Lévy walks evolve through interaction between movement and environmental complexity

Abstract

Ecological theory predicts that animal movement is shaped by its efficiency of resource acquisition. Focusing solely on efficiency, however, ignores that animal activity can impact 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 due to 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.
Introduction

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 (Bartumeus et al., 2005; Sims et al., 2008) 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 (Viswanathan et al., 2000; Bartumeus et al., 2005; Sims et al., 2008; Bartumeus, 2009). 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 (See Appendix; Viswanathan et al., 2000; Codling et al., 2008; Viswanathan, 2010), where many short steps are occasionally alternated with a long step. Model simulations have shown that a Lévy walk provides faster dispersal (Bartumeus et al., 2005; Bartumeus, 2009), more newly visited sites (Bartumeus et al., 2005; Sims et al., 2008), and less intra-specific competition than Brownian walks (Viswanathan et al., 2000); it is therefore considered the most efficient random search strategy in resource-limited environments where food occurs patchily at locations unknown to the searcher (Bartumeus et al., 2005; Sims et al., 2008; Bartumeus, 2009) and, most importantly, where the resource distribution is largely unaffected by the activities of the searching animal (Viswanathan et al., 1999; Reynolds & Bartumeus, 2009). Although shown to be optimal for only these specific conditions, Lévy walks are broadly found in nature (Ramos-Fernandez et al., 2004; Reynolds et al., 2007; Sims et al., 2008; Humphries et al., 2010), suggesting that they are actually adaptive over a wider range of conditions. We hypothesize that this wide occurrence is due to the fact that organisms themselves affect the availability and spatial distribution of the resources upon which they depend (Jones et al., 1994). 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 (See Appendix; Maas Geesteranus, 1942; Van de Koppel et al., 2008). In particular, pattern formation in mussel beds is
attributable to two opposing mechanisms: cooperation and competition (Van de Koppel et al., 2005). Through movement 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 (Van de Koppel et al., 2008). 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 whether the interplay between movement strategy and habitat complexity results in the emergence of Lévy walks in these self-organizing mussel beds.

Methods & Results

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 (Nolet & Mooij, 2002; Benhamou, 2007; Reynolds & Rhodes, 2009). 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 (See Appendix). 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 one. The exponent \( \mu \) 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 \( \mu \) approaches 1, the movement is approximately ballistic, while it is approximately Brownian when \( \mu \) approaches 3 (and for \( \mu > 3 \)) (See Appendix; Fig. 2.5; Bartumeus et al., 2005; Reynolds & Rhodes, 2009). The Lévy walks found in nature typically have an exponent \( \mu \) of approximately 2 (Ramos-Fernandez et al., 2004; Reynolds et al., 2007; Sims et al., 2008; Humphries et al., 2010).
Figure 2.1: 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 (18 mussels, 15,764 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.

Our results show that mussels use a Lévy walk during the process of pattern formation. Based on maximum likelihood estimation and the derived Goodness-of-fit (G), Akaike Information Criterion (AIC) and the fraction of variance explained by the model (R²), 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 2 orders of magnitude (See Appendix, Table 2.1; Fig. 2.1; Table 2.2). A possible alternative explanation is that mussel movement follows a composite Brownian walk, where movement speeds are adjusted to local environmental conditions (Nolet & Mooij, 2002; Benhamou, 2007; Reynolds, 2008; Benhamou, 2008; Reynolds & Rhodes, 2009). Such a strategy can have a similar step length distribution as 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)
Table 2.1: Summary of the model fits to the step length data. Here, we only used the ‘angle method’ to calculate the step lengths from the movement data. The maximum likelihood estimation (ML) and the subsequent weighed Akaike Information Criterion (wAIC) show that a truncated Lévy walk with $\mu = 1.9$ best (out of these three movement strategies) approximates the movement strategy of solitary mussels.

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<th>ML</th>
<th>wAIC</th>
<th>Lévy exponent</th>
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<td>1.9</td>
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<tr>
<td>Lévy walk</td>
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<td>Brownian walk</td>
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<td>0</td>
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</table>

and long-range density (the density of mussels within a radius of 22.5 cm) categories, 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 (See Appendix, Table 2.3). 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 (See Appendix). 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 prior study to estimate the parameters of this stop-or-move behavior (See Appendix; Fig. 2.5; Van de Koppel et al., 2008). Although step length distributions are unaffected by mussel density, we discovered 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). Based on 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 travelled 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
Figure 2.2: The rate of pattern formation for various movement strategies. As 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.

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 was formed (See Appendix).

Simulations reveal that movement strategies differ strongly in terms of the rate at which they create patterns (Fig. 2.2). 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 $\mu$ prevented quick formation of tight clusters, while a larger value of $\mu$ 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.

As pattern formation both improves mussel survival and decreases competition between mussels (Maas Geesteranus, 1942), 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 (Reynolds & Rhodes, 2009). To determine the long-term outcome of selection acting on mussels differing in strategy (i.e. their exponent $\mu$) we created a pairwise invasibility plot (PIP, Fig. 2.3) by performing an evolutionary invasibility analysis (See Appendix; Geritz et al., 1998; Dercole & Rinaldi, 2008). 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 $\mu_{\text{res}}$. The y-axis represents the exponents $\mu_{\text{mut}}$ of potential mutant strategies. The colors indicate whether or not a mutant strategy $\mu_{\text{mut}}$ can successfully invade a resident strategy $\mu_{\text{res}}$, i.e. whether or not 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) (See Appendix).

The PIP reveals that a Lévy walk with $\mu \approx 2$ is the unique evolutionary attractor of the system (Fig. 2.3; Geritz et al., 1998; Dercole & Rinaldi, 2008). 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. 2.1) not only has a high patterning efficiency (Fig. 2.2) but is also an evolutionarily stable strategy (Fig. 2.3).
Figure 2.3: Pairwise invasibility plot (PIP) indicating that the movement strategy evolves towards 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 or not a mutant can invade the resident population (Geritz et al., 1998). Here, the PIP shows that a Lévy walk with $\mu \approx 2$ is the sole evolutionarily stable strategy (ESS).

Conclusion & Discussion

Our study demonstrates an evolutionary feedback between individual movement behavior and higher level complexity, and it provides a possible explanation for 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, as resource patterns reflect the movement patterns of their consumers. This applies, for instance, to the interaction between herbivores and vegetation, which shapes grasslands globally (Adler et al., 2001). 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 [Boyer & Lopez-Corona, 2009]). We conclude that the interaction between animal movement and habitat complexity is a key component in understanding the evolution of animal movement strategies.
Appendix: Supplementary Materials & Methods

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 (Maas Geesteranus, 1942). 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.

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). 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, 68 mussels were used for the experiments, resulting in 19,401 steps. Tracks of 18 of these mussels (15,764 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. 2.1B). 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
Figure 2.4: 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).

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). In the ‘error radius method’ (illustrated in Fig. 2.4a), 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.

Turchin’s ‘angle method’ (illustrated in Fig. 2.4b) 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 $\beta_{\text{max}}$. When this value is exceeded after the nth movement, the corresponding point becomes the starting point for the next step. The threshold value $\beta_{\text{max}}$ was also chosen iteratively, starting with a small angle and gradually increasing it until oversampling was minimized ($\beta_{\text{max}} = 30^\circ$).

As the method used for estimating step lengths does not affect our conclusions, we chose to calculate the step lengths using the ‘angle method’. Without all steps smaller than the lower truncation boundary (0.2 mm), the step length data now contains 6996 data points.

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. 2.1a). 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 (Sims et al., 2007; Edwards et al., 2007; White et al., 2008). We therefore used a more robust method (Edwards et al., 2007) 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. 2.1b 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.
Figure 2.5: The Lévy exponent $\mu$ determines the shape of the step length distribution and thus the movement strategy. When $\mu$ 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 $\mu$ 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 $\mu = 1.01$, 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 $\mu = 1.01$, 2, and 3, respectively.

**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 $\lambda > 0$:

$$f(l) = \lambda e^{-\lambda(l-l_{\text{min}})}, \quad (2.1)$$

where $l_{\text{min}}$ is the lower truncation boundary ($l_{\text{min}} = 0.2$ mm).
**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 (Clauset et al., 2009) was used:

\[ f(l) = C_\mu l^{-\mu}. \] (2.2)

The shape parameter \( \mu \) (which has to exceed 1) is known as the Lévy exponent or scaling exponent and determines the movement strategy (see Fig. 2.5). When \( \mu \) 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 \( \mu \) approaches 1, the movement is approximately ballistic, while it is approximately Brownian when \( \mu \) approaches 3 (and for \( \mu > 3 \)). The Lévy walks found in nature typically have an exponent \( \mu \) of approximately 2 (Ramos-Fernandez et al., 2004; Reynolds et al., 2007; Sims et al., 2007; Humphries et al., 2010). \( C_\mu \) 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 \( L_{\text{min}} \) (0 < \( L_{\text{min}} \)), this constant is given by

\[ C_\mu = (\mu - 1)L_{\text{min}}^{\mu - 1}. \] (2.3)

When fitting our data to a Lévy walk, we used the value of \( L_{\text{min}} \) that provided the most accurate movement data (without the small-scale measuring errors; \( L_{\text{min}} = 0.2 \) mm).

**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 \( C_\mu \):

\[
C_\mu = \frac{\mu - 1}{\frac{1}{l_{\text{min}}} - \frac{1}{l_{\text{max}}}}.
\]

(2.4)

In a truncated Lévy walk, step lengths are constrained to the interval \( l_{\text{min}} < l < l_{\text{max}} \). When fitting our data to a truncated Lévy walk, we used those values of \( l_{\text{min}} \) that provided the most accurate movement data (without the small-scale measuring errors; \( l_{\text{min}} = 0.2 \) mm). We used the maximum step length as the upper truncation boundary (\( l_{\text{max}} \)).

**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 (ML) estimation:

\[
ML_{\text{BW}} = n \cdot \log(\lambda) - \lambda \cdot \sum (l - l_{\text{min}}),
\]

(2.5)

\[
ML_{\text{LW}} = n \cdot \log(\mu - 1) + n \cdot (\mu - 1) \cdot \log(l_{\text{min}}) - \sum \log(l),
\]

(2.6)

\[
ML_{\text{TLW}} = \frac{n}{\mu - 1} + \frac{n \cdot (l_{\text{min}}/l_{\text{max}})^{\mu - 1} \cdot \log(l_{\text{min}}/l_{\text{max}})}{1 - (l_{\text{min}}/l_{\text{max}})^{\mu - 1}} - \sum (\log(l) - \log(l_{\text{min}})),
\]

(2.7)

where \( n \) is the number of data points. Subsequently, we calculated the AIC:

\[
AIC_i = -2 \cdot ML_i + 2 \cdot K_i,
\]

(2.8)

where \( K \) is the number of parameters of model \( i \). Using the AIC’s of the three movement strategies, we were able to calculate the weighed AIC (wAIC):

\[
wAIC_i = e^{-0.5 \cdot (AIC_i - AIC_{\text{min}})} / \sum e^{-0.5 \cdot (AIC_i - AIC_{\text{min}})},
\]

(2.9)
Table 2.2: Lévy exponent during pattern formation. The Lévy exponent (calculated with the ‘angle method’ step length data when n > 50) increases with local and long-range mussel density (df = 21, F = 15.46, r^2 = 0.557, p < 0.001). This increase in μ with mussel density may be accounted for by collisions with conspecifics, which cause truncation of steps.

<table>
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where \( AIC_{min} \) is the lowest AIC of the three movement strategies. The movement strategy with the highest weighed AIC provides the best fit to the mussel movement data (out of the three models). This method was used for the analysis of the movement strategies of the 12 solitary mussels (see Fig. 2.4). 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 2.2).

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). Whereas they modeled pattern formation in mussel beds by adjusting the movement speed to the short- and long-range densities (Van de Koppel et al., 2008), 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, R² = 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. 2.6), 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:

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

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 (Newman, 2005) with a given Lévy exponent $\mu > 1$:

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

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 (Clauset et al., 2009), 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.
Figure 2.6: 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.

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 \(\mu\). 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 (Geritz et al., 1998; Dercole & Rinaldi, 2008). 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:

$$F_{mut} = \frac{D_{1,mut}}{D_{1,res}} * \frac{D_{2,res}}{D_{2,mut}} * \frac{X_{res}}{X_{mut}}.$$  \hspace{1cm} (2.12)

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 (Dercole & Rinaldi, 2008; see Fig. 2.3). 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 (Geritz et al., 1998; Dercole & Rinaldi, 2008).
Comment & Reply I:

Emergent properties of the Lévy walk are not adaptive strategies

Comment by: Frank van Langevelde, Willem F. de Boer, Hendrik J. de Knegt, Herbert H. T. Prins

Comment

M. de Jager et al.’s fascinating study on the interaction between animal movement and habitat complexity demonstrates that mussels move from random distributions to self-organized mussel beds (De Jager et al., 2011). Mussel movements show properties of Lévy walks with the characteristic $\mu \approx 2$, which is the most efficient random search strategy (Sims et al., 2008; Humphries et al., 2010). De Jager et al. argue that mussels doing a Lévy walk with $\mu \approx 2$ create a spatial environment in which this strategy is evolutionarily stable. The conclusion that Lévy walks are selectively advantageous is important, as it could explain why animal movements are often superdiffusive (Viswanathan et al., 1999; De Knegt et al., 2007). Yet we contest that a Lévy walk is an adaptive strategy, and argue that it is merely an emergent property that arises through interaction with the environment.

Our simulations show that observed movement patterns differ from the innate movement strategy (Hengeveld et al., 2007). The typical step-length distribution of Lévy walks ($\mu_{\text{observed}} \approx 2$) can be generated simply by truncations of long steps in walks with $\mu_{\text{innate}} < 2$: Finding targets decreases the step lengths and increases $\mu$. Hence, $\mu_{\text{observed}}$ is larger than $\mu_{\text{innate}}$ (Fig. 2.7). With increasing target density, the deviation between $\mu_{\text{observed}}$ and $\mu_{\text{innate}}$ increases. The observed $\mu \approx 2$ in mussels can thus not be the innate $\mu$ that is selected to create mussel beds.

Consequently, we predict that $\mu_{\text{innate}}$ measured using solitary mussels is smaller than $\mu_{\text{observed}}$ in mussel bed pattern formation. Secondly, we expect that $\mu_{\text{observed}}$ of the modeled mussels is larger than $\mu_{\text{innate}}$ used in the model, due to truncation of large steps by obstruction from conspecifics. Therefore, we challenge the evolutionarily stable strategy of $\mu \approx 2$, and predict that $\mu_{\text{innate}} < \mu_{\text{observed}}$. We hypothesize that the $\mu_{\text{observed}}$ at which the strategy is stable increases with mussel density (Viswanathan et al., 1999; De Knegt et al., 2007). More work is needed to understand how movement patterns are shaped by the interaction between the innate $\mu$ and habitat complexity.
Figure 2.7: Observed $\mu_{\text{observed}}$ vs. innate $\mu_{\text{innate}}$ (Hengeveld et al., 2007). The slopes of the downward part of the log-log frequency distribution of the observed flights ($\mu_{\text{observed}}$) are plotted against the slopes of the distribution of flight used to generate the paths ($\mu_{\text{innate}}$). The relationship is plotted for 4 (triangle) resource densities (measured by the mean free path between targets $\delta$): $\delta = 10$ (square), $\delta = 10^2$ (◊), $\delta = 10^3$ (Δ), $\delta = 10^4$ (•). The solid line is the reference line $\mu_{\text{innate}} = \mu_{\text{observed}}$.

Reply

F. van Langevelde et al. argue that the Lévy walks found in nature are not innate search strategies but rather emergent properties of the interplay between animal movement and environmental complexity. Their line of reasoning is that steps become truncated whenever an animal finds a target resource. Hence, they claim that the scaling exponent $\mu$ of the truncated Lévy walk that we observed in mussel movements should be larger than the $\mu$ of the innate search strategy, and that a Lévy walk therefore cannot be an adaptive strategy in dense mussel beds.
We agree with Van Langevelde et al. that the truncation of intended steps by resource encounter indeed can alter the movement pattern and increases the observed value of $\mu$. However, the data that are presented in Figure 1B of our Report (de Jager et al., 2011) are based on movements of solitary mussels, and therefore collisions with other mussels do not influence their movement. Hence, as Lévy movement is observed in the absence of conspecifics, it must reflect their innate strategy.

In the Supporting Online Material of our Report, however, we presented an analysis of the step size distribution of mussel movements in clumps of different densities, in which collisions do occur. Here, we concluded that the density of neighbors, the main determinant of the chances of a collision, did not affect the observed Lévy exponent $\mu$, which was found to approximate a value of 2 for all. However, the results of our analysis reflected our choice to fit only a non-truncated power law to the data and to include samples of size $n < 50$. When we reanalyzed the data by fitting truncated Lévy walks, we found that $\mu$ indeed changes with mussel density: $\mu$ increases with local and long-range mussel density (Fig. 2.8; df $= 21$, $F = 15.46$, $r^2 = 0.557$, $p < 0.001$).

This increase in $\mu$ with mussel density may be accounted for by collisions with conspecifics, which cause truncation of steps, supporting the hypothesis posed by Van Langevelde et al. (2011). Importantly, however, we do not concur with Van Langevelde et al. that these observations challenge our result that a $\mu$ close to 2 is the evolutionarily stable strategy. Collisions with conspecifics may indeed alter the observed $\mu$, but selection acts on the innate movement strategy of organisms, rather than on the movements that we observe. The invasibility analysis presented in our Report (de Jager et al., 2011) was based on the innate value of $\mu$ and not on the value of $\mu$ characterizing the observed movement pattern. Hence, we maintain our conclusion that a $\mu$ of approximately 2 is the evolutionarily stable strategy for mussels in self-organizing mussel beds, as is reflected by their innate strategy observed in the absence of conspecifics.
Figure 2.8: (A) The inverse cumulative step length frequency distributions ($F[L>l]$) of the mussel movements in clumps of different sizes diverges from that of the solitary mussels, resulting in a higher estimate of $\mu$. $D_1$ here indicates the mussel density within a radius of 3.3 cm. (B) When the steps are divided into groups based on the local and long-range mussel density, we find that the estimated $\mu$ of the fitted truncated Lévy walks increase with local mussel density.
Comment & Reply II:

Comment on ‘Lévy walks evolve through interaction between movement and environmental complexity’

Comment by: Vincent A. A. Jansen, Alla Mashanova, Sergei Petrovskii.

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

Science 335, 918 (2012)
Comment

De Jager et al. (2011) 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. (2011) studied the movements of individual mussels and concluded that mussels move according to a Lévy walk.

The argument of De Jager et al. (2011) 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 (Burnham & Anderson, 2002). This methodology is used to infer types of movements of animals (Edwards et al., 2007) and has led to a number of studies that claim Lévy walks are often encountered in the movement of animals. The methodology in De Jager et al. (2011) 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 (Benhamou, 2007; Petrovskii & Morozov, 2009; Petrovskii et al., 2011). Mussels’ movement is heterogeneous as they switch between moving very little or not at all, and moving much farther (De Jager et al., 2011; Van de Koppel et al., 2008). 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.
Figure 2.9: The step length distribution for mussel movement [as in De Jager et al. (2011)] 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 De Jager et al. (2011) (2029 steps). (B) The full untruncated data set (3584 steps).

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. 2.9A). We applied a model selection procedure based on the Akaike information criterion (AIC) (Burnham & Anderson, 2002; Edwards et al., 2007). 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 De Jager et al. (2011) (Fig. 2.9A) as well as all the full, untruncated data set (Fig. 2.9B). In both cases, we found that the composite Brownian walk consisting of the sum of three exponentials was the best model (Fig. 2.9 and Table 2.3). This convincingly shows that the mussels described in De Jager et al. (2011) 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 De Jager et al. (2011).

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 2.3; 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 (De Jager et al., 2011). We speculate that the mode with the smallest average movement (~0.4 mm) is related to non-movement, 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 (2011) 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 (Grünbaum, 2011). Having included the option of a composite Brownian walk, which was discussed in De Jager et al. (2011) 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 (Burnham & Anderson, 2002). Heterogeneous random movement often provides such an alternative and has the additional advantage that it can suggest a simple
Table 2.3: Model parameters and Akaike weights. The maximum likelihood parameter estimates, log maximum likelihoods (ML), AIC values, and Akaike weights are calculated for the data shown in Fig. 2.8, A and B. The Akaike weights without the composite Brownian walks are given in brackets. We analyzed the full data set (*) with $x_{\text{min}} = 0.02236$ mm, and the data set truncated as in De Jager et al. (2011) (†) with $x_{\text{min}} = 0.21095$ mm. For $x_{\text{max}}$, the longest observed step length (103.9 mm) 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.

<table>
<thead>
<tr>
<th>Models</th>
<th>Formula</th>
<th>Parameters*</th>
<th>Parameters†</th>
<th>ML</th>
<th>AIC</th>
<th>Weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>Exponential (Brownian motion)</td>
<td>$P(X = x) = \lambda e^{-\lambda(x-x_{\text{min}})}$</td>
<td>$\lambda = 1.133$</td>
<td>$\lambda = 0.770$</td>
<td>$-3136.89^*$</td>
<td>$6275.78^*$</td>
<td>0 (0)*</td>
</tr>
<tr>
<td>Power Law (Lévy walk)</td>
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<td>$\mu = 1.975$</td>
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<td>$4582.20^*$</td>
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<tr>
<td>Truncated power law</td>
<td>$P(X = x) = \frac{1}{x_{\text{min}}} x^{-\mu} \mathbb{1}<em>{{x \leq x</em>{\text{max}}}}$</td>
<td>$\mu = 1.320$</td>
<td>$\mu = 1.960$</td>
<td>$-2119.55^*$</td>
<td>$4241.10^*$</td>
<td>0 (1)*</td>
</tr>
<tr>
<td>Mix of two exponentials</td>
<td>$P(X = x) = \sum_{i=1}^{2} \rho_i e^{-(x-x_{\text{min}})/\lambda_i}$</td>
<td>$\lambda_1 = 0.122$</td>
<td>$\lambda_1 = 0.123$</td>
<td>$-1022.44^*$</td>
<td>$2050.87^*$</td>
<td>0 †</td>
</tr>
<tr>
<td>Brownian walk</td>
<td>$P(X = x) = \sum_{i=1}^{2} \rho_i e^{-(x-x_{\text{min}})/\lambda_i}$</td>
<td>$\lambda_1 = 3.328$</td>
<td>$\lambda_2 = 3.275$</td>
<td>$-906.15^*$</td>
<td>$1818.31^*$</td>
<td>0 †</td>
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<tr>
<td>Mix of three exponentials</td>
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<td>$\lambda_1 = 0.034$</td>
<td>$\lambda_2 = 0.103$</td>
<td>$-861.55^*$</td>
<td>$1733.11^*$</td>
<td>0.881†</td>
</tr>
<tr>
<td>Brownian walk</td>
<td>$P(X = x) = \sum_{i=1}^{3} \rho_i e^{-(x-x_{\text{min}})/\lambda_i}$</td>
<td>$\lambda_1 = 0.034$</td>
<td>$\lambda_2 = 0.103$</td>
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<td>$1733.11^*$</td>
<td>0.881†</td>
</tr>
<tr>
<td>Mix of four exponentials</td>
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<td>$\lambda_2 = 0.103$</td>
<td>$-861.55^*$</td>
<td>$1733.11^*$</td>
<td>0.881†</td>
</tr>
</tbody>
</table>

mechanism for the observed behavior.

Reply

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 (de Jager et al., 2011; de Jager et al., 2012a) 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 $\mu$) 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. (2012). 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.
Table 2.4: 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 (Burnham & Anderson, 2002). For all model fits, we used a lower boundary (l_{\text{min}}) of 0.2 mm.

<table>
<thead>
<tr>
<th>Mussel</th>
<th>BW</th>
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<th>LW</th>
<th>wAIC</th>
<th>TLW</th>
<th>wAIC</th>
<th>CBW2</th>
<th>wAIC</th>
<th>CBW3</th>
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<td>1236.6</td>
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<td>1192.4</td>
<td>0.006</td>
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<tr>
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<td>2030.8</td>
<td>0.000</td>
<td>1618.1</td>
<td>0.000</td>
<td>1297.2</td>
<td>0.117</td>
<td>1301.2</td>
<td>0.016</td>
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<tr>
<td>D</td>
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<td>0.000</td>
<td>282.5</td>
<td>0.000</td>
<td>256.1</td>
<td>0.000</td>
<td>209.1</td>
<td>0.502</td>
<td>209.2</td>
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<td>F</td>
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<td>642.3</td>
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<td>0.002</td>
<td>1123.2</td>
<td>0.033</td>
<td>1116.4</td>
<td>0.966</td>
</tr>
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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 (Benhamou, 2007; Plank & James, 2008; Reynolds, 2009). 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 (Petrovskii et al., 2008) — 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. 2.10); 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. (de Jager et al. 2012a, Jansen et al., 2012). The analysis (Table 2.4 and Fig. 2.11) reveals that, in

Figure 2.11: 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).
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 (de Jager et al., 2011; de Jager et al., 2012a) 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 practice. 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. (2012) 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. (2012) does not change the overall conclusion of our paper (de Jager et al., 2011), but it may contribute to a better understanding of the behavioral mechanisms by which animals achieve their optimal movement strategy.