Composite Brownian Walks Best Describe Livestock Mobility Patterns across Species

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Abstract

In quantitative studies on animal movements and foraging, there has been ongoing debate over the relevance of Lévy walk and related stochastic models to understanding mobility patterns of diverse organisms. In this study, we collected and analyzed a large number of GPS logs that tracked the movements of different livestock species in northwestern Kenya. Statistically principled analysis has only found scant evidence for the scale-free movement patterns of the Lévy walk and its variants. Instead, the analysis has given strong support to composite exponential distributions (composite Brownian walks) as the best description of livestock movement trajectories in a wide array of parameter settings. Furthermore, this support has become overwhelming and near universal under an alternative criterion for model selection. These results illuminate the multi-scale and multi-modal nature of livestock spatial behavior. They also have broader theoretical and empirical implications for the related literature.

Keywords

Lévy walk; composite Brownian walk; foraging; searching; mobility; GPS; mobility; Kenya

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Introduction

Over the past two decades, quantitative studies on animal movements and foraging have expanded considerably. Apart from the huge advancement in tracking technologies, one of the driving forces behind this expansion has been the ongoing debate over Lévy flight/walk and related stochastic models in describing these movements [1-3]. A Lévy walk is a class of random walk where a walker's step length at each move is drawn from a fat-tailed power law distribution with a certain range of exponent (see the next section) [4]. Ever since the seminal, somewhat controversial works by Viswanathan and his colleagues [5, 6], arguments and counter-arguments concerning the ability of this model to describe the mobility patterns of moving organisms have brought a great variety of theoretical [7-13], methodological [14-17], and empirical works [18-20].

In this debate, a wide array of organisms has been reported to follow Lévy walk or its variants (e.g., 'truncated' Lévy walk). Examples include bacteria [21], cells [22], mussels [23], insects [6, 24], marine predators [18, 19], herbivores [6], primates [25, 26], and even ancient extinct species [27]. Human beings are no exception [2, 3, 28]. Lévy walk models have been considered to represent the movements of such diverse populations as African hunter-gatherers [29, 30], Peruvian anchovy fishermen [31], US travellers [32], and UK burglars [33]. Although strong counter-examples always exist [14, 15], mounting evidence seems to suggest that diverse living organisms actually adopt Lévy walk-like scale-free mobility patterns, especially in harsh environments with few resources [6, 18].

In the study reported here, we examined the applicability of these patterns to yet another group of organisms: livestock animals such as cattle, goats, sheep, and camels. These domesticated herbivores have had close relationships with human beings for thousands of years. Naturally, one might expect some characteristic traits that carry a trace of this long history in the livestock movements. Moreover, livestock animals are major contributors to human livelihood as well as its disruption, for example, by carrying deadly diseases such as sleeping sickness. Thus, seeking formal descriptions of livestock mobility has wider practical implications.

In the recent literature on animal husbandry and pastoralism, livestock movements have been actively tracked with GPS devices [34-42]. Most of these

studies, however, have not been done from the dynamic perspective that pursues direct representations of the spatio-temporal behavior of livestock animals. Rather, obtained GPS data points are quickly aggregated into static summary variables such as a total walked distance and an average speed for use in ensuing statistical analyses. Furthermore, one experimental study that explicitly investigated Lévy walks in the context of goat movements [43] suffers from a common methodological flaw that affects many other works. That is, in fitting the power law to mobility data, this study applied linear regression to the log-transformed distribution of step lengths. Such an operation, which tends to cause a systematic bias in an estimated parameter, has largely been discredited [14, 17, 44]. This casts a serious doubt on the assumed presence of Lévy patterns that the authors derived from their analyses.

Thus, a significant gap still exists regarding the relevance of the Lévy walk or any other stochastic representations to livestock mobility patterns. We aim to bridge this gap by analyzing a large dataset on livestock movements in a statistically principled manner.

Materials and Methods

We tracked livestock movements during daily herding in northwest Kenya from 2012 to 2014. The study area surrounds a small town named Tangulbei (0°48'18.3"N 36°16'48.3"E) in the Rift Valley Province, and 20 Pokot households residing there collaborated with the data collection. In each collection trial, in each household, we attached a GPS logger (Holux wireless M-241) to one selected animal in a livestock corral in the early morning and released the individual. The device was retrieved in the same place in the evening after several (mostly one or two) days of daily herding. For the 20 households, we repeated such a trial 151 times (excluding failed ones such as accidental abortion of tracking) in different periods of time with the total number of days approaching 200. Most of the trials occurred from October 2012 to February 2013, but some of the data was taken as late as in June 2014. The tracked individuals, 42 in total, consists of 20 goats, 11 cattle, 10 calves, and 1 camel. The GPS loggers recorded their locations at 5-second intervals. The total number of the data points obtained amounts to 2,126,457.

We then converted this huge dataset into a collection of step length distributions.

For each set of the GPS logs that were obtained in each data collection trial, we first extracted its subsets according to the date and the time of measurement. Regarding the measurement time, we used only data points that were recorded during 5:00-17:00, as typical daily herding take places within this duration. For each daily subset of data thus extracted, we further discretized the location history of an individual animal into a series of movement 'steps'. Following a prominent work on Tanzanian hunter-gatherers [30], we define a movement step as a geodesic line segment between two locations on the recorded trajectory (1) whose length is longer than some minimum threshold value (Δx_{min}) and (2) along which change in the direction of the individual does not exceed some maximum threshold angle ($\Delta\theta_{max}$). Following the same work again, we also investigated the 'outbound' case (δ_{out}=1) where a movement trajectory only consists of locations between the first data point (x_0) and the point farthest away from x_0, in addition to the 'round-trip' case (δ_{out}=0) where all the data points are used. The three parameters (Δx_{min}, $\Delta\theta_{max}$, and δ_{out}) were systematically manipulated ({1.0, 2.0, …, 9.0, 10.0} for Δx_{min}; {5.0, 10.0, …, 85.0, 90.0} for $\Delta\theta_{max}$; {0, 1} for δ_{out}; thus 10 x 18 x 2 = 360 combinations in total) in order to obtain robust results.

For each parameter combination, we derived step length distributions from daily livestock trajectories and repeated model estimation/selection procedures against each of these distributions to obtain an overall distribution of best-fit models. The following random walk models, where L denotes the random variable for step lengths and l its realization, were investigated as possible descriptions of livestock mobility patterns. This expanded set of models ensures stringent assessment of the validity of a given model [15, 30].

Power Law

$$P(L=l)=\frac{\mu-1}{l_{\min}^{1-\mu}}l^{-\mu} \tag{1}$$

Truncated Power Law

$$P(L=l)=\frac{\mu-1}{l_{\min}^{1-\mu}-l_{\max}^{1-\mu}}l^{-\mu} \tag{2}$$

Exponential Distribution (Brownian)

$$P(L=l)=\lambda e^{-\lambda(l-l_{\min})} \tag{3}$$

Composite Exponential Distributions (Composite Brownian)

$$\begin{aligned} P(L=l)&=\sum_{j=1}^{k} p_j \lambda_j e^{-\lambda_j(l-l_{\min})} \\ p_k&=1-\sum_{j=1}^{k-1} p_j \end{aligned} \tag{4}$$

We estimated two-composite (k=2), three-composite (k=3), and four-composite (k=4) exponential distributions.

Among the parameters that appear in the above equations, the left and the right truncation cutoffs ($l_{\min}$ and $l_{\max}$) were just assigned the minimum and the maximum values of a given step length distribution, respectively. Regarding the other parameters, we employed the standard, mostly reliable maximum-likelihood estimation (MLE) [14, 17, 44]. We then calculated the likelihood of a given distribution under each of the estimated models and, considering the number of free-moving parameters, computed Akaike's information criterion (AIC) for each model. The random walk model that minimizes AIC can be considered as the model that best fits the given livestock trajectory.

Results

The results of these analyses give very strong support to the composite Brownian walks against the Lévy models (the power law and the truncated power law) across livestock species. Figure 1 illustrates the overall picture. Each panel in the figure is a heat map that displays relative frequencies (0.0-1.0) of a given type of model becoming the best-fit model in various combinations of Δx_{min} and $\Delta\theta_{max}$. The candidate models are grouped into either composite Brownian walks [panels (a) and (c)] or Lévy walks (power law or truncated power law) [(b) and (d)]. The simple exponential distribution is omitted because of the negligible support it received. Results are shown for both the round-trip (δ_{out}=0) cases [(a) and (b)] and the outbound (δ_{out}=1) cases [(c) and (d)]. As the figure shows, in a broad range of parameter combinations, one of the composite Brownian models (k=2, 3, or 4 in equation (4)) minimized AIC for the greater part of step length distributions

(typically more than 85%; total average 82.6%). This support became weak only in limited conditions, notably those with Δx_{min}=1.0. In these cases, the Lévy models, mostly the truncated version, best described the majority of livestock trajectories (total average 17.4%).

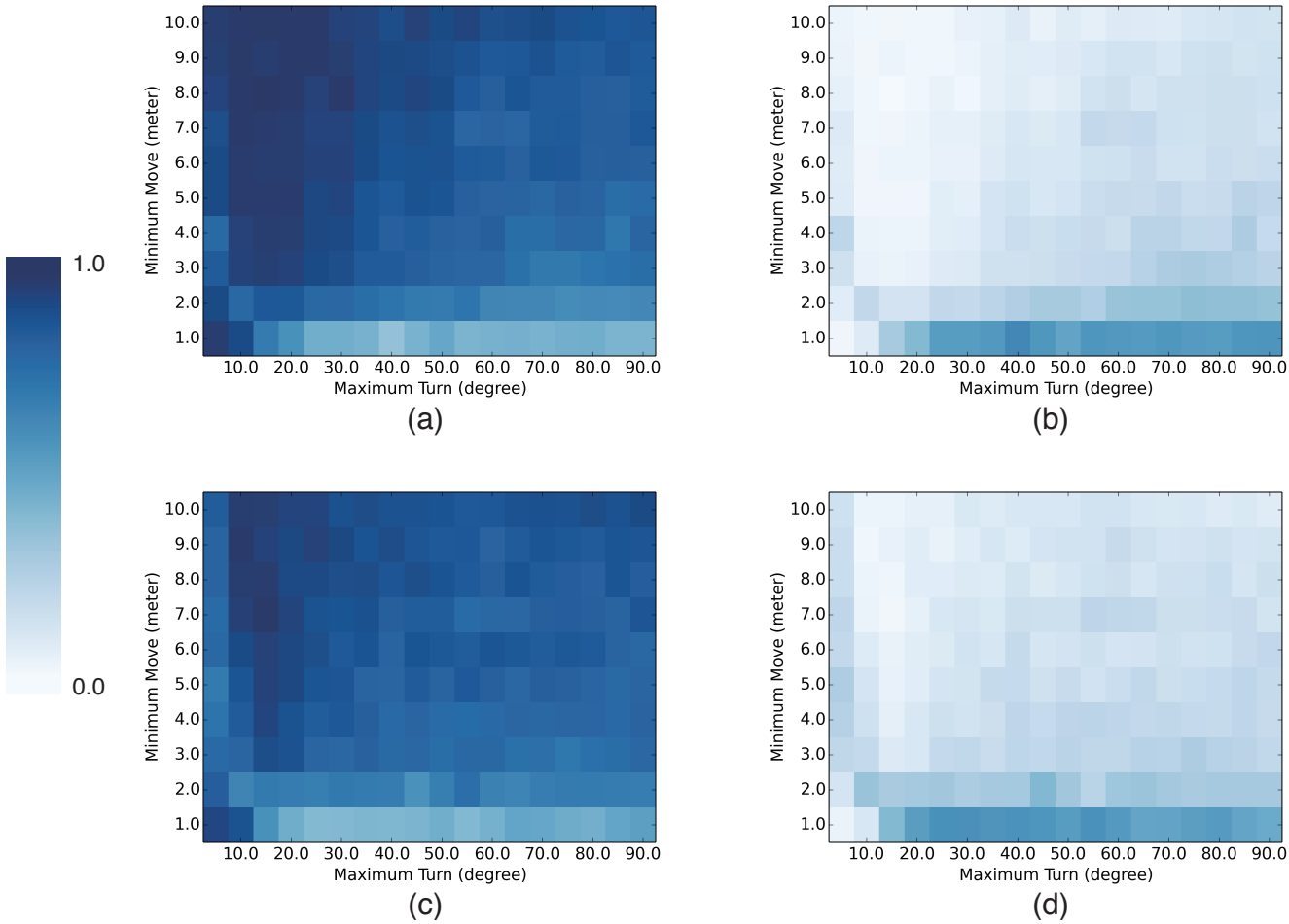


Figure 1. Heat maps showing best-fit frequencies

The x-axes denote changes in $\Delta\theta_{max}$, whereas the y-axes denote changes in Δx_{min}. (a) Composite Brownian walks (k=2, 3, or 4) in round-trips (δ_{out}=0); (b) Lévy walks (power law or truncated power law) in round-trips; (c) composite Brownian walks in outbound trips (δ_{out}=1); (d) Lévy walks in outbound trips.

Moreover, even this limited support for the Lévy walks becomes untenable if one changes ways of perceiving the 'best' model. Figure 2 illuminates this point. Here, we computed, for each combination of Δx_{min} and $\Delta\theta_{max}$, the frequency in which a given type of model maximized the likelihood of each step-length distribution, rather than minimized the AIC. In other words, in determining best-fit models, we now focus on the accuracy of a model's description of data regardless of the number of parameters. As the figure clearly demonstrates, this change has made the noted contrast even more pronounced. The support for the composite Brownians has become overwhelming (total average 98.0%) in any combination of parameters, while that for the Lévys has been rendered almost negligible (1.9%).

Two graphs in Figure 3 give examples of detailed composition of best-fit models (selected in the AIC criterion) in each combination of Δx_{min} and $\Delta\theta_{max}$. It shows that the relative strength of the models can change considerably depending on the parameters even in the same group of models. Among the composite Brownian walks, the tendency is that step-length distributions that were derived with larger $\Delta\theta_{max}$, that is, coarser data, are likely to support simpler models with smaller k values (k=2 or 3). Similarly, the truncated power law is more likely to be selected for larger $\Delta\theta_{max}$, even though the overall level of this frequency is critically dependent on the other parameter, Δx_{min}, as the two graphs demonstrate.

Regarding parameter estimation, Table 1 shows examples of MLE parameters computed for a composite Brownian model. The estimation was done against the round-trip data (δ_{out}=0) with Δx_{min}=5.0 and $\Delta\theta_{max}$=30.0. The 3-composite Brownian walk (k=3), for which these parameters were estimated, best described the majority of the step-length distributions (125 out of 193) obtained in this combination of δ_{out}, Δx_{min}, and $\Delta\theta_{max}$. In the table, $1/\lambda_j$ (j=1,2,3) gives a component scale (in meters) for an animal's step length and p_j denotes its contribution to that length (see Equation (4)). Although one can easily see substantial individual variations, the parameters also contain useful information on general properties of livestock mobility. For example, one can find that the average move of each animal more or less consists of the following distinctive scales of movement (note that the estimated parameters are relative to l_{min}, which, given Δx_{min} is no less than 5.0 meters): several-hundred meters of relatively infrequent long-range jump, around 10.0 meters of short-range move, and relatively frequent displacement of slightly above 5.0 meters.

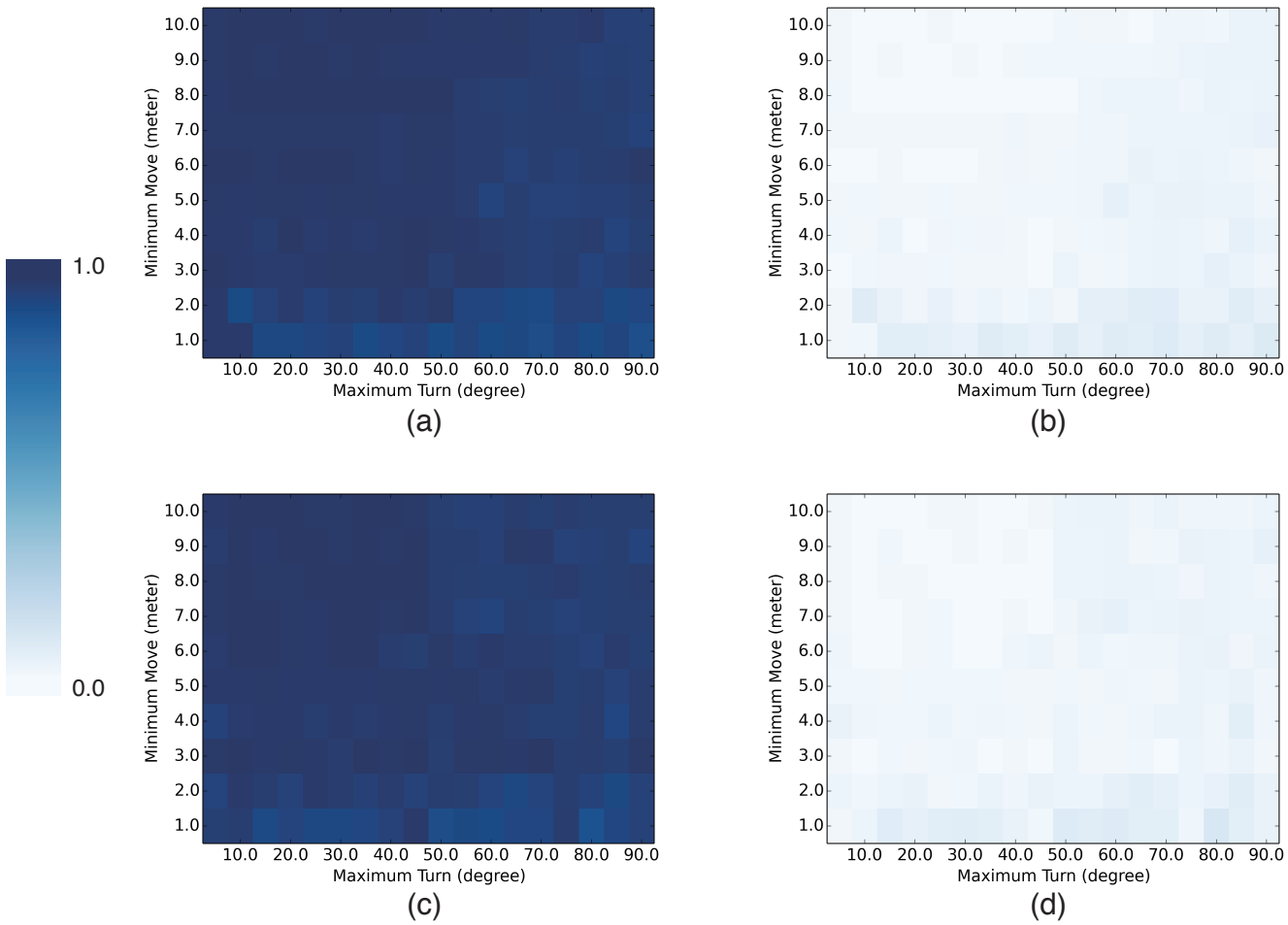
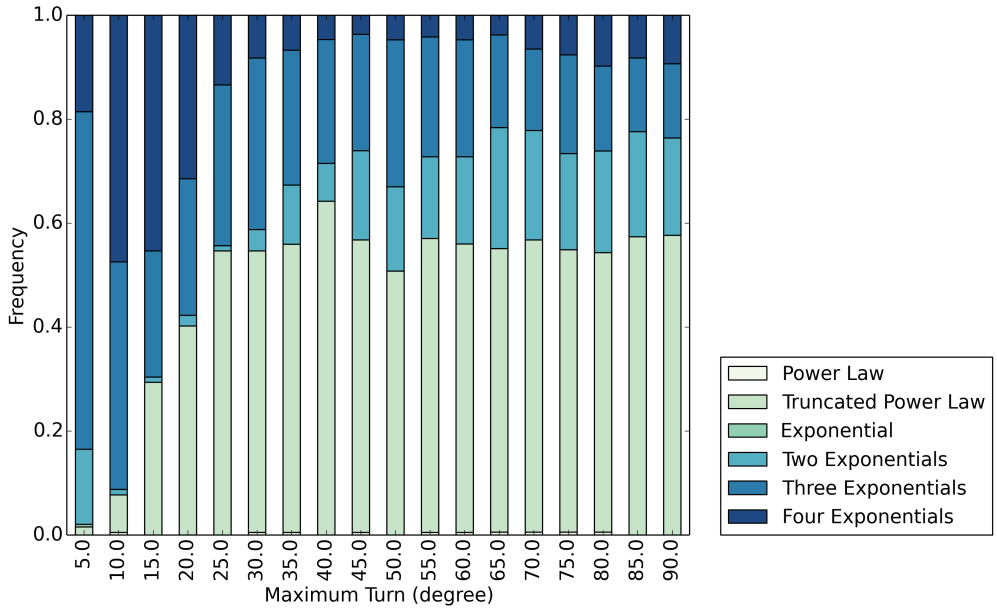
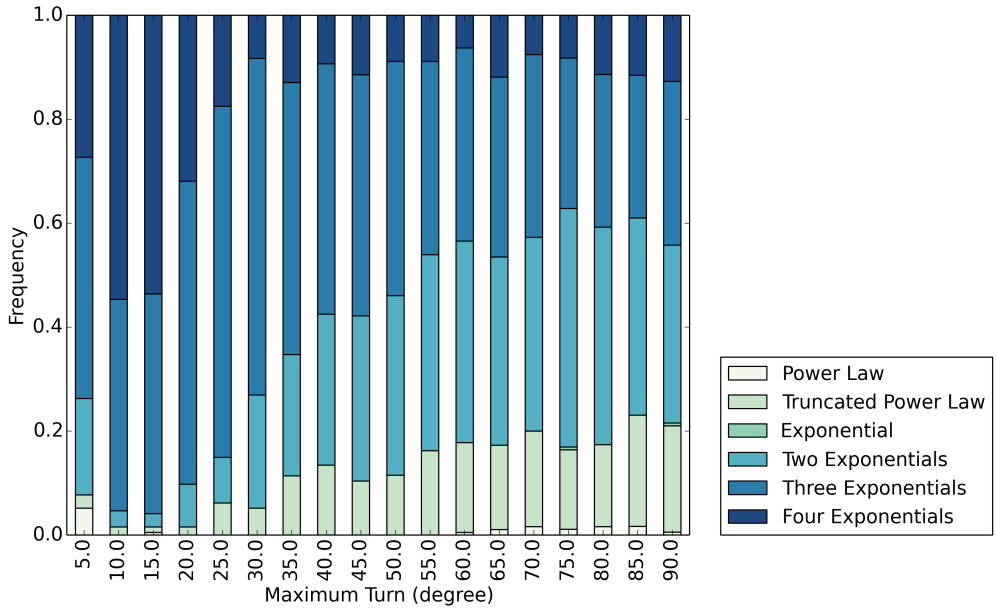


Figure 2. Heat maps showing best-fit frequencies (maximum likelihood)

The same as Figure 1, except that the best-fit criterion is now changed to the maximum likelihood criterion. (a) Composite Brownian walks (k=2, 3, or 4) in round-trips (δ_{out}=0); (b) Lévy walks (power law or truncated power law) in round-trips; (c) composite Brownian walks in outbound trips (δ_{out}=1); (d) Lévy walks in outbound trips.



(a)



(b)

Figure 3. Frequency distributions of best-fit models

Each bar represents a stacked histogram that displays the frequency of each candidate model becoming the best-fit model for a given value of $\Delta\theta_{max}$. (a) Δx_{min}=1.0; (b) Δx_{min}=5.0. Both were computed from the round-trip data (δ_{out}=0).

Table 1. Parameters estimated for composite Brownian walks (k=3)

Livestock	Date	n	p1	p2	p3	1/λ1(m)	1/λ2 (m)	1/λ3 (m)	Avg scale (m)
Calf	2012/10/15	85	0.264	0.339	0.397	24.090	2.440	0.363	7.330
Calf	2012/10/23	89	0.083	0.286	0.631	51.469	2.099	0.624	5.261
Calf	2012/11/9	66	0.345	0.420	0.235	35.675	3.217	0.328	13.747
Calf	2012/11/21	42	0.243	0.645	0.111	70.154	2.318	0.037	18.562
Calf	2013/2/12	86	0.106	0.220	0.674	106.398	6.470	0.771	13.255
Calf	2013/2/15	223	0.063	0.380	0.557	31.153	1.731	0.332	2.808
Calf	2013/2/19	41	0.166	0.467	0.367	170.733	2.030	0.302	29.464
Cow	2012/10/17	85	0.132	0.190	0.678	149.458	11.836	0.816	22.508
Cow	2012/10/23	39	0.116	0.280	0.604	450.200	6.647	0.778	54.483
Cow	2012/11/6	65	0.105	0.163	0.732	256.083	23.468	1.266	31.530
Cow	2012/11/17	35	0.069	0.597	0.334	127.137	6.463	0.294	12.701
Cow	2013/2/22	36	0.191	0.453	0.356	599.650	4.493	0.373	116.818
Goat	2012/10/15	89	0.156	0.296	0.548	279.036	5.856	0.867	45.638
Goat	2012/10/25	51	0.187	0.245	0.568	339.213	12.777	1.323	67.228
Goat	2012/11/10	68	0.205	0.364	0.430	52.467	1.675	0.242	11.485
Goat	2012/11/15	134	0.098	0.511	0.391	191.515	3.344	0.428	20.632
Goat	2012/11/22	20	0.070	0.426	0.504	301.475	24.355	0.696	31.691
Goat	2012/11/25	59	0.346	0.138	0.515	252.115	20.263	1.907	91.084
Goat	2012/12/6	24	0.399	0.401	0.200	171.550	4.062	0.240	70.106
Goat	2013/1/2	101	0.094	0.523	0.383	240.674	2.981	0.456	24.337
Goat	2013/1/9	23	0.345	0.213	0.442	516.854	10.494	1.947	181.298
Goat	2013/2/11	150	0.061	0.248	0.691	134.968	7.028	0.874	10.591
Goat	2013/2/12	63	0.213	0.438	0.349	137.715	3.706	0.402	31.083
Goat	2013/2/15	21	0.112	0.211	0.677	338.591	9.704	1.317	40.718
Goat	2013/2/16	66	0.194	0.257	0.548	112.442	6.012	0.565	23.717
Goat	2013/2/20	20	0.157	0.679	0.164	370.353	2.467	0.169	59.982
Goat	2013/2/22	123	0.199	0.549	0.252	214.757	2.166	0.298	44.036
Goat	2014/6/12	44	0.082	0.161	0.757	498.789	23.330	1.913	46.020
Goat	2014/6/14	117	0.161	0.530	0.309	87.525	4.578	0.541	16.659

Note: The table shows examples of MLE parameters of composite Brownian walks. These were computed for the round-trip tracks (δ_{out}=0) in the setting of Δx_{min}=5.0 and $\Delta\theta_{max}$=30.0. Out of 193 step-length distributions derived from these tracks, 125 support the 3-composite Brownian walk as their best description. The table details information on 32 cases extracted from these 125 cases. n denotes the number of move steps in the corresponding step-length distribution, p_j and λ_j (j=1,2,3) the MLE parameters computed against that distribution (see Equation (4)), and 'Avg scale' the average mobility scale (in meters) of the animal concerned that is computed from these parameters.

Discussion

Given the accumulation of studies that indicate the prevalence of Lévy walks in organism movements, the above results, which clearly suggest otherwise, might seem somewhat surprising. However, these results allow straightforward biological and ecological interpretations. The robust and widespread support given to the composite Brownian walks confirms a simple fact: moving organisms have several distinctive modes of spatial behavior. Livestock animals rest, graze, walk and run during daily herding [36, 40, 45]. These animals sometimes intensively exploit nearby resources while they extensively search for distant pasture and water at other times [34]. The composite Brownian models and their estimated parameters might contain useful quantitative information on these different modes of behavior observed at multiple spatial scales. These findings are also relevant to formal modeling of animal movements and foraging [10-12, 46].

In a much broader context, there are two ways of interpreting this apparent deviation from the assumed ubiquity of Lévy walks. Firstly, one can argue that the Lévy-type scale-free mobility pattern is not ubiquitous at all because many of the previous works that gave support to this pattern did so in a methodologically flawed manner. In fact, several high-profile studies on 'Lévy foraging hypotheses' lost ground in re-examination of their findings based on statistically enhanced approaches [5, 14, 15, 23]. These approaches, including model estimation based on MLE and model selection in a sufficiently large set of candidate models, also gave the present study a solid methodological foundation.

Moreover, we also showed that empirical support to Lévy walks could critically depend on contingent aspects of a model selection criterion. In the case of AIC, the truncated Lévy walk occasionally beat other competing models mostly because of the fewer number of parameters it has rather than the inherent accuracy of data description. Although AIC is one of the established statistics in model selection and has also been widely employed in the preceding studies on organism movements, it is not necessarily an obvious choice. Other selection criteria such as those based on the likelihood ratio should also be tried in selecting best-fit models [44, 47].

On the other hand, one can also claim that there is something special about domesticated animals, which might contribute to any systematic discrepancy in movement patterns between livestock and other 'wild' organisms. For example,

livestock animals, even if extensively herded under open access or communal land tenure regimes, typically have some limited grazing ranges ('herding radius') set by their owners for management or other social purposes (e.g., conflict avoidance) [36, 40, 48, 49]. These ranges, normally encircling main homesteads and water points, can effectively constrain the inherent mobility of the animals concerned. Thus, possibly except in extreme circumstances such as severe drought, these animals might be unlikely to show extraordinarily long jumps in their movement trajectories, which characterize scale free mobility patterns such as the Lévy walk. The increasing trend toward sedentarization in the contemporary pastoralism [50] seems to make these considerations even more important.

The two interpretations discussed so far are not mutually exclusive and both are worth exploring by further analysis. Sound methodologies combined with broad consideration of causal mechanisms can lead to balanced assessment of movement patterns of living organisms.

Conclusions

We carried out a comprehensive investigation into a large dataset on livestock mobility and obtained highly robust, clear results concerning stochastic representation of livestock movements. However, these are only a part of what can be derived from our dataset. First of all, the analysis can be made more rigorous with additional application of statistical procedures. For example, before the model selection, we can screen candidate random walk models by means of some goodness-of-fit test such as the Kolmogorov-Smirnov test [44]. We can also extend the analysis to other aspects of livestock mobility, including diffusion statistics, velocity statistics, directional persistency and bias, and distributions of flight times and waiting times. These will help us obtain more complete stochastic descriptions of livestock movements, which are then amenable to the whole set of mathematical tools provided by random walk theory [2, 51, 52].

Beyond the framework of random movements and foraging, the inquiry can be directed more deeply into livestock spatio-temporal behavior and its driving mechanism. The first task along this direction will be to examine possible effects of species and seasonal differences on various aspects of livestock mobility. We will also greatly benefit from the use of other data such as vegetation distributions

derived from satellite imagery [53-56] since these data enable us to place livestock movement trajectories in a proper spatial context. We will continue to work on the livestock mobility dataset from these diverse angles.

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Author Contributions

TS conceived the study; NI collected and provided the data; TS and LS planned, coded and performed the analysis of the data; TS wrote the paper.

References

1. Pyke GH. Understanding movements of organisms: it's time to abandon the Lévy foraging hypothesis. Methods in Ecology and Evolution. 2015;6(1):1-16. doi: 10.1111/2041-210X.12298.

2. Zaburdaev V, Denisov S, Klafter J. Lévy walks. Reviews of Modern Physics. 2015;87(2):483-530.

3. Viswanathan GM, da Luz MGE, Raposo EP, Stanley HE. The physics of foraging : an introduction to random searches and biological encounters. Cambridge ; New York: Cambridge University Press; 2011. xiii, 164 p. p.

4. Tsallis C. Lévy distributions. Physics World. 1997;10:42-5.

5. Viswanathan GM, Afanasyev V, Buldyrev SV, Murphy EJ, Prince PA, Stanley HE. Levy flight search patterns of wandering albatrosses. Nature. 1996;381(6581):413-5.

6. Viswanathan GM, Buldyrev SV, Havlin S, da Luz MGE, Raposo EP, Stanley HE. Optimizing the success of random searches. Nature. 1999;401(6756):911-4.

7. Bartumeus F, Catalan J, Fulco UL, Lyra ML, Viswanathan GM. Optimizing the encounter rate in biological interactions: Levy versus Brownian strategies. Phys Rev Lett. 2002;88(9):097901. doi: 10.1103/PhysRevLett.88.097901.

PubMed PMID: 11864054.

8. Bartumeus F, da Luz MGE, Viswanathan GM, Catalan J. Animal search strategies: a quantitative random-walk analysis. Ecology. 2005;86(11):3078-87. doi: 10.1890/04-1806.

9. James A, Plank MJ, Brown R. Optimizing the encounter rate in biological interactions: Ballistic versus Levy versus Brownian strategies. Phys Rev E Stat Nonlin Soft Matter Phys. 2008;78(5 Pt 1):051128. doi: 10.1103/PhysRevE.78.051128. PubMed PMID: 19113116.

10. Plank MJ, James A. Optimal foraging: Lévy pattern or process? Journal of The Royal Society Interface. 2008;5(26):1077-86. doi: 10.1098/rsif.2008.0006.

11. Benhamou S. How Many Animals Really Do the Lévy Walk? Ecology. 2007;88(8):1962-9.

12. Lomholt MA, Tal K, Metzler R, Joseph K. Lévy strategies in intermittent search processes are advantageous. Proceedings of the National Academy of Sciences. 2008;105(32):11055-9. doi: 10.1073/pnas.0803117105.

13. Boyer D, Miramontes O, Ramos-Fernández G, Mateos JL, Cocho G. Modeling the searching behavior of social monkeys. Physica A: Statistical Mechanics and its Applications. 2004;342(1–2):329-35. doi: http://dx.doi.org/10.1016/j.physa.2004.04.091.

14. Edwards AM, Phillips RA, Watkins NW, Freeman MP, Murphy EJ, Afanasyev V, et al. Revisiting Levy flight search patterns of wandering albatrosses, bumblebees and deer. Nature. 2007;449(7165):1044-8. doi: http://www.nature.com/nature/journal/v449/n7165/suppinfo/nature06199_S1.html.

15. Jansen VAA, Mashanova A, Petrovskii S. Comment on "Lévy Walks Evolve Through Interaction Between Movement and Environmental Complexity". Science. 2012;335(6071):918. doi: 10.1126/science.1215747.

16. Humphries NE, Weimerskirch H, Sims DW. A new approach for objective identification of turns and steps in organism movement data relevant to random walk modelling. Methods in Ecology and Evolution. 2013;4(10):930-8. doi: 10.1111/2041-210X.12096.

17. White EP, Enquist BJ, Green JL. On estimating the exponent of power-law frequency distributions. Ecology. 2008;89(4):905-12. doi: 10.1890/07-1288.1.

18. Humphries NE, Queiroz N, Dyer JRM, Pade NG, Musyl MK, Schaefer KM, et al. Environmental context explains Lévy and Brownian movement patterns of marine predators. Nature. 2010;465(7301):1066-9. doi: http://www.nature.com/nature/journal/v465/n7301/suppinfo/nature09116_S1.html.

19. Sims DW, Southall EJ, Humphries NE, Hays GC, Bradshaw CJA, Pitchford JW, et al. Scaling laws of marine predator search behaviour. Nature. 2008;451(7182):1098-102. doi: http://www.nature.com/nature/journal/v451/n7182/suppinfo/nature06518_S1.html.

20. Bartumeus F, Peters F, Pueyo S, Marrasé C, Catalan J. Helical Lévy walks: Adjusting searching statistics to resource availability in microzooplankton. Proceedings of the National Academy of Sciences. 2003;100(22):12771-5. doi: 10.1073/pnas.2137243100.

21. Ariel G, Rabani A, Benisty S, Partridge JD, Harshey RM, Be'er A. Swarming bacteria migrate by Levy Walk. Nat Commun. 2015;6. doi: 10.1038/ncomms9396.

22. Harris TH, Banigan EJ, Christian DA, Konradt C, Tait Wojno ED, Norose K, et al. Generalized Levy walks and the role of chemokines in migration of effector CD8+ T cells. Nature. 2012;486(7404):545-8. doi: http://www.nature.com/nature/journal/v486/n7404/abs/nature11098.html -supplementary-information.

23. de Jager M, Weissing FJ, Herman PMJ, Nolet BA, van de Koppel J. Lévy Walks Evolve Through Interaction Between Movement and Environmental Complexity. Science. 2011;332(6037):1551-3. doi: 10.1126/science.1201187.

24. Reynolds AM, Leprêtre L, Bohan DA. Movement patterns of Tenebrio beetles demonstrate empirically that correlated-random-walks have similitude with a Lévy walk. Scientific Reports. 2013;3:3158. doi: 10.1038/srep03158.

25. Boyer D, Ramos-Fernández G, Miramontes O, Mateos JL, Cocho G, Larralde H, et al. Scale-free foraging by primates emerges from their interaction with a complex environment. Proceedings of the Royal Society B: Biological Sciences. 2006;273(1595):1743-50. doi: 10.1098/rspb.2005.3462. PubMed PMID: PMC1634795.

26. Ramos-Fernández G, Mateos J, Miramontes O, Cocho G, Larralde H, Ayala-Orozco B. Lévy walk patterns in the foraging movements of spider monkeys

(Ateles geoffroyi). Behavioral Ecology and Sociobiology. 2004;55(3):223-30. doi: 10.1007/s00265-003-0700-6.

27. Sims DW, Reynolds AM, Humphries NE, Southall EJ, Wearmouth VJ, Metcalfe B, et al. Hierarchical random walks in trace fossils and the origin of optimal search behavior. Proceedings of the National Academy of Sciences. 2014;111(30):11073-8. doi: 10.1073/pnas.1405966111.

28. Baronchelli A, Radicchi F. Lévy flights in human behavior and cognition. Chaos, Solitons & Fractals. 2013;56(0):101-5. doi: http://dx.doi.org/10.1016/j.chaos.2013.07.013.

29. Brown C, Liebovitch L, Glendon R. Lévy Flights in Dobe Ju/'hoansi Foraging Patterns. Hum Ecol. 2007;35(1):129-38. doi: 10.1007/s10745-006-9083-4.

30. Raichlen DA, Wood BM, Gordon AD, Mabulla AZP, Marlowe FW, Pontzer H. Evidence of Lévy walk foraging patterns in human hunter–gatherers. Proceedings of the National Academy of Sciences. 2014;111(2):728-33. doi: 10.1073/pnas.1318616111.

31. Bertrand S, Bertrand A, Guevara-Carrasco R, Gerlotto F. Scale-invariant movements of fishermen: the same foraging strategy as natural predators. Ecological Applications. 2007;17(2):331-7. doi: 10.1890/06-0303.

32. Brockmann D, Hufnagel L, Geisel T. The scaling laws of human travel. Nature. 2006;439(7075):462-5. doi: http://www.nature.com/nature/journal/v439/n7075/suppinfo/nature04292_S1.html.

33. Johnson SD. How do offenders choose where to offend? Perspectives from animal foraging. Legal and Criminological Psychology. 2014;19(2):193-210. doi: 10.1111/lcrp.12061.

34. Adriansen HK, Nielsen TT. The geography of pastoral mobility: A spatio-temporal analysis of GPS data from Sahelian Senegal. GeoJournal. 2005;64(3):177-88. doi: 10.1007/s10708-005-5646-y.

35. Bertiller MB, Ares JO. Sheep Spatial Grazing Strategies at the Arid Patagonian Monte, Argentina. Rangeland Ecology & Management. 2008;61(1):38-47. doi: http://dx.doi.org/10.2111/07-130.1.

36. Butt B. Seasonal space-time dynamics of cattle behavior and mobility among Maasai pastoralists in semi-arid Kenya. Journal of Arid Environments. 2010;74(3):403-13. doi: http://dx.doi.org/10.1016/j.jaridenv.2009.09.025.

37. Butt B. Pastoral resource access and utilization: Quantifying the spatial and temporal relationships between livestock mobility, density and biomass availability in southern Kenya. Land Degradation & Development. 2010;21(6):520-39. doi: 10.1002/ldr.989.

38. Butt B, Shortridge A, WinklerPrins AMGA. Pastoral Herd Management, Drought Coping Strategies, and Cattle Mobility in Southern Kenya. Annals of the Association of American Geographers. 2009;99(2):309-34. doi: 10.1080/00045600802685895.

39. Feldt T, Schlecht E. Analysis of GPS trajectories to assess spatio-temporal differences in grazing patterns and land use preferences of domestic livestock in southwestern Madagascar. Pastoralism. 2016;6(1):1-17. doi: 10.1186/s13570-016-0052-2.

40. Moritz M, Soma E, Scholte P, Xiao N, Taylor L, Juran T, et al. An Integrated Approach to Modeling Grazing Pressure in Pastoral Systems: The Case of the Logone Floodplain (Cameroon). Hum Ecol. 2010;38(6):775-89. doi: 10.1007/s10745-010-9361-z.

41. Raizman EA, Rasmussen HB, King LE, Ihwagi FW, Douglas-Hamilton I. Feasibility study on the spatial and temporal movement of Samburu's cattle and wildlife in Kenya using GPS radio-tracking, remote sensing and GIS. Prev Vet Med. 2013;111(1-2):76-80. doi: 10.1016/j.prevetmed.2013.04.007. PubMed PMID: 23711505.

42. Zengeya FM, Murwira A, de Garine-Witchatitsky M. Inference of herder presence from GPS collar data of semi-free range cattle. Geocarto International. 2015;30(8):905-18. doi: 10.1080/10106049.2015.1004129.

43. de Knegt HJ, Hengeveld GM, van Langevelde F, de Boer WF, Kirkman KP. Patch density determines movement patterns and foraging efficiency of large herbivores. Behavioral Ecology. 2007;18(6):1065-72. doi: 10.1093/beheco/arm080.

44. Clauset A, Shalizi CR, Newman MEJ. Power-Law Distributions in Empirical Data. SIAM Review. 2009;51(4):661-703. doi: doi:10.1137/070710111.

45. Schlecht E, Hülsebusch C, Mahler F, Becker K. The use of differentially corrected global positioning system to monitor activities of cattle at pasture. Applied Animal Behaviour Science. 2004;85(3):185-202. doi: 10.1016/j.applanim.2003.11.003.

46. Fauchald P. Foraging in a Hierarchical Patch System. The American Naturalist. 1999;153(6):603-13. doi: 10.1086/303203.

47. Vuong QH. Likelihood Ratio Tests for Model Selection and Non-Nested Hypotheses. Econometrica. 1989;57(2):307-33. doi: 10.2307/1912557.

48. Coppolillo PB. The Landscape Ecology of Pastoral Herding: Spatial Analysis of Land Use and Livestock Production in East Africa. Hum Ecol. 2000;28(4):527-60. doi: 10.1023/A:1026435714109.

49. Coppolillo PB. Central-place analysis and modeling of landscape-scale resource use in an East African agropastoral system. Landscape Ecology. 2001;16(3):205-19. doi: 10.1023/A:1011148503303.

50. Fratkin EM, Roth EA. As pastoralists settle : social, health, and economic consequences of the pastoral sedentarization in Marsabit District, Kenya. New York: Kluwer Academic/Plenum Publishers; 2004.

51. Codling EA, Plank MJ, Benhamou S. Random walk models in biology. Journal of The Royal Society Interface. 2008;5(25):813-34. doi: 10.1098/rsif.2008.0014.

52. Turchin P. Quantitative analysis of movement : measuring and modeling population redistribution in animals and plants. Sunderland, Mass.: Sinauer Associates; 1998. ix, 396 p. p.

53. Booth DT, Tueller PT. Rangeland Monitoring Using Remote Sensing. Arid Land Research and Management. 2003;17(4):455-67. doi: 10.1080/713936105.

54. Egeru A, Wasonga O, Kyagulanyi J, Majaliwa G, MacOpiyo L, Mburu J. Spatio-temporal dynamics of forage and land cover changes in Karamoja sub-region, Uganda. Pastoralism: Research, Policy and Practice. 2014;4(1):6. PubMed PMID: doi:10.1186/2041-7136-4-6.

55. Miller BW. Using Geospatial Analysis to Assess the Influence of Land-Use Change and Conservation on Pastoralist Access to Drought Resources. Nomadic Peoples. 2015;19(1):120-45. doi: 10.3197/np.2015.190108.

56. Tueller PT. Remote sensing technology for rangeland management applications. Journal of Range Management. 1989;42(6):442-53.