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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. Pekala for constructive discussions.

Supporting Online Material

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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

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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

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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	–

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 is formed (5).

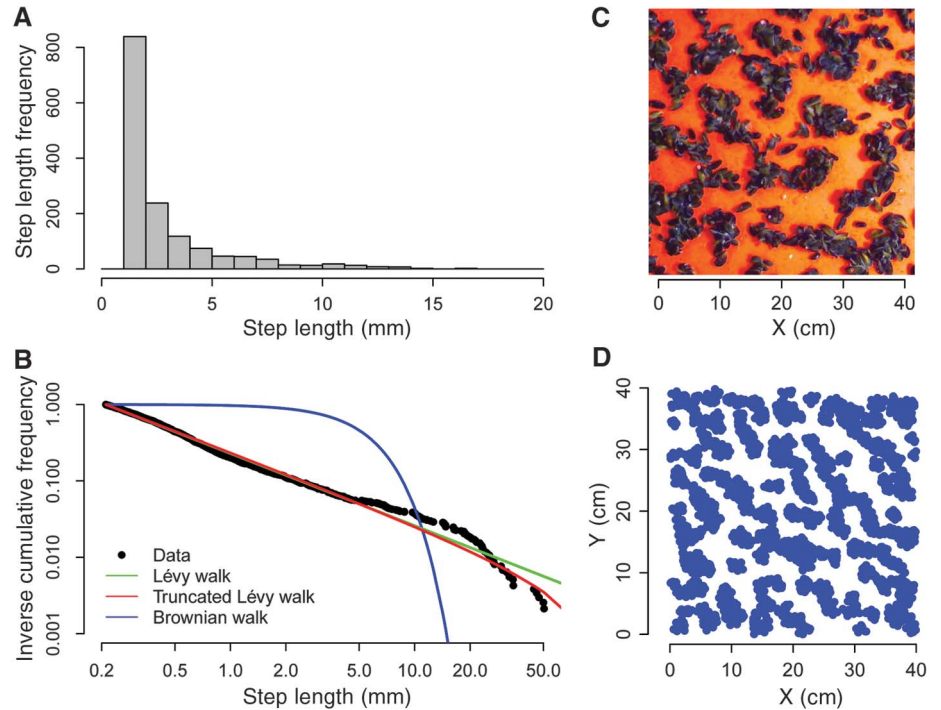


Fig. 1. Experimental and model results showing that mussel movement, which is best described by a Lévy walk, generates patterns in mussel beds. (A) Frequency distribution of step lengths of all solitary mussels (12 mussels, 12,401 steps). (B) Inverse cumulative frequency distribution of the step lengths.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

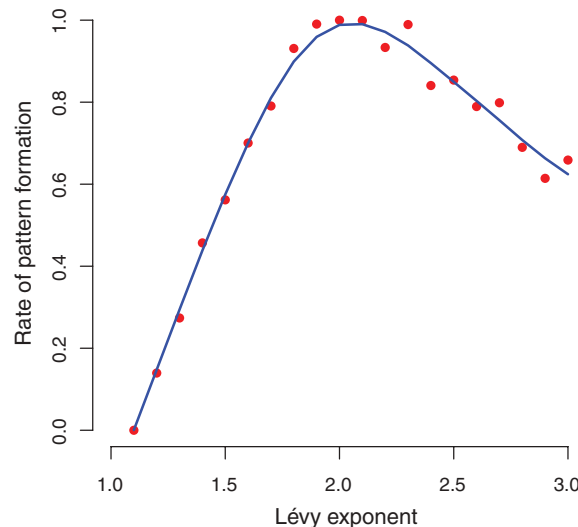


Fig. 2. The rate of pattern formation for various movement strategies. Because we assume that movement speed is constant, we can calculate the rate of patterning as the normalized inverse of the distance traversed until a pattern is formed. A Lévy walk with exponent $\mu \approx 2$ minimizes the time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

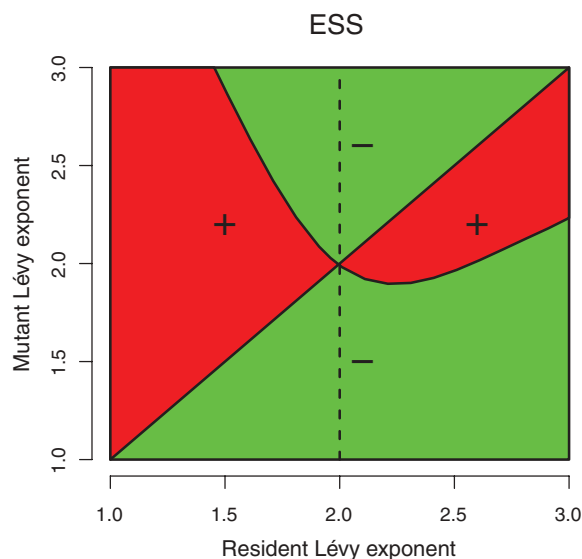
Fitness was given by the product of mussel survival (which is proportional to short-range mussel density) and fecundity (which is inversely proportional to long-range mussel density and the energy invested in movement) (5).

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).



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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

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 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