Scaling law in free walking of mice in circular open fields of various diameters

Hiroto Shoji¹

Received: 21 April 2015 / Accepted: 29 November 2015 / Published online: 18 January 2016
© Springer Science+Business Media Dordrecht 2016

Abstract Open-field tests are routinely used to study locomotor activity in rodents. I studied the effects of apparatus size on rodent locomotor activity, specifically with respect to how resting and walking periods are interwoven. I explored the open-field behavior of mice utilizing circular open fields of various diameters. When the diameter of the test apparatus was greater than 75 cm, the durations of the resting and moving periods of free walking behavior obeyed bounded power-law distribution functions. I found that the properties of the scaling exponents and model selection became similar for test apparatus diameters greater than 75 cm. These results can provide a guide for the selection of the size of the test apparatus for use in the study of the open-field behavior of rodents.

Keywords Power law · Locomotor activity · Exponential distribution

1 Introduction

Open-field tests are widely used to assess qualitative and quantitative measures of general locomotor activity and willingness to explore in rodents [1]. Measurement of locomotor activity in rodents is one of the most widespread behavioral tests used in psychopharmacology, behavioral genetics, and neurobiology [1, 2].

Recently, the scale-invariant properties of animal behavior have been utilized for characterization of locomotor activity to assess the influence of genotypes or drugs [3–9]. Paulus and

Submitted to the Journal of Biological Physics on April 21, 2015

✉ Hiroto Shoji
shoji@koto.kpu-m.ac.jp

¹ Department of Physics, Graduate School of Medical Science, Kyoto Prefectural University of Medicine, Sakyo-ku, Kyoto 606-0823, Japan

Geyer [3] developed an index to characterize the behavior of drug-induced rats by temporal scaling exponents based on power laws.

Interestingly, recent studies have suggested that power-law relations appear in a wide variety of physical [10–13], social [14], and biological systems [9, 15]. How these processes are generated in termites [15] and *Escherichia coli* [9] has also been investigated by examining the fractal nature of movement patterns and by mathematical modeling, respectively.

Researchers have also examined which models best describe the exploring movement of animals. Researchers have shown that the movement patterns of bees [16, 17], jackals [18], and marine predators [19, 20] can be described by power-law models with tail exponents μ between 1 and 3. These movements are called Lévy flights or walks [21–26]. De Jager et al. [27] found that the movement patterns of blue mussel could be approximated by a Lévy walk by adopting an intrinsic composite correlated random walk (CCRW) model in which switching between different models was triggered internally, rather than externally. De Jager et al. [27] advised caution in inferring the presence of Lévy walk behavior in biological systems [28].

In terms of pharmacological or neurological effects, many researchers have reported that not only the active periods [3–8] but also the resting periods of animal behavior [4, 5, 9] are related to their frequencies and that these relations can be expressed by power laws or exponential statistical models. Nakamura et al. [4, 5] developed an index to characterize the behavior of abnormal psychiatric diseases and clock gene-deficient mice by fitting the cumulative distributions of the durations of resting and active periods of locomotor activity in mice to a power law and a simple exponential model, respectively. Shoji et al. [6] characterized the behavior of drug-induced mice by developing an index based on the concept that the durations of active periods of locomotor activity could best be fitted to combinations of exponential statistical distributions. Kafkafi et al. [7, 8] developed variations of shared exponential statistical distributions of walking speed to describe the behavior of drug-induced rats.

In this study, I considered the effect of apparatus size on locomotor activity in rodents. Nakamura et al. [4, 5] measured the locomotor activity of mice in a rectangular field 25 cm $\times$ 15 cm and concluded that the distributions of the durations of resting and active periods of locomotor activity in mice could best be fitted to power laws and simple exponential statistical models, respectively. In contrast, when the locomotor activity in mice or rats was measured in a larger apparatus, the distributions of the durations of active periods could best be fitted to combinations of two or three exponential statistical distributions. In Shoji et al. [6], we measured the locomotor activity of mice in a circular open field with a 60-cm diameter. Kafkafi et al. [7, 8] measured the walking speeds of rats in a circular open field with a 650-cm diameter.

In this study, I examined the scaling law of the distributions of the durations of resting and active periods in an open field, depending on the size of the apparatus. Utilizing circular open fields of various diameters (45, 60, 75, 90, 120, and 150 cm), I analyzed locomotor activity data for free-walking mice, capturing the data using a digital video camera, as shown in Fig. 1a. I then selected the best-fitting models from among not only simple power-law models and exponential models but also bounded power-law and Poisson statistic models. I computed the scaling exponents for the test groups depending on the test apparatus diameters.

Fig. 1 Experimental procedures. **a** Photo used for image analysis illustrating the ordinate of a mouse in an open field with a 60-cm diameter. **b** Frequency distribution of movements per 1/29.97 s (video frame) summed for ten mice for the 60-cm-diameter apparatus. Following the procedure developed by Draï et al. [30], the speed threshold between the moving and resting states was determined at 0.8 pixels for the circular open field with a 60-cm diameter by the position of the fixation point. **c** A sample of the time series of a 20-s movement step length of a mouse tested in an open field with a 60-cm diameter

2 Materials and methods

2.1 Animals

Six-week-old male C57BL/6 N mice were purchased from the Shimizu Laboratory Supplies Co., Kyoto, Japan. The mice were housed in groups of six in standard breeding cages (27 × 21 × 12 cm) with freely available food and water under a 12-h light/12-h dark cycle (lights on at 08:00). The mice were acclimatized to these conditions for 2 weeks before the tests. The experiments were performed in accordance with the National Research Council's Guidelines for the Care and Use of Mammals in Neuroscience and Behavioral Research and with the approval of the Committee for Animal Research at the Kyoto Prefectural University of Medicine.

2.2 Open-field measurements

The mice were tested once during the light phase of the photoperiodic cycle. Before the experiment, I performed the following handling treatment to prevent any psychological influences due to frustration mice feel when they do not acclimatize to a place. Between 7

and 9 days before the experiment, each mouse was handled daily for 3 min and then exposed to an environment in which observation was performed for 5 min. This protocol was followed until the day of the experiment.

On the day of the experiment, the animals were transported from the animal facility to the experimental room at least 60 min before the start of the experiment. After having its body weight measured, each mouse was placed in an open-field test apparatus to assess its locomotor activity. The test apparatus surrounded a circular open field either 45, 60, 75, 90, 120, and 150 cm in diameter. Each mouse was removed from its cage and placed at the center of the apparatus. I examined ten mice for each diameter. Figure 1a shows an example of a 60-cm circular open field and a mouse.

The experiments were performed out of the sight of the experimenter. The locomotor activity was recorded for 30 min using a video camera (HDR-CX700V; SONY, Japan). Because recording movement data for mice at a high resolution would produce very large computer files, an easy-to-use Linux program was used for processing of the output file. We developed a program in Linux for this purpose, called glana, using the C language [6, 29]. I measured the coordinates of the center of gravity of each mouse after discriminating the mouse image as $\vec{p} = (x(t), y(t))$ using the glana program. The program automatically computed the coordinates of the center of gravity of the mouse after discriminating the mouse image from the background at a high resolution (29.97 frames per second).

During a so-called stop state (i.e., when the mouse is resting), a mouse may perform many local movements, such as rearing backward and stepping sideways. Therefore, even if a mouse appears to be resting, its speed is not necessarily zero. Draï et al. [30] developed a procedure to classify a rodent's behavior as 'stop state' or 'moving state' activity. Comparing the time evolution of the walking speed of a rodent's behavior (walking freely or sleeping), they found that the inflexion point of the estimated density function of the walking speed could be interpreted as indicating the speed threshold between the 'stop state' and the 'moving state'. This procedure has been applied in other studies [6–8].

Following the procedure developed by Draï et al. [30] described above, I determined the movement threshold for the test group for each circular open-field diameter. Figure 1b shows the estimated density function of the experimental group of mice tested in the circular open field with a 60-cm diameter. I measured 1.2, 0.8, 0.6, 0.4, 0.3, and 0.2 pixels/time frame as the movement thresholds of the experimental groups of the circular open fields with 45-cm, 60-cm, 75-cm, 90-cm, 120-cm, and 150-cm diameters, respectively. Values below these thresholds were considered to indicate rest periods and values above these thresholds were considered to indicate movement periods (as indicated by the intervals separated by arrows in Fig. 1c). The gaps between the moving durations represent the resting states.

2.3 Data analysis

2.3.1 Fitting the statistical models

I counted the number of video frames to determine the lengths of the resting and moving periods, which I termed the resting and moving durations. Data were summed for ten mice for each circular open-field diameter. The rest durations and moving durations were plotted against the frequency of moving events (Figs. 2 and 3).

It is well known that the distribution of the Lévy walk takes the form of a power-law distribution with a power-law exponent between 1 and 3 [23, 24]. Thus, a power law with an exponent between 1 and 3 could be used to determine the exponents of the distributions of the rest periods and walking periods. To derive the effect in walking behavior depending on the diameters of the open field, I

Fig. 2 **a–c** Plots of frequency distributions of resting-period durations for free walking behavior in circular open fields with 45-cm (**a**), 75-cm (**b**) and 120-cm (**c**) diameters. The *dots* indicate the data obtained. The *black*, *blue*, *green*, and *red* lines indicate the fitted statistical models using Model PL ($Cx^{-\mu}$, $x \leq a$), Model PLB ($Cx^{-\mu}$, $x \in [a, b]$), Model Exp ($\lambda e^{-\lambda(x-a)}$, $x \leq a$) and Model ExpB ($\lambda e^{-\lambda x}$, $x \in [a, b]$), respectively. The values of parameters C , μ and λ were estimated and the values of a and b were set to the minimum and maximum values indicated by the data, as explained in the text. Among the models tested, Model PLB yielded the best results (data shown in Table 1). The *insets* show the log-log plots of frequency distributions and the best-fitted models

compared the power-law and exponential models using the likelihood method and model selection approach (the Akaike information criterion (AIC)) explained in Ref. [23, 24]. Here, I examined four candidate models: a simple power-law tail model (PL), a bounded power law (PLB), an exponential model (Exp) and a bounded exponential model (ExpB). The bounded versions of the power law and exponential models were tested due to lack of support for the unbounded power-law model.

The models are as follows. A simple power-law tail (PL) model has the form:

$$f(x) = Cx^{-\mu} \quad x \leq a \quad (1)$$

with a normalization constant $C = (\mu - 1)a^{\mu-1}$.

A simple exponential (Exp) model has the form:

$$f(x) = \lambda e^{-\lambda(x-a)} \quad x \leq a \quad (2)$$

A bounded power law (PLB) has the form:

$$f(x) = Cx^{-\mu} \quad x \in [a, b] \quad (3)$$

Fig. 3 **a–c** Plots of frequency distributions of active-period durations for free walking behavior in circular open fields with 45-cm (**a**), 75-cm (**b**) and 120-cm (**c**) diameters. The *dots* indicate the data obtained. The *black*, *red*, *blue*, and *green* lines indicate the fitted statistical models using Model PL, PLB, Exp, and ExpB shown in the text and in the caption for Fig. 2, respectively. Among the models tested, Model PLB yielded the best results (data shown in Table 1). The *insets* show the log-log plots of frequency distributions and the best-fitted models

Table 1 Summary of AIC values and parameters of the models fitted to data for an individual mouse

	PL: MLE for μ (95% CI)		PLB: MLE for μ (95% CI)		Exp: MLE for λ (95% CI)		Exp B: MLE for λ (95% CI)		AIC	
	G, P		G, P		G, P		G, P		PL	ExpB
Rest										
45 cm	1.17 (1.16, 1.18)	1.18 (1.17, 1.19)	0.0561 (0.0550, 0.0573)	0.0575 (0.0558, 0.0591)					-1047.5	-652.7
	299, 0.00161	232, 0.000409	196, 0.0277	211, 0.00630						
60 cm	1.21 (1.20, 1.21)	1.22 (1.20, 1.24)	0.0886 (0.064, 0.0903)	0.0866 (0.0849, 0.0894)					-889.5	-643.0
	301, 0.00142	274, 0.00391	297, 0.0188	0.0866						
75 cm	1.15 (1.14, 1.16)	1.15 (1.13, 1.16)	0.041628 (0.0382, 0.0436)	0.040628 (0.0375, 0.0423)					-783.5	-680.1
	294, 0.0242	299, 0.0109	307, 0.00714	304, 0.00679						
90 cm	1.18 (0.17, 1.19)	1.17 (1.16, 1.19)	0.053289 (0.0508, 0.0573)	0.06032 (0.0573, 0.0639)					-771.2	-663.2
	358, 0.0118	374, 0.00233	344, 0.0407	351, 0.0227						
120 cm	1.16 (1.15, 1.17)	1.17 (1.16, 1.19)	0.04893 (0.0463, 0.0501)	0.04935 (0.0451, 0.0513)					-783.3	-672.1
	364, 0.00668	374, 0.00233	349, 0.02694615	353, 0.0190						
150 cm	1.19 (1.18, 1.20)	1.19 (1.18, 1.21)	0.04932 (0.0472, 0.0520)	0.05092 (0.0482, 0.0525)					-662.2	-605.2
	375, 0.00830	383, 0.00443	374, 0.00233	377, 0.00167						
Walking										
45 cm	1.62 (1.54, 1.59)	1.61 (1.53, 1.58)	0.0568 (0.0531, 0.05)	0.0570 (0.0541, 0.0589)					-1029.1	-827.3
	159, 0.00970	213, 0.00138	232, 0.0201	232, 0.0197						
60 cm	1.57	1.56	0.0627	0.0625					-905.5	-644.3

Table 1 (continued)

	PL: MLE for μ (95% CI)		PLB: MLE for μ (95% CI)		Exp: MLE for λ (95% CI)		Exp B: MLE for λ (95% CI)		AIC	
	G, P		G, P		G, P		G, P		PL	ExpB
75 cm	(1.55, 1.58)		(1.54, 1.58)		(0.0610, 0.0645)		(0.0606, 0.0663)			
	332, 0.00305		353, 0.000905		383, 0.0283		390, 0.0109		-983.5	
	1.32		1.31		0.0601		0.0598		-992.2	-653.8
90 cm	(1.31, 1.34)		(1.29, 1.33)		(0.0579, 0.0631)		(0.0565, 0.0630)			
	371, 0.00510		401, 0.00243		356, 0.0142		362, 0.00829		-902.4	
	1.42		1.41		0.0593		0.0590		-910.5	-663.2
120 cm	(1.41, 1.43)		(1.39, 1.43)		(0.0573, 0.0622)		(0.0587, 0.0617)			
	318, 0.0202		341, 0.00892		328, 0.0277		330, 0.0199		-1002.4	
	1.40		1.40		0.0588		0.0590		-1017.3	-719.5
150 cm	(1.39, 1.41)		(1.38, 1.41)		(0.0561, 0.0612)		(0.0567, 0.0613)			
	278, 0.00988		320, 0.00357		319, 0.0429		329, 0.0150		-894.2	
	1.36		1.35		0.0574		0.0578		-916.6	-643.2
	(1.35, 1.37)		(1.34, 1.36)		(0.0553, 0.0609)		(0.0559, 0.0611)			
	346, 0.00960		421, 0.00417		328, 0.0183		334, 0.0102		-894.2	-659.2

with a normalization constant given by $C=(\mu-1)/(a^{1-\mu}-b^{1-\mu})$ for $\mu \neq 1$ and $C=1/(\log b - \log a)$ for $\mu = 1$.

A bounded exponential model (ExpB) has the form:

$$f(x) = Ae^{-\lambda x} \quad x \in [a, b] \quad (4)$$

with a normalization constant $A = \lambda/(e^{-\lambda a} - e^{-\lambda b})$.

The parameter a is the start of the tail of the data and b is the maximum allowable value of the data for the bounded models.

For each data set, the maximum likelihood estimate (MLE) of μ or λ was estimated for each model, together with 95% confidence intervals obtained using the profile likelihood ratio test [31]. The Akaike weight was considered to be the weight of evidence in favor of the model being tested [32].

Goodness-of-fit tests were performed on distributions with evidence ratios of 1.0 to determine whether the data were, in fact, consistent with the best model. The G test (likelihood ratio test) with Williams's correction was used.

2.3.2 Statistical analysis

The results obtained for the scaling exponents and their related index values among the groups, depending on the diameter of the test apparatus, were compared using the two-tailed Mann–Whitney U test. The statistical analyses were performed using SPSS 16.0 for Macintosh (SPSS Inc., Chicago, IL, USA).

3 Results and discussion

3.1 Distribution laws of resting and walking periods

Plots of the rest-step (move-step) frequency versus rest (moving) duration of free walking behavior summed for ten individual mice are shown in Figs. 2a–c (Figs. 3a–c), respectively. I found that the model with the lowest AIC values (i.e., the best model) was PLB for both periods, as shown in Figs. 2 and 3 and Table 1.

Once the best-fit model for each individual mouse was determined (Table 1), the number of individuals for each best-fit model was identified, as shown in Table 2.

Table 2 Total numbers of fitted statistical models among ten individual rest durations and walking durations

Diameter of field	Rest				Walking			
	PL	PLB	Exp	ExpB	PL	PLB	Exp	ExpB
45 cm	1	8	0	1	0	6	0	4
60 cm	0	8	0	2	0	8	0	2
75 cm	0	10	0	0	0	10	0	0
90 cm	0	10	0	0	0	10	0	0
120 cm	0	10	0	0	0	10	0	0
150 cm	0	10	0	0	0	10	0	0

Fig. 4 Change in the scaling components μ_j in the fitting functions to the plots of the rest-period durations in circular open fields. No significant differences were observed among the data sets for the different apparatus diameters

Although the total number of fitted statistical models was different for free walking in the circular open fields with 45-cm and 60-cm diameters, the frequency distributions of individual walking behavior in circular open fields with 75-cm, 90-cm, 120-cm and 150-cm diameters were best fitted by the PLB model for resting and walking periods.

Fig. 5 Change in the scaling components μ_j in the fitting functions to the plots of the active periods in circular open fields of various diameters. The number of stars indicates the statistical level of significance (*: $p \leq 0.05$, **: $p \leq 0.01$)

3.2 Scaling exponents

3.2.1 Scaling exponents of rest period

Next, I examined the scaling exponent μ_j of the frequency distribution of the rest periods of each individual mouse's free walking behavior, where j is a number identifying the individual mouse.

Figure 4 shows the ranges of μ_j . Although the means of the μ_j values were not very different, the ranges of μ_j were narrower for the 60-cm and 75-cm diameters, as is evident in Fig. 4. I compared the scaling exponent μ_j among the test groups for the different apparatus diameters. No significant differences were observed among the data sets depending on the diameter of the apparatus.

3.2.2 Scaling exponents of walking period

I examined the scaling exponent μ_j of the frequency distribution of the walking period of each individual mouse's free walking behavior. Figure 5 shows the ranges of μ_j . The abrupt transition from a large variance of μ_j values to a small variance between the 60-cm and 75-cm diameters is evident in Fig. 5. I compared the scaling exponent μ_j among the test groups for the different apparatus diameters. Significant differences were observed among the data sets depending on the diameter of the apparatus (data shown in Fig. 5).

4 Conclusions

In this study, I examined the locomotor activity of mice in circular open fields of various diameters, using the AIC to determine whether the mice performed Lévy walks (PLB with $1 \leq \mu \leq 3$). The results can be summarized by the following three points. First, the distributions of the rest periods could best be fitted by bounded power-law distribution functions with power-law exponents between 1 and 3. This finding indicates that the free walking behavior of mice belongs to an analogical class of power-law distributions, like the waiting time distributions in the exploring behavior of animals [24, 26], in human communication [14] and in neuronal avalanches [33]. Second, the moving periods of free walking behavior in circular open fields also obeyed bounded power-law models. Third, in free walking behavior in circular open fields with diameters greater than 75 cm, the range of exponents of the bounded power laws becomes narrower.

The results of this study suggest that the size of the apparatus used in open-field tests should be as large as possible to minimize the variance in the data obtained. I suggest that the diameter of the test apparatus used in open-field testing be at least ten times greater than the length of the test animal, excluding its tail, because the body sizes of the tested mice were 7.52 ± 0.44 cm, excluding their tails.

I commented on the movement thresholds for each experimental group and determined the pixels/time frame of the movement threshold for each experimental group, measured in the manner proposed by Draai et al. [8, 30]. However, I also performed the same analysis for model selection purposes using different movement thresholds. I found that the trends exhibited by the scaling law described above were the same, even if the movement threshold was twice as large or half as large; however, the start points of the tail parameter a have to be changed (data not shown).

A wide variety of approaches is currently being used to estimate the parameters in candidate models [34–36] and there has been discussion in the ecological literature concerning how the choice of methodology influences the parameter estimates [35]. Edwards et al. [24] proposed alternative robust and accurate statistical methods for this purpose, including the maximum likelihood estimation method (MLE) and the Akaike information criterion (AIC) for use in model comparisons; these methods were utilized in the present study.

It has been noted that thigmotaxis, i.e., the inclination to explore mainly the peripheral zone of a test apparatus, has an effect on the free walking behavior in a test apparatus [37] and an index related to thigmotaxis has been said to be one of the best indices available to assess the influence of drugs or genotypes on rodents' behavior [37, 38]. When too small a test apparatus is used, the influence of thigmotaxis cannot be observed but individual differences in the mobility of mice might be manifested in larger variations in the distributions. Researchers have studied this type of walking behavior, called Lambertian Lévy walking, from a theoretical perspective [36, 39]. Because the tested animals came into contact with the test apparatus each time, they were found to continue to walk while being dispersed at certain angles that may result in Lévy distributions.

Acknowledgments I would like to thank K. Hanai for his technical assistance and K. Yoshii for his helpful comments. This research was supported by JSPS KAKENHI Grant Numbers 26800225 and 15H01125.

References

1. Gould, T.D., Dao, D.T., Kovacsics, C.E.: The open field test mood and anxiety related phenotypes in mice. *Neuromethods* **42**, 1–20 (2009)
2. Meyer, J.S., Quenzer, L.F.: *Psychopharmacology: Drugs, the Brain, and Behavior*. Sinauer Associates, Inc. Publishers, Massachusetts (2005)
3. Paulus, M.P., Geyer, M.A.: Three independent factors characterize spontaneous rat motor activity. *Behav. Brain Res.* **53**, 11–20 (1991)
4. Nakamura, T., Takumi, T., Takano, A., Aoyagi, N., Yoshiuchi, K., Struzik, Z.R., Yamamoto, Y.: Of mice and men: Universality and breakdown of behavioral organization. *PLoS ONE* **3**, e2050 (2005)
5. Nakamura, T., Takumi, T., Takano, A., Hatanaka, F., Yamamoto, Y.: Characterization and modeling of intermittent locomotor dynamics in clock gene-deficient mice. *PLoS ONE* **8**, e58884 (2013)
6. Shoji, H., Nakatomi, Y., Yokoyama, C., Fukui, K., Hanai, K.: New index based on the physical separation of motion into three categories for characterizing the effect of cocaine in mice. *J. Theor. Biol.* **333**, 68–77 (2013)
7. Benjamini, Y., Lipkind, D., Horev, G., Kafkafi, N., Golani, I.: Ten ways to improve the quality of descriptions of whole-animal movement. *Neurosci. Biobehav. Rev.* **131**, 11014–11026 (2010)
8. Kafkafi, N., Mayo, C.L., Drai, D., Golani, I., Elmer, G.: Natural segmentation of the locomotor behavior of drug-induced rats in a photobeam cage. *J. Neurosci. Meth.* **109**, 111–121 (2001)
9. Matthus, F., Mommer, M.S., Curk, T., Dobnikar, J.: On the origin and characteristics of noise-induced Lévy walks of *E. coli*. *PLoS ONE* **6**, e17623 (2011)
10. Bak, P.: *How Nature Works: The Science of Self-Organized Criticality*. Springer, New York (1996)
11. Brown, J.H., Gupta, V.K., Li, B.L., Milne, B.T., Restrepo, C., West, G.B.: The fractal nature of nature: power laws, ecological complexity and biodiversity. *Philos. Trans. R. Soc. B.* **357**, 619–626 (2002)
12. Clauset, A., Shalizi, C.R., Newman, M.E.J.: Power-law distributions in empirical data. *SIAM Rev.* **51**, 661–703 (2009)
13. Newman, M.E.J.: Power laws Pareto distributions and Zipf's law. *Contemp. Phys.* **46**, 323–351 (2005)
14. Barabasi, A.-L.: Origin of bursts and heavy tails in human dynamics. *Nature* **435**, 207–211 (2005)
15. Miramontes, O., DeSouza, O., Paiva, L.R., Marins, A., Orozco, S.: Lévy flights and self-similar exploratory behavior of termite workers: beyond model fitting. *PLoS ONE* **9**, e111183 (2014)
16. Reynolds, A.M., Smith, A.D., Menzel, R., Greggers, U., Reynolds, D.R., Riley, J.R.: Displaced honey bees perform optimal scale-free search flights. *Ecology* **88**, 1955–1961 (2007)

17. Vismanathan, G.M., Buldyrev, S.V., Havlin, S., da Luz, M.G.E., Raposo, E.P., Stanley, H.E.: Optimizing the success of random search. *Nature* **401**, 911–914 (1999)
18. Atkinson, R.P.D., Rhodes, C.J., Macdonald, D.W., Anderson, R.M.: Scale-free dynamics in the movement patterns of jackals. *Oikos* **98**, 134–140 (2002)
19. Humphries, N.E., Queiroz, N., Dyer, J.R.M., Pade, N.G., Musyl, M.K., Schaefer, K.M., Fuller, D.W., Brunnenschweiler, J.M., Doyle, T.K., Houghton, J.D.R., Hays, G.C., Jones, C.S., Noble, L.R., Wearmouth, V.J., Southall, E.J., Sims, D.W.: Environmental context explains Lévy and Brownian movement patterns of marine predators. *Nature* **465**, 1066–1069 (2010)
20. Sims, D.W., Southall, E.J., Humphries, N.E., Hays, G.C., Bradshaw, C.J.A., Pitchford, J.W., James, A., Ahmed, M.Z., Brierley, A.S., Hindell, M.A., Morritt, D., Musyl, M.K., Righton, D., Shepard, E.L.C., Wearmouth, V.J., Wilson, R.P., Witt, M.J., Metcalfe, J.D.: Scaling laws of marine predator search behaviour. *Nature* **451**, 1098–1102 (2008)
21. Mashanova, A., Oliver, T.H., Jansen, V.A.A.: Evidence for intermittency and a truncated power law from highly resolved aphid movement data. *J. R. Soc. Interface* **6**, 199–208 (2010)
22. Vandercone, R., Premachandra, K., Wijethunga, G.P., Dinadh, C., Ranawana, K., Bahar, S.: Random walk analysis of ranging patterns of sympatric langurs in a complex resource landscape. *Am J. Primatol* **75**, 1209–1219 (2013)
23. Edwards, A.M.: Overturning conclusions of Lévy flight movement patterns by fishing boats and foraging animals. *Ecology* **92**, 1247–1257 (2011)
24. Edwards, A.M., Phillips, R.A., Watkins, N.W., Freeman, M.P., Murphy, E.J., Afanasyev, V., Buldyrev, S.B., da Luz, M.G.E., Raposo, E.P., Stanley, H.E., Viswanathan, G.M.: Revisiting Lévy flight search patterns of wandering albatrosses, bumblebees, and deer. *Nature* **449**, 1044–1048 (2007)
25. Benhamou, S.: How many animals really do the Lévy walk? *Ecology* **88**, 1962–1969 (2007)
26. Viswanathan, G.M., Afanasyev, V., Buldyrev, S.V., Murphy, E.J., Price, P.A., Stanley, H.E.: Lévy flight search patterns of wandering albatrosses. *Nature* **381**, 413–415 (1996)
27. de Jager, M., Weissing, F.J., Herman, P.M.J., Nolet, B.A., Van de Koppe, J.: Lévy walk evolves through interaction between movement and environmental complexity. *Science* **332**, 1551–1553 (2011)
28. Reynolds, A.: Liberating Lévy walk research from the shackles of optimal foraging. *Phys. Life Rev.* **14**, 59–83 (2015)
29. Hanai, K., Ozaki, M., Yamauchi, D., Nakatomi, Y., Yokoyama, C., Fukui, K.: Scale-free dynamics involved in locomotor activity of ant and mouse. *WSEAS Trans. Biol. Biomed.* **6**, 511–515 (2006)
30. Draï, D., Benjamini, Y., Golani, I.: Statistical discrimination of natural modes of motion in rat exploratory behavior. *J. Neurosci. Meth.* **96**, 119–131 (2000)
31. Burnham, K.P., Anderson, D.R.: Model selection and multimodel inference: A practical information-theoretic approach. Springer, New York (2002)
32. Reynolds, A.M.: Mussels realized Weierstrassian Lévy walks as composite correlated random walks. *Sci. Rep.* **4**, 4409 (2014)
33. Beggs, J.M., Plenz, D.: Neuronal avalanches in neocortical circuits. *J. Neurosci.* **23**, 11167–11172 (2003)
34. Sims, D.W., Righton, D., Pitchford, J.W.: Minimizing errors in identifying Lévy flight behavior of organisms. *J. Anim. Ecol.* **76**, 222–229 (2007)
35. White, E.P., Ernest, S.K.M., Kerkhoff, A.J., Enquist, B.J.: Relationships between body size and abundance in ecology. *Trends Ecol. Evol.* **22**, 323–350 (2007)
36. White, E.P., Enquist, B.J., Green, J.L.: On estimating the exponents of power-law frequency distribution. *Ecology* **89**, 905–912 (2008)
37. Geyer, M.A.: Approaches to the characterization of drug effects on locomotor activity in rodents. In Adler, M.W., and Cowan, A. (eds.). *Modern Methods in Pharmacology Vol. 6 Testing and Evaluation of Drug Abuse*, Wiley Liss, 81–100 (1990)
38. Barnett, S.H.: The rat: A study in behavior. Aldine Publishing Co., Chicago (2007)
39. Miramontes, O.: Divorcing physics from biology? Optimal foraging and Lévy flights. Comment on Liberating Lévy walk research from the shackles of optimal foraging by A.M. Reynolds. *Phys. Life Rev.* **14**, 108–110 (2015)