

# Response to Comment on “Lévy Walks Evolve Through Interaction Between Movement and Environmental Complexity”

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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  $\mu$ ) distinguishes between the different movement strategies. We intentionally chose a one-dimensional strategy space that can easily be used in pairwise invisibility analyses and the subsequent pair-

wise invisibility 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.

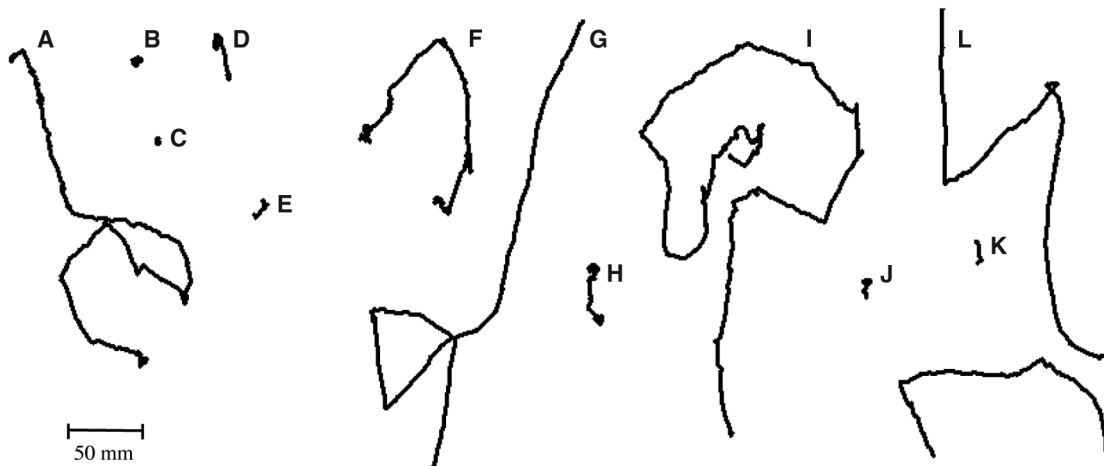
Nevertheless, it might be interesting to examine the mechanisms behind the composite Brownian walk that was observed in our mussel movement data by Jansen *et al.* (3). Below, we investigate three possible causes of the observed movement pattern: (i) mussels switch between multiple movement modes because 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).

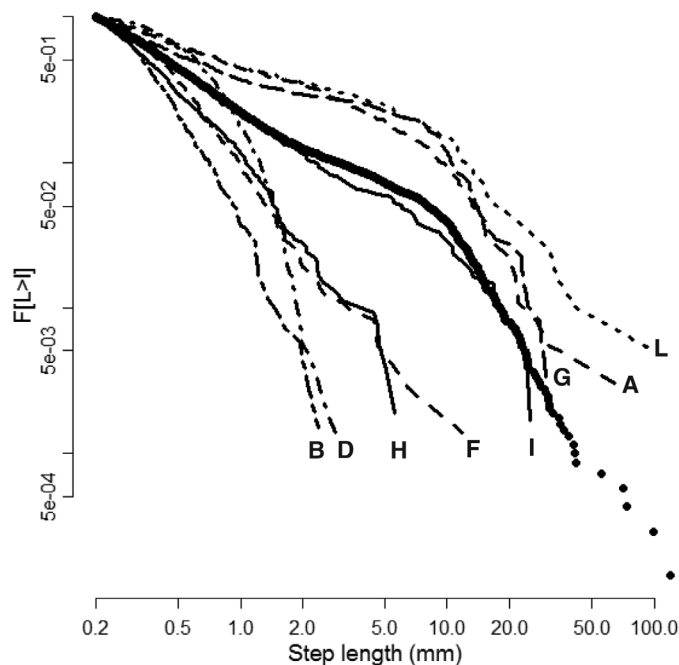
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**Table 1.** Comparison of five movement models (Brownian walk, BW; Lévy walk, LW; truncated Lévy walk, TLW; composite Brownian walk with two movement modes, CBW2; composite Brownian walk with three movement modes, CBW3) for the eight mussels for which 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 ( $\delta$ ). 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
<b>A</b>	1917.4	0.000	1262.7	0.000	1236.6	0.000	1192.4	0.006	<b>1182.12</b>	<b>0.994</b>
<b>B</b>	<b>1293.2</b>	<b>0.867</b>	2030.8	0.000	1618.1	0.000	1297.2	0.117	1301.2	0.016
<b>D</b>	330.4	0.000	282.5	0.000	256.1	0.000	<b>209.1</b>	<b>0.502</b>	209.2	0.498
<b>F</b>	1101.7	0.000	642.3	0.000	628.9	0.054	638.8	0.000	<b>623.2</b>	<b>0.945</b>
<b>G</b>	1410.7	0.000	792.4	0.000	770.8	0.000	761.6	0.001	<b>748.5</b>	<b>0.998</b>
<b>H</b>	625.5	0.000	775.6	0.000	750.3	0.000	<b>519.9</b>	<b>0.881</b>	523.9	0.119
<b>I</b>	2177.2	0.000	1650.0	0.000	1592.5	0.003	<b>1582.1</b>	<b>0.620</b>	1583.1	0.376
<b>L</b>	1455.8	0.000	1179.0	0.000	1129.0	0.002	1123.2	0.033	<b>1116.4</b>	<b>0.966</b>

**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).



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.

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