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

Vincent A. A. Jansen, *et al.*

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

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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;

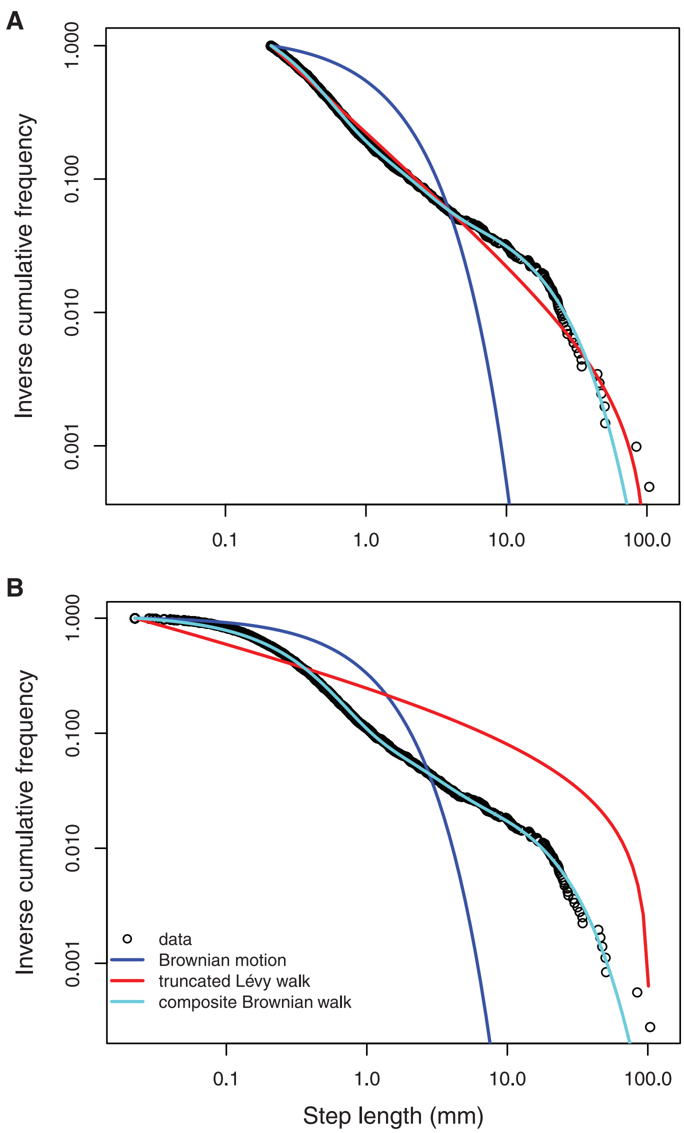

Fig. 1. The step length distribution for mussel movement [as in (*10*)] and curves depicting some of the models. The circles represent the inverse cumulative frequency of step lengths, The curves represent Brownian motion (blue), a truncated power law (red), and a composite Brownian walk consisting of 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).

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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).

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Materials and Methods
SOM Text
References

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