to the relative likelihood of each model (*8*). For all model fits, we used a lower boundary (l_{min}) of 0.2 mm.

Mussel	BW		LW		TLW		CBW2		CBW3	
	AIC	wAIC	AIC	wAIC	AIC	wAIC	AIC	wAIC	AIC	wAIC
A	1917.4	0.000	1262.7	0.000	1236.6	0.000	1192.4	0.006	**1182.12**	**0.994**
B	**1293.2**	**0.867**	2030.8	0.000	1618.1	0.000	1297.2	0.117	1301.2	0.016
D	330.4	0.000	282.5	0.000	256.1	0.000	**209.1**	**0.502**	209.2	0.498
F	1101.7	0.000	642.3	0.000	628.9	0.054	638.8	0.000	**623.2**	**0.945**
G	1410.7	0.000	792.4	0.000	770.8	0.000	761.6	0.001	**748.5**	**0.998**
H	625.5	0.000	775.6	0.000	750.3	0.000	**519.9**	**0.881**	523.9	0.119
I	2177.2	0.000	1650.0	0.000	1592.5	0.003	**1582.1**	**0.620**	1583.1	0.376
L	1455.8	0.000	1179.0	0.000	1129.0	0.002	1123.2	0.033	**1116.4**	**0.966**

Fig. 2. Inverse cumulative frequency distribution (e.g., the fraction of step lengths that is larger than or equal to a given step length) of the movement patterns of 12 individual mussels (thin dashed and dotted lines) and the combined data set (thick line and large dots).



References and Notes

1. M. de Jager, F. J. Weissing, P. M. J. Herman, B. A. Nolet, J. van de Koppel, *Science* **332**, 1551 (2011).
2. M. de Jager, F. J. Weissing, P. M. J. Herman, B. A. Nolet, J. van de Koppel, *Science* **334**, 1641 (2012).
3. V. A. A. Jansen, A. Mashanova, S. Petrovskii, *Science* **335**, 918 (2012); www.sciencemag.org/cgi/content/full/335/6071/918-c.
4. M. J. Plank, A. James, *J. R. Soc. Interface* **5**, 1077 (2008).
5. S. Benhamou, *Ecology* **88**, 1962 (2007).
6. A. M. Reynolds, *Physica A* **388**, 561 (2009).
7. S. Petrovskii, A. Mashanova, V. A. A. Jansen, *Proc. Natl. Acad. Sci. U.S.A.* **108**, 8704 (2011).
8. K. P. Burnham, D. R. Anderson, *Model Selection and Multimodal Inference: A Practical Information-Theoretic Approach* (Springer-Verlag, New York, ed. 2, 2002).

Acknowledgments: We thank A. Edwards, F. van Langevelde, and V. Jansen *et al.* for their comments and suggestions. The authors declare no competing financial interests. The research of M.d.J. is supported by a grant from the Netherlands Organization of Scientific Research/Earth and Life Sciences (NWO-ALW). This is publication 5183 of the Netherlands Institute of Ecology (NIOO-KNAW).

18 November 2011; accepted 13 January 2012
10.1126/science.1215903