Comments

Sampling rate and misidentification of Lévy and non-Lévy movement paths: comment

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In a recent paper, Plank and Codling (2009) critique the use of Lévy walks to describe animal movement, arguing that non-Lévy walk processes could be misidentified as Lévy patterns and, conversely, movement patterns actually generated by Lévy processes may be wrongly attributed to other mechanisms. The authors suggest that this ambiguity is partly caused by sampling paths at scales that do not reflect actual movement decisions and this despite the theoretical scale-independence of Lévy walks. These findings, if true, would be an important contribution, as the Lévy walk is a popular, although controversial, model in the animal movement literature.

Here, we support Plank and Codling's (2009) contention that movement patterns must be attributed to the correct process and that animal movement is likely not truly scale-invariant. However, we challenge their methodology, and hence that they showed that Lévy and non-Lévy processes could be misidentified for one another and that this ambiguity partly depends on the sampling scale. Our main criticism is that using the relative fit of poorly chosen models, without verifying for the absolute fit of the best model, is insufficient evidence for either the identification or the misidentification of a process. To demonstrate this methodological problem, we first describe the models used to simulate the data and thus representing the movement processes. Then we describe how the models that were fitted to the data differed from the ones used to simulate the data. Finally, we argue that the authors failed to consider the importance of examining the absolute fit of the best model. Without this information, it is impossible to determine whether either model provides a reasonable explanation for a given data set, whether those data are generated by simulations or actual animals.

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Simulating ecological processes: the movement simulations of Plank and Codling (2009)

Plank and Codling (2009) simulated two types of datasets: one representing a Lévy walk and one representing a composite correlated random walk (CCRW). To simulate the Lévy walk they used a non-correlated random walk with a truncated Pareto distribution for the step length distribution. The CCRW was chosen as an alternative movement process to the Lévy walk because this distinct behavioral process produces a similar movement pattern to the Lévy walk (Benhamou 2007, Plank and James 2008). The CCRW was composed of two phases: an intensive phase with tortuous movement and small step lengths and an extensive phase with nearly straight movement with long step lengths.

Discrepancy between the models used to simulate the processes and those to explain the patterns

The two models Plank and Codling (2009) fitted to recover the simulated process differed from those used to produce the data, making it likely that the absolute fits of these models would be poor. The authors fitted a non-truncated Pareto distribution to recover a process simulated with the truncated version of this distribution. The non-truncated distribution is scale-invariant at all measurable scales. In contrast, the truncated Pareto distribution has an upper limit on the size of the step lengths and is thus scale invariant for only a limited range of scales. Plank and Codling (2009) state that they used the non-truncated Pareto distribution to fit the data because it is the distribution most commonly used. However, most studies using the non-truncated Pareto distribution also used the now-obsolete histogram-based method to test for Lévy walks (but see Focardi et al. 2009). This histogram-based method did not allow for a truncated version of the Lévy walk. Because the more modern maximum likelihood method used by Plank and Codling (2009) allows to fit a truncated Pareto distribution (Edwards 2008, White et al. 2008), the authors should have additionally fitted the truncated Pareto distribution to their simulated data.

Not only did Plank and Codling (2009) use two different models to simulate and recover the Lévy process, they used two different models to simulate and recover the CCRW. In this case these two models are not merely two different versions of the same model but completely distinct. Thus, the absolute fit is expected to be poor. They fitted an exponential distribution to recover a process simulated with CCRW. An exponential distribution is often used to model a simple random Poisson process and

has been an alternative model against which Pareto distribution has been compared in Lévy walk studies (Edwards et al. 2007, Edwards 2008, Humphries et al. 2010). However, the exponential distribution is not a good representation of a CCRW and we cannot expect the exponential distribution to adequately fit a CCRW. Plank and Codling (2009) state that they used the exponential distribution because the only likelihood function that could recover a CCRW process is complicated and uses Bayesian statistics (see Morales et al. 2004). This indicates the need for a simple likelihood function that describes the step length distribution of a CCRW.

Comparing two poor models with Akaike weights is insufficient evidence for process identification

The main goals of the study by Plank and Codling (2009) were to verify whether a Lévy walk can be misidentified for a Poisson process and whether CCRW can be misidentified as a Lévy walk. To do so, they compared the fit of the non-truncated Pareto and the exponential distributions using Akaike weights. By definition, Akaike weights can only measure the relative fit of the candidate models, not their absolute fit to the data (Burnham and Anderson 2002). Thus, the best model according to Akaike weights may still be a poor model for the data. However, when the Akaike weights favored the wrong model, Plank and Codling (2009) concluded that a misidentification was likely to occur. For example, when Akaike weights favored the Pareto over the exponential distribution for data simulated with the CCRW, Plank and Codling (2009) concluded that the CCRW was likely to be misidentified as a Lévy walk.

For Plank and Codling (2009) to suggest that CCRW could be misidentified as a Lévy walk, they would have needed to investigate the absolute fit of the best model. While Akaike weights can identify the best of the candidate models, only a measure of absolute fit can identify whether the best model adequately fits data. In the articles that introduced Akaike weights as a method to compare Lévy walks to other movement models (Edwards et al. 2007, Edwards 2008), goodness-of-fit tests (G-tests) were used to verify that the best model fitted the data. In other recent studies that applied Lévy walks to animal movement using maximum-likelihood methods similar to Plank and Codling (2009), the absolute fit was demonstrated by the analysis of the residuals (e.g., Focardi et al. 2009), statistical tests (e.g., Schreier and Grove 2010), and by visual inspection of the fit of the best model to the data (e.g., Focardi et al. 2009, Humphries et al. 2010). Without such verification of absolute model fit, the conclusion that CCRW can be misidentified as Lévy walks is unwarranted.

A visual assessment of Fig. 3 in Plank and Codling (2009) suggests that neither the Pareto nor the exponential distribution fits the CCRW. This reveals that, even if the Pareto distribution fits the data simulated with a CCRW better than the exponential distribution according to Akaike weights, the Pareto distribution does not appear to adequately describe the CCRW. Whether a goodness-of-fit test, such as a G test, would have confirmed such discrepancy needs to be investigated. Therefore, even though Plank and Codling (2009) importantly showed that Akaike weights can be misleading, their suggestion that CCRW is easily misidentified as a Lévy walk is unfounded. This reasoning also extends to their other conclusions, such as that a Lévy walk could be misidentified for a Poisson process and that the assumption of scale invariance of Lévy walks is tenuous.

Conclusion

The important study by Plank and Codling (2009) appropriately cautions ecologists not to blindly assume that pattern is equivalent to process in the study of animal movement and that animal movement is likely not truly scale-invariant. Despite the identification of these potential problems, Plank and Codling (2009) have not provided definitive tests for their detection, and our analysis of their study should extend the caution to promote the investigation of both the relative and the absolute fit of movement models. Because Plank and Codling (2009) did not emphasize the importance of the absolute fit of the best model, they did not demonstrate whether a CCRW actually would be misidentified as a Lévy walk, or a Lévy walk as a Poison process. Nonetheless, Plank and Codling (2009) highlighted an important and perennial problem associated with applying the Lévy walk to empirical data. The Lévy walk is too often compared to simplistic alternative models, and rarely against strong alternative models. The two-phase searching strategy associated with a CCRW produces a similar movement pattern as the Lévy walk strategy, yet the CCRW is rarely used as an alternative model in studies of Lévy walks. One reason for this tendency is that there is no simple likelihood function for CCRWs. A logical next step is to develop such a function so ecologists can rigorously compare the Lévy walk against this strong alternative model. By distinguishing between these two processes, we will be a step further in elucidating the mechanisms that diverse organisms, including humans, use to find resources.

Literature cited

Benhamou, S. 2007. How many animals really do the Lévy walk? Ecology 88:1962–1969.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer, New York, New York, USA.

Edwards, A. M. 2008. Using likelihood to test for Lévy flight search patterns and for general power-law distributions in nature. Journal of Animal Ecology 77:1212–1222.

Edwards, A. M., R. A. Phillips, N. W. Watkins, M. P. Freeman, E. J. Murphy, V. Afanasyev, S. V. Buldyrev, M. G. E. da Luz, E. P. Raposo, and H. E. Stanley. 2007. Revisiting Lévy flight search patterns of wandering albatrosses, bumblebees and deer. Nature 449:1044–1048.

Focardi, S., P. Montanaro, and E. Pecchioli. 2009. Adaptive Lévy walks in foraging fallow deer. PLoS ONE 4:e6587.

Humphries, N. E., N. Queiroz, J. R. M. Dyer, N. G. Pade, M. K. Musyl, K. M. Schaefer, D. W. Fuller, J. M. Brunnschweiler, T. K. Doyle, and J. D. R. Houghton. 2010. Environmental context explains Lévy and Brownian movement patterns of marine predators. Nature 465:1066–1069.

Morales, J. M., D. T. Haydon, J. Frair, K. E. Holsinger, and J. M. Fryxell. 2004. Extracting more out of relocation data: building movement models as mixtures of random walks. Ecology 85:2436–2445.

Plank, M. J., and E. A. Codling. 2009. Sampling rate and misidentification of Lévy and non-Lévy movement paths. Ecology 90:3546–3553.

Plank, M. J., and A. James. 2008. Optimal foraging: Lévy pattern or process? Journal of The Royal Society Interface 5:1077–1086.

Schreier, A. L., and M. Grove. 2010. Ranging patterns of hamadryas baboons: random walk analyses. Animal Behaviour 80:75–87.

White, E. P., B. J. Enquist, and J. L. Green. 2008. On estimating the exponent of power-law frequency distributions. Ecology 89:905–912.

Sampling rate and misidentification of Lévy and non-Lévy movement paths: reply

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Auger-Méthé et al. (2011), in their comment on our paper (Plank and Codling 2009), raised two main criticisms of our methodology and conclusions. The first of these concerns the discrepancy between the models

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used to simulate the movement paths and those fitted to the resulting data; the second is that the absolute fit of the candidate models should be tested, as well as the relative fit. We will focus on these two issues in this reply.

Discrepancy between the models used to simulate the processes and those to explain the patterns

In Plank and Codling (2009), we used two different random walk models to simulate movement paths: (1) a truncated Lévy walk (TLW), in which step lengths are drawn from a truncated Pareto distribution; and (2) a composite correlated random walk (CCRW), in which the walker alternates between two phases, with each phase corresponding to a correlated random walk (CRW) with distinct parameter values. The walker's location was sampled at regular intervals and the straight-line distances between successive observed locations recorded. This is similar to the sampling methods used in several empirical studies (e.g., Mårell et al. 2002, Fritz et al. 2003, Austin et al. 2004, Ramos-Fernández et al. 2004). We then used a maximum likelihood method (e.g., Edwards 2008, White et al. 2008) to fit two simple candidate distributions to the observed data: an untruncated Pareto distribution and an exponential distribution.

Auger-Méthé et al. (2011) point to the discrepancy between the movement models and the fitted distributions as a flaw in our methodology, claiming that we should instead have fitted distributions corresponding to the step-length distributions used in the movement models. The situation we were attempting to replicate in Plank and Codling (2009) was one in which there is no a priori knowledge of the movement mechanisms. We therefore chose the two simplest candidate distributions that assume the least information about the process they are being used to describe. These are also two of the distributions most commonly used to fit observational data. We agree with Auger-Méthé et al. (2011) that testing a wider range of distributions, including for example a truncated Pareto distribution (e.g., Edwards et al. 2007, Edwards 2008) and a distribution describing the step lengths of a CCRW, would be sensible. However, we stress that, in the absence of specific information about the underlying mechanisms, the choice of candidate distributions is always somewhat arbitrary.

It should also be noted that it is unrealistic to expect that the forager's location will be sampled exactly at the end of every random walk step. This motivated our study of the effects of subsampling on the outcomes of the statistical analysis. One of these effects is that the observed travel-distance distribution may bear little resemblance to the underlying step-length distribution. Hence, even with a priori knowledge of the underlying movement mechanism, fitting the corresponding step-length distribution may not provide a good fit to the observed data.

One way of improving the capacity of the observed data to infer information about movement mechanisms is to attempt to identify points at which the forager undergoes a significant change in direction. This was originally proposed by Turchin et al. (1991) and subsequently adapted by Reynolds et al. (2007b). Codling and Plank (2010) applied this "turn designation" method to TLW and CCRW simulation data, showing that the details of how turning points are identified can also influence the relative fit of the two (simplistic) candidate models. This highlights the fact that there is not yet a definitive means of distinguishing a TLW from a CCRW.

Comparing two poor models with Akaike weights is insufficient evidence for process identification

We agree with Auger-Méthé et al. (2011) that comparing the relative fit of two models is not sufficient to identify the process that generated the data. Indeed the aim of our paper was to demonstrate that this approach, which has been adopted in a number of empirical analyses (e.g., Reynolds 2009, Reynolds et al. 2009), is flawed and can give potentially misleading results. An essential prerequisite for any successful model is that it has a good absolute fit (Edwards 2008), yet this has been overlooked in a number of studies (e.g., Ramos-Fernández et al. 2004, Reynolds et al. 2007a, b). Augur-Méthé et al. (2011) propose "visual inspection of the fit" (e.g., Focardi et al. 2009, Humphries et al. 2010) as one possible means of checking this. This visual "test" is at best subjective and at worst misleading, being reminiscent of the obsolete regression-based methods originally used in this area. For instance, the importance of individual data points plotted on log-log axes can easily be distorted. It is possible to get a good apparent fit to a straight line on log-log axes when the absolute fit of the model is actually very poor (i.e., has a negligibly small P value).

Conclusion

The points raised by Auger-Méthé et al. (2011) about our paper (Plank and Codling 2009) are largely valid and serve to reiterate our intended meaning. We deliberately employed a flawed, yet widely used, methodology. It was not our intention to advocate this methodology, but rather to caution against its use by demonstrating the erroneous conclusions to which it can lead. Extreme caution should be employed when inferring Lévy walk behavior from step length data. The use of a quantitative goodness-of-fit test, as well as a relative test, is important, although even this can be misleading when dealing with relatively small sample sizes. Furthermore, the conclusions of such tests can depend on how the available data are processed. It is therefore advisable to test the sensitivity of statistical tests to the processing methods where possible (Codling and Plank 2010). The development of stronger, mech-anism-based models that can be fitted to data of the type commonly recorded will greatly enhance our ability to infer movement processes from observed patterns.

Literature cited

Auger-Méthé, M., C. C. St. Clair, M. A. Lewis, and A. E. Derocher. 2011. Sampling rate and misidentification of Lévy and non-Lévy movement paths: comment. Ecology 92:1699–1701.

Austin, D., W. D. Bowen, and J. I. McMillan. 2004. Intraspecific variation in movement patterns: modelling individual behaviour in a large marine predator. Oikos 105:15–30.

Codling, E. A., and M. J. Plank. 2010. Turn designation, sampling rate and the misidentification of power laws in movement path data using maximum likelihood estimates. [doi:10.1007/s12080-010-0086-9]

Edwards, A. M. 2008. Using likelihood to test for Lévy flight search patterns and for general power-law distributions in nature. Journal of Animal Ecology 77:1212–1222.

Edwards, A. M., R. A. Phillips, N. W. Watkins, M. P. Freeman, E. J. Murphy, V. Afanasyev, S. V. Buldyrev, M. G. E. da Luz, E. P. Raposo, H. E. Stanley, and G. M. Viswanathan. 2007. Revisiting Lévy flight search patterns of wandering albatrosses, bumblebees and deer. Nature 449:1044–1049.

Focardi, S., P. Montanaro, and E. Pecchioli. 2009. Adaptive Lévy walks in foraging fallow deer. PLoS ONE 4:e6587.

Fritz, H., S. Said, and H. Weimerskirch. 2003. Scale-dependent hierarchical adjustments of movement patterns in a long-range foraging seabird. Proceedings of the Royal Society B 270:1143–1148.

Humphries, N. E., et al. 2010. Environmental context explains Lévy and Brownian movement patterns of marine predators. Nature 465:1066–1069.

Mårell, A., J. P. Ball, and A. Hofgaard. 2002. Foraging and movement paths of female reindeer: insights from fractal analysis, correlated random walks, and Lévy flights. Canadian Journal of Zoology 80:854–865.

Plank, M. J., and E. A. Codling. 2009. Sampling rate and misidentification of Lévy and non-Lévy movement paths. Ecology 90:3546–3553.

Ramos-Fernández, G., J. L. Mateos, O. Miramontes, G. Cocho, H. Larralde, and B. Ayala-Orozco. 2004. Lévy walk patterns in the foraging movements of spider monkeys (Ateles geoffroyi). Behavioral Ecology and Sociobiology 55:223–230.

Reynolds, A. M. 2009. Lévy flight patterns are predicted to be an emergent property of a bumblebees' foraging strategy. Behavioral Ecology and Sociobiology 64:19–23.

Reynolds, A. M., D. R. Reynolds, A. D. Smith, G. P. Svensson, and C. Löfstedt. 2007a. Appetitive flight patterns of male Agrotis segetum moths over landscape scales. Journal of Theoretical Biology 245:141–149.

Reynolds, A. M., A. D. Smith, R. Menzel, U. Greggers, D. R. Reynolds, and J. R. Riley. 2007b. Displaced honey bees perform optimal scale-free search flights. Ecology 88:1955–1961.

Reynolds, A. M., J. L. Swain, A. D. Smith, A. P. Martin, and J. L. Osborne. 2009. Honeybees use a Lévy flight search strategy and odour-mediated anemotaxis to relocate food sources. Behavioral Ecology and Sociobiology 64:115–123.

Turchin, P., F. J. Odendall, and M. D. Rausher. 1991. Quantifying insect movement in the field. Environmental Entomology 20:955–963.

White, E. P., B. J. Enquist, and J. L. Green. 2008. On estimating the exponent of power-law frequency distributions. Ecology 89:905–912.