Overturning conclusions of Lévy flight movement patterns by fishing boats and foraging animals

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Abstract. A surprisingly diverse variety of foragers have previously been concluded to exhibit movement patterns known as Lévy flights, a special type of random walk. These foragers range in size from microzooplankton in experiments to fishermen in the Pacific Ocean and the North Sea. The Lévy flight conclusion implies that all the foragers have similar scale-free movement patterns that can be described by a single dimensionless parameter, the exponent μ of a power-law (Pareto) distribution. However, the previous conclusions have been made using methods that have since been shown to be problematic: inaccurate techniques were used to estimate μ, and the power-law distribution was usually assumed to hold without testing any alternative hypotheses.

Therefore, I address the open question of whether the previous data still support the Lévy flight hypothesis, and thus determine whether Lévy flights really are so ubiquitous in ecology. I present a comprehensive reanalysis of 17 data sets from seven previous studies for which Lévy flight behavior had been concluded, covering marine, terrestrial, and experimental systems from four continents. I use the modern likelihood and Akaike weights approach to test whether simple alternative models are more supported by the data than Lévy flights.

The previously estimated values of the power-law exponent μ do not match those calculated here using the accurate likelihood approach, and almost all of them lie outside of the likelihood-based 95% confidence intervals. Furthermore, the original power-law Lévy flight model is overwhelmingly rejected for 16 out of the 17 data sets when tested against three other simple models. For one data set, the data are consistent with coming from a bounded power-law distribution (a truncated Lévy flight). For three other data sets, an exponential distribution corresponding to a simple Poisson process is suitable. Thus, Lévy flight movement patterns are not the common phenomena that was once thought, and are not suitable for use as ecosystem indicators for fisheries management, as has been proposed.

Key words: AIC; fisheries management; Lévy flight; likelihood; movement patterns; optimal foraging strategy; power laws; random walk.

Introduction

It is appealing to try to deduce a wide-ranging yet simple theory to explain the search behavior of a variety of organisms. Over the past decade, an increasingly popular way to analyze animal movement data is in the context of Lévy flights. A Lévy flight is a random walk for which each movement step is independently drawn from a probability distribution that has a heavy power-law tail (ben-Avraham and Havlin 2000). The power-law tail means that occasionally there will be a very large step. The resulting pattern is of clusters of short steps that are connected by the rare long steps. For example, Plank and Codling (2009) show the typical two-dimensional case, which assumes random angles between steps. A suggested application of Lévy flight movements of fishing boats is as an indicator of fish

vulnerability, perhaps to serve as a warning signal for fisheries management (Bertrand et al. 2007).

Viswanathan et al. (1996, 1999) presented evidence of Lévy flight movement patterns by Wandering Albatrosses, bumble bees, and deer. Then followed many similar conclusions, such as those concerning the movements of Peruvian purse-seiner fishing boats (Bertrand et al. 2007), Dutch beam-trawler fishing boats (Marchal et al. 2007), microzooplankton (dinoflagellates) in experiments (Bartumeus et al. 2003), gray seals in the North Atlantic Ocean (Austin et al. 2004), reindeer in Sweden (Mårell et al. 2002), side-striped jackals in Zimbabwe (Atkinson et al. 2002), and Dobe Ju/'hoansi human hunter-gatherers in Botswana and Namibia (Brown et al. 2007). For all except the gray seals and reindeer, the Lévy flight conclusion was the main focus of the original paper.

Motivation for such studies came from the claim that, under certain conditions, a Lévy flight with an exponent of two represents an optimal foraging strategy (Viswanathan et al. 1999). Furthermore, the Lévy flight model is a simple alternative to Brownian motion, and showing

TABLE 1. Summary of data sets reanalyzed for Lévy flight conclusions.

Foragers	Data collection method	Movement length (units)	Reported conclusion
Peruvian fishermen	hourly GPS locations	distance moved in a straight line, turning <10° (nautical miles)	all 691 vessels had $1 < \mu < 3$, with mean $\mu = 2.00$
Dutch fishermen	satellite vessel monitoring system	distance moved between hauls in month (nautical miles)	mainly $1.0 < \mu < 1.9$
Microzooplankton	controlled experiments	time spent between tumbles of >100° (s)	flight times switched from exponential to Lévy as prey decreased
Gray seals	Argos satellite locations	distance moved per day (km)	9 out of 27 daily sampled seals fit Lévy flight
Reindeer	laser range-finding binoculars	distance moved between 30-s observations (m)	Lévy flights for all three time periods
Side-striped jackals	radio-tracked from vehicle	distance traveled in 10 min (100s of meters)	all 7 jackals were Lévy, $\mu = 2.02 \pm 0.30$
Human hunter-gatherers	measured from a map	distance moved between successive camps (km)	Lévy flight with $\mu = 1.97$

Notes: Definitions of movement length or step used in each original analysis are given, followed by the units of measurement (1 nautical mile = 1.852 km). Reported conclusions summarize the Lévy flight aspect of each study, where μ is the power-law exponent, $1 < \mu \leq 3$ corresponds to a Lévy flight, and $\mu = 2$ represents an optimal foraging strategy under certain conditions. See original sources for further details of data analysis, data filtering, and conclusions.

Sources: Peruvian fishermen, Bertrand et al. (2007); Dutch fishermen, Marchal et al. (2007); microzooplankton, Bartumeus et al. (2003); gray seals, Austin et al. (2004); reindeer, Mårell et al. (2002); side-striped jackals, Atkinson et al. (2002); human hunter-gatherers, Brown et al. (2007).

that movements could not simply be described as Brownian motion was a useful step forward (Anders Mårell, *personal communication*).

However, the influential empirical conclusions of the first two studies (Viswanathan et al. 1996, 1999) have since been overturned (Edwards et al. 2007); data were originally misinterpreted, and inaccurate methods were originally used. Similar methods were subsequently adopted for the later studies, but such methods have since been shown to be inaccurate and problematic (Edwards et al. 2007, Sims et al. 2007, Edwards 2008, White et al. 2008). This raises the question of whether these studies do, in fact, provide evidence for Lévy flights in ecology, and thus motivates the present work, which reanalyzes 17 data sets from the seven studies just cited.

The inaccurate methods in question involve the estimation of the dimensionless parameter μ, which is the exponent of the power-law probability density function (explicitly given in Eq. 1). Sims et al. (2007) showed that one of the methods, simple log-transformation (LT) of a histogram, is inaccurate; they recommended the log-binning with normalization (LBN) method. White et al. (2008) and Edwards (2008) then showed that this method is also inaccurate, and that likelihood correctly determines μ from simulated data. See those references for full descriptions of the methods.

The other problems with the original approaches were the lack of proper testing of alternative hypotheses and the lack of testing of goodness of fit. A power-law distribution was usually assumed, and the parameter μ estimated, without consideration of possible alternatives (see Edwards et al. 2007). Therefore, I reanalyze the original data sets using likelihood and calculate Akaike weights to test alternative models. I also test goodness of fit to check if the best model of those tested is actually a suitable model for the data (some authors had reported r^2 values related to regression methods, but these are not statistical goodness-of-fit tests; see Edwards 2008).

METHODS

A brief summary of the data sets from each previous study is given in Table 1. The data collection methods used were somewhat varied across studies, as necessitated by the diverse nature of the organisms being studied. Table 1 demonstrates that the working definition of "movement length" also varies between studies (e.g., the distance moved in a straight line for Peruvian fishing boats, compared to distance moved in a day for gray seals). Thus the Lévy flight hypothesis was being tested for different types of data, and, consequently, the hypotheses really being tested were somewhat different than the original concept of Viswanathan et al. (1996) of power-law-distributed movements between feeding events.

The approach here was to reanalyze the specific data sets from each previous study that had been explicitly shown in a figure to be a power law. Typically, a regression based on the figure (some sort of histogram on log–log axes) was originally used to determine μ. This was done using the LT or LBN methods (based on Viswanathan et al. 1996, 1999) that have now been shown to be inaccurate, as noted above.

An unbounded power-law model (PL model) is what was concluded in each of the previous studies. Here, I tested it against the simplest alternative of an exponential model, which naturally arises as the distribution of intervals between events of a simple Poisson random process (Grimmett and Stirzaker 1990, Brown et al. 2007). The bounded versions of these models were also tested, due to the lack of support for the unbounded

power-law model in previous work (Edwards et al. 2007).

The likelihood and Akaike weights approach outlined in Edwards et al. (2007) and Edwards (2008) was used. The four models and corresponding probability density functions $f(x)$ for movements of length x, are: the classic Lévy flight model of an unbounded power-law tail (PL model)

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

with normalization constant $C = (\mu - 1)a^{\mu-1}$; the simplest alternative of an unbounded exponential tail (Exp)

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

a bounded power law (PLB)

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

with 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 $\mu = 1$ (see Appendix); and a bounded exponential distribution (ExpB)

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

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

The Lévy flight hypothesis is that the distribution of movements has a power-law tail with $1 < \mu \leq 3$. This is the PL model, where the hypothesis is not directly concerned with data $<a$.

Clearly, movement lengths (and other data) naturally have some maximum value. While more familiar distributions (such as the Gaussian) are widely used in ecology in their unbounded form, this is because they decay away fast enough that unrealistically large values are extremely unlikely (there is no need to bound a Gaussian distribution to avoid large values). But power laws, by definition, can decay away slowly enough to produce huge values, and so would seem to require an explicit upper bound to be logically reasonable (e.g., Page [1968] used the PLB model in the context of earthquakes). Note that the PL and PLB models are also called the Pareto and truncated Pareto distributions (see White et al. 2008 and references therein).

The value of a generally has not been explicitly stated, so for each data set tested here, I determined a from what was implied by the corresponding log–log plots in the original papers. This may be the minimum of the full data set. Or if the lowest point of an LT or LBN plot had been excluded in the computation of μ (as in Edwards et al. 2007: Fig. 4), then I set a to be the minimum value of the lowest bin that was included. Thus for each data set I am explicitly testing the model that was implied in the original paper, that of a power-law tail for data greater than a. The value of b was taken to be the maximum value of the data, rounded up to the nearest integer. Values of a and b are given in the Appendix: Table A2.

For each data set, the appropriate maximum likelihood estimate (MLE) of μ or λ was calculated for each model, together with 95% confidence intervals obtained using the profile likelihood-ratio test (Hilborn and Mangel 1997). Akaike weights were computed, where the Akaike weight for a particular model is considered to be the weight of evidence in favor of that model being the best model for that data set, out of the models being tested (Burnham and Anderson 2002). The results are presented in terms of evidence ratios, calculated for a particular data set by dividing each Akaike weight by the highest Akaike weight (Burnham and Anderson 2002), such that the best model has an evidence ratio of 1.0, and the other models have evidence ratios >1.0. For further background to the approach see Burnham and Anderson (2002) and Johnson and Omland (2004), and for further specifics to the current analyses see Edwards et al. (2007), Edwards (2008), and the Appendix, which includes derivations of the likelihood functions for the PLB and ExpB models, and for all models when only prebinned data are available.

Goodness-of-fit tests were performed on the distribution that has evidence ratio 1.0, to ask whether the data are, in fact, consistent with the best model. The best model might simply be the best out of four poor models, and thus may be far from suitable. Previously, the unbounded power-law distribution was generally fitted and plotted, without consideration of other models or goodness of fit. The G test (likelihood ratio test) with Williams's correction was used (Sokal and Rohlf 1995), for which the null hypothesis is that the data are consistent with the tested distribution. Therefore if $P > 0.05$, the null hypothesis is not rejected, and the data are considered to be consistent (at the 0.05 level) with the distribution. See the Appendix for full details.

Where possible, raw data were obtained from the original authors of each study, as now described. For the Peruvian fishing boats, data were analyzed for the three boats shown in Bertrand et al. (2007: Fig. 1d–f); data courtesy S. Bertrand (*personal communication*). For each boat, Bertrand et al. (2007) excluded the data in the first bin, and so a for each boat was set to the lower bound of the second bin.

For the Dutch fishing boats, the original raw data for large Dutch beam-trawlers were obtained from P. Marchal (*personal communication*). I would have used the data set for the example specifically shown in Marchal et al. (2007: Fig. 4a), but it was not available. So I analyzed data for the two months that contained the most move lengths, where the move lengths are distances moved between hauls (specifically, May 2001 and July 2003; the full time series of calculated μ values is shown in Marchal et al. [2007: Fig. 5]).

For the microzooplankton, the raw data were not available. The values plotted in Bartumeus et al. (2003: Fig. 4) were obtained from F. Bartumeus (*personal*
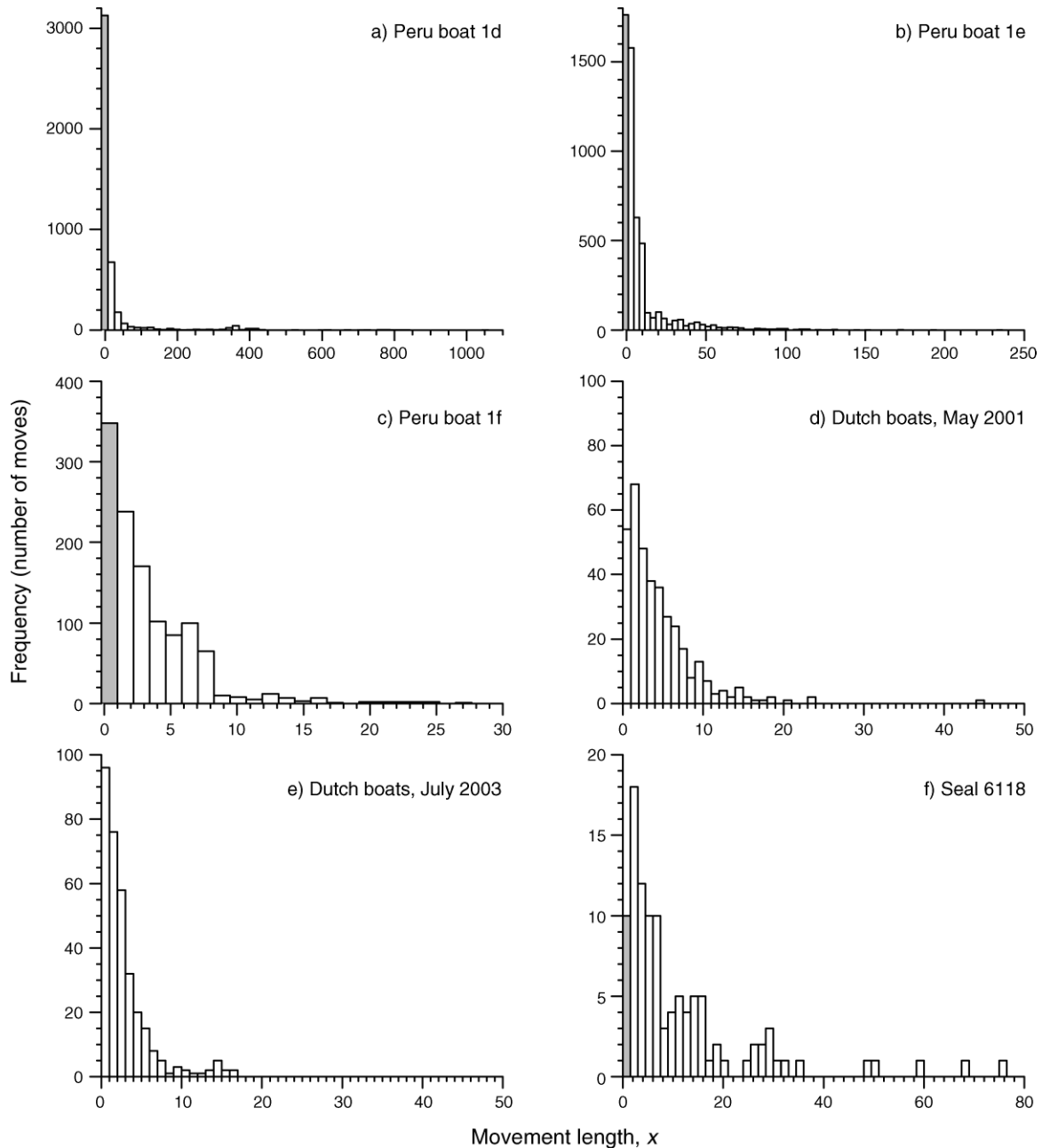
Fig. 1.   Raw movement data were available for 12 of the 17 data sets and are shown as standard histograms. The 12 data sets are from three Peruvian fishing boats, Dutch fishing boats in two seasons, three individual seals, reindeer from three time periods, and human hunter-gatherers. Gray-shaded bars indicate data $<a$ for each data set, where a was considered in each original study to be the start of the power-law tail (values of a are given in the Appendix: Table A 2). Table 1 gives definitions of movement length and corresponding units, which differ for each type of data set.

communication). These data are $\log_{10}$ of the frequency density in each bin plotted against $\log_{10}$ of the geometric midpoint of each bin. Knowing that bins progressively doubled in size and that the geometric midpoints were equally spaced on a $\log_{10}$ scale, I calculated what the original bin breaks must have been and derived the appropriate likelihood functions for data binned in such a way, similar to Edwards et al. (2007); see the

Appendix. The four situations for which power laws were concluded were reanalyzed here: namely experiment A with medium food (Am), experiment B with medium food (Bm), experiment A with low food (Al), and experiment B with low food (Bl).

The gray seal (*Halichoerus grypus*) data analyzed were for the three seals (numbered 6118, 6124, and 6125) whose movements were plotted in Austin et al. (2004:
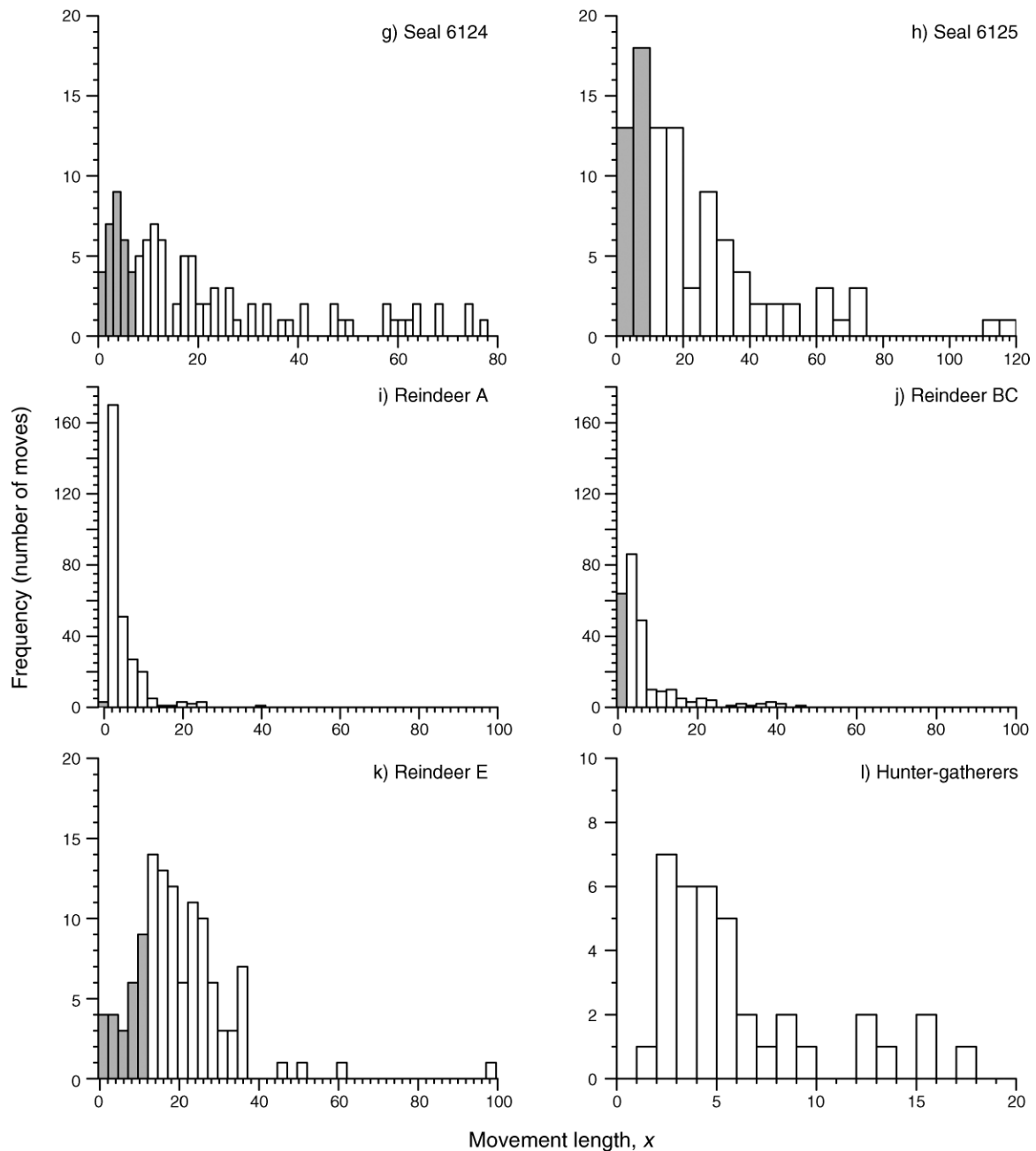
FIG. 1. Continued.

Fig. 3). As outlined in Edwards (2008), where data for seal 6118 were reanalyzed, the data were incorrectly plotted in those figures, so here I use the true raw data, courtesy of D. Austin (*personal communication*).

Mårell et al. (2002: Fig. 2) show three data sets of reindeer (*Rangifer tarandus*) movements. These are movements of female reindeer grouped into three time periods, denoted A (end of May to mid-June), BC (mid-June to end of July), and E (mid-August to mid-September), and are reanalyzed here. Original raw data were provided by A. Mårell (*personal communication*).

Atkinson et al. (2002) analyzed movements of side-striped jackals (*Canis adustus*), and stated that "The distribution of step lengths (Fig. 2) does not fit a Gaussian distribution... ." However, their Fig. 2, in fact, does not show such a distribution of step lengths, and the raw data are no longer available (C. Rhodes, *personal communication*). Atkinson (1997: Fig. 2) gives a histogram of step lengths for jackal F4, so I use that data set in the analysis here (actual counts in each bin were given in the figure). Because the data are only available in binned form, I use the likelihood functions

TABLE 2.   Likelihood calculations of the Lévy exponent μ for the 17 data sets.

Data set	Reported μ	PL: MLE for μ	PLB: MLE for μ
Peru boat 1d	1.43	1.72 (1.68–1.76)	**1.60 (1.56–1.65)**
Peru boat 1e	2.00	1.59 (1.58–1.61)	**1.45 (1.43–1.48)**
Peru boat 1f	2.43	1.79 (1.74–1.85)	1.46 (1.38–1.53)
Dutch boats, May 2001	1.60	1.41 (1.37–1.45)	1.07 (1.00–1.13)
Dutch boats, July 2003	1.65	1.53 (1.48–1.59)	1.15 (1.06–1.24)
Microzooplankton Am	2.1	1.89 (1.82–1.96)	**1.82 (1.74–1.90)**
Microzooplankton Al	2.1	1.74 (1.70–1.77)	1.62 (1.58–1.66)
Microzooplankton Bm	2.2	2.03 (1.93–2.14)	1.86 (1.74–1.99)
Microzooplankton Bl	2.2	2.03 (1.94–2.13)	1.86 (1.75–1.97)
Gray seal 6118	1.26	1.60 (1.49–1.73)	**1.25 (1.07–1.43)**
Gray seal 6124	1.12	1.93 (1.73–2.16)	**1.21 (0.86–1.56)**
Gray seal 6125	1.30	2.04 (1.80–2.32)	1.55 (1.20–1.92)
Reindeer A	2.0	1.91 (1.81–2.02)	**1.73 (1.61–1.86)**
Reindeer BC	1.8	1.95 (1.82–2.09)	**1.64 (1.47–1.82)**
Reindeer E	1.8	2.68 (2.36–3.05)	2.41 (2.01–2.84)
Jackal F4	2.02	2.79 (2.60–3.00)	**2.71 (2.51–2.93)**
Hunter-gatherers	1.97	1.93 (1.66–2.26)	1.20 (0.73–1.69)

Notes: For each data set, the previously reported μ is given, followed by the maximum likelihood estimate (MLE) and 95% confidence interval of μ for the PL (power law unbounded) and PLB (power law bounded) models. Corresponding estimates of λ for the Exp (exponential unbounded) and ExpB (exponential bounded) models are deferred to the Appendix: Table A1. Boldface indicates the model with the most support as determined by the evidence ratios of 1.0 in Table 3; if no bold is shown here for a data set, then one of the exponential models was most supported. For gray seals, reported μ values are those originally incorrectly calculated by Austin et al. (2004; see Edwards 2008), but the results here are for the true raw data. For the Dutch boats, reported values are calculated using the LT method as used by Marchal et al. (2007). For jackal F4, a value of μ was not given in Atkinson (1997), although μ = 2.02 ± 0.30 (SD) was reported by Atkinson et al. (2002) for seven animals, so I have reported μ = 2.02 here.

for prebinned data derived in the supplementary information of Edwards et al. (2007).

For the hunter-gatherers, the data were taken directly from Brown et al. (2007: Table 1). In that study, alternative distributions were considered (including an exponential), and the power law was concluded to be superior. However, the exponential distribution was incorrectly analyzed (see Appendix).

Computations were performed using the statistical software R (R Development Core Team 2009), versions 2.2.0 onward. In particular, the function nlm() was used for numerical optimization of analytically intractable likelihood functions.

Results

Fig. 1 shows standard histograms for the 12 data sets for which there are raw (unbinned) data. There is substantial variability between individuals of the same type, demonstrated by the fact that, except for the Dutch fishing boats, different axes ranges were needed between individuals of the same type to adequately display the data.

For each individual data set, the power-law tail was assumed in the original study to start at the value of *a*, which is at the right-hand end of the shaded bar (values of *a* are given in the Appendix: Table A2), or at the minimum data value if all data were originally fitted to. For every organism (except the Dutch boats) for which multiple data sets were investigated, *a* differs between individuals. Thus, the original studies were fitting power-law tails, yet the definition of tail varied between individuals.

An initial conclusion from Fig. 1 is that no data set spans several orders of magnitude. In fact, the ratios *b*/*a* range from roughly 8 to 200. Over half of the data sets have ratios ≤ 32, such that the largest value is at most only 32 times the smallest (*a*). Simulated data from a pure power-law distribution with μ = 2 will be expected to have 1% of values larger than 100*a* (e.g., Edwards 2008: Fig. 1d), and such values will sometimes be huge. Thus, simply looking at the ranges of the data sets (and those of Viswanathan et al. 1996, 1999), the tails do not seem "heavy" enough to be pure power laws. Appendix: Fig. A2 reproduces the original binned figures for the four microzooplankton data sets, for which standard unlogged histograms cannot be plotted.

Table 2 lists the μ values reported for the PL model in the previous studies. These all lie within the Lévy range of 1 < μ ≤ 3, and were previously calculated using regression-based methods (LT, LBN, or, for the hunter-gatherers, a multi-histogram approach). The next column of Table 2 gives the MLE for μ calculated here, together with its 95% confidence interval. Remarkably, for 12 out of the 14 data sets, the previously reported μ lies outside of the 95% CI, demonstrating the unreliability of the original approaches. (The 14 data sets exclude the gray seals, whose reported values were originally incorrectly determined.) Such unreliability of the methods has been clearly demonstrated using simulated data (Edwards 2008, White et al. 2008), whereas the MLE was shown to accurately estimate μ.

For the PLB model (Table 2), the MLE for μ is always lower than that for the PL model. This is to be expected,

TABLE 3. Evidence ratios and goodness-of-fit results.

Data set	Evidence ratios				Goodness of fit for best model	
	PL	Exp	PLB	ExpB	n	P
Peru boat 1d	10^{20}	10^{306}	**1.0**	10^{306}	1224	0
Peru boat 1e	10^{92}	10^{201}	**1.0**	10^{201}	3498	0
Peru boat 1f	10^{83}	**1.0**	10^{41}	1.8	824	10^{-11}
Dutch boats, May 2001	10^{82}	**1.0**	10^{42}	2.7	364	0.64
Dutch boats, July 2003	10^{33}	**1.0**	8100	1.9	329	10^{-5}
Microzooplankton Am	10^{5}	10^{32}	**1.0**	10^{32}	641	10^{-8}
Microzooplankton Al	10^{57}	**1.0**	10^{30}	2.7	1743	0
Microzooplankton Bm	10^{7}	**1.0**	220	2.7	374	10^{-4}
Microzooplankton Bl	10^{14}	**1.0**	10^{7}	2.7	471	0.001
Gray seal 6118	10^{6}	2.2	**1.0**	5.3	96	0.016
Gray seal 6124	10^{6}	200	**1.0**	27	71	0.84
Gray seal 6125	3500	**1.0**	2.5	1.7	63	0.74
Reindeer A	10^{5}	10^{9}	**1.0**	10^{9}	284	10^{-10}
Reindeer BC	10^{7}	10^{4}	**1.0**	10^{5}	193	10^{-5}
Reindeer E	10^{4}	**1.0**	990	2.6	89	0.93
Jackal F4	4.0	910	**1.0**	2500	414	0.0081
Hunter-gatherers	2200	1.05	1.3	**1.0**	37	0.15

Notes: Evidence ratios give the relative degree of support for each model, with 1.0 being the most supported (shown in boldface). Sample size is n, and P is the value for the goodness-of-fit tests (G test with Williams' correction; Sokal and Rohlf 1995) for the model with evidence ratio 1.0 (degrees of freedom and G values are given in the Appendix: Table A2). If $P > 0.05$, then the data are considered to be consistent with the tested distribution.

because for the region $>b$, the tail in the PL model must decay away (because there are no data in this region to support a heavier tail), but this region is excluded in the PLB model, thus permitting a shallower (lower μ) probability density function. The MLEs of λ for the Exp and ExpB models are deferred to the Appendix: Table A1.

Table 3 gives the evidence ratios for the four models for each data set. An evidence ratio of 1.0 occurs for the model that is most supported by the data, highlighted in boldface.

The PL model is not the best model for any of the data sets. The evidence ratio for the PL model is $\geq 10^{7}$ for over half of the data sets, and >2000 for all but one data set. Yet the PL model had previously been concluded for each data set. Only for the jackal data set does the PL model have any support.

The Exp model is most supported for eight of the data sets, although in each case the evidence ratio for the ExpB model is <3, such that the ExpB model cannot be ruled out. For the May 2001 Dutch boats data and three of the microzooplankton data sets, the evidence ratio for ExpB takes the value $2.7 \approx e$, which essentially means that the likelihoods for the Exp and ExpB models are the same, but the ExpB model gets penalized because of the extra parameter. For the other four data sets, the ExpB evidence ratio is <2.7, such that the extra parameter b does increase the likelihood of the ExpB model.

The PLB model is also most supported for eight of the data sets, overwhelmingly in five cases. The ExpB model is most supported only for the hunter-gatherers, although for that data set, the Exp and PLB evidence ratios are both very close to 1.0, such that the data are not sufficient to distinguish a best model.

The fact that the PLB model was supported for eight of the data sets implies that such a power-law model, albeit not the originally concluded PL model, may still be suitable. Thus, such a truncated Lévy flight might be a good model. However, the goodness-of-fit tests suggest otherwise. The P values in Table 3 are $P \leq 10^{-5}$ for the data for Peru boats 1d and 1e, microzooplankton Am, and reindeer A and BC, and $P \leq 0.02$ for gray seal 6118 and the jackal. Thus, none of these data sets are consistent (at the 0.05 level) with the PLB model, despite the PLB model being the best of the four tested. Therefore, none of the models are suitable descriptions for these data sets. The only data set for which the PLB model is most supported and the data are consistent with the PLB model (from the goodness-of-fit test) is gray seal 6124 ($P = 0.84$). I also used an alternative procedure for determining bins for the goodness-of-fit tests to ensure that the general rejection of the PLB model was not a consequence of the binning procedure; however, the conclusions remain unchanged (see Appendix).

The jackal data set was the only one for which the classic PL model had some support, with an evidence ratio of 4.0 compared to the PLB model. However, the data are not consistent with the PLB model ($P = 0.008$).

Table 3 shows that the Exp model is only deemed to be consistent with the data for three out of the eight data sets for which it was the most supported model, namely the Dutch boats in May 2001, gray seal 6125, and reindeer E. Thus the Exp model is a suitable model for these data sets. Finally, for the hunter-gatherers, the ExpB model is the most supported model (although only marginally), and is consistent with the data.

Fig. 2 shows the raw data and model fits on a rank/frequency plot with logarithmic axes. Such plots of the
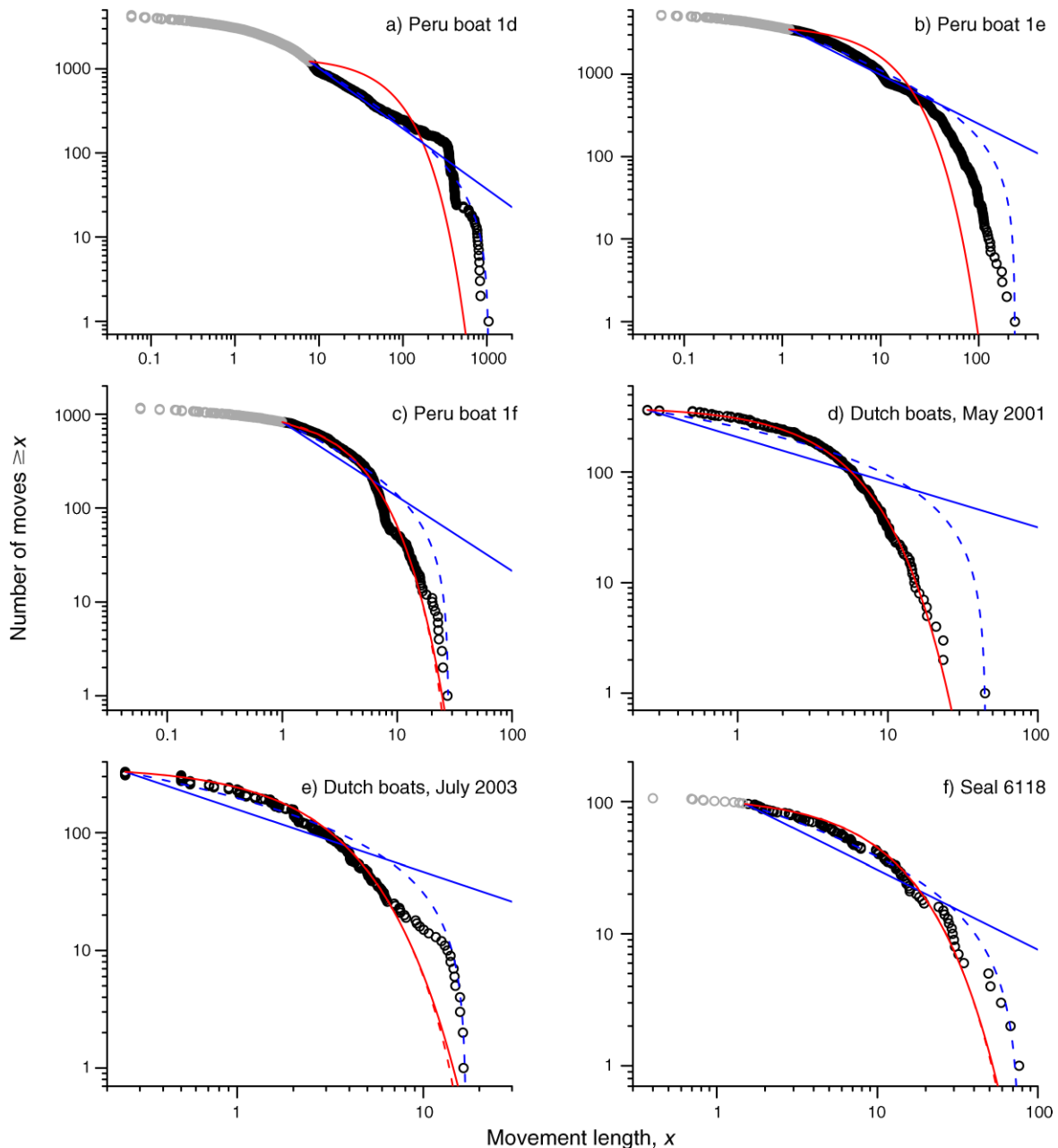
FIG. 2.   Rank/frequency plots of data and model fits on logarithmic axes, using the data sets depicted in Fig. 1. Black circles are values ≥*a* for each data set; gray circles are values <*a* (models are only fitted for values ≥*a*, as for the original studies, which each considered *a* to be the start of the power-law tail). The four model fits are PL (power law; blue straight line), Exp (exponential unbounded; red curved line), PLB (power law bounded; blue dashed curved line), and ExpB (exponential bounded; red dashed curved line, mostly overlapping with Exp). Fig. A1 (in the Appendix) shows the same plots on linear axes to show the data and model fits without the distortion from the logarithmic axes. Table 1 gives definitions of movement length and corresponding units, which differ for each type of data set.

data are often used in power-law studies, because if data do come from an unbounded power law, then they will appear straight due to the logarithmic axes (with a slight curvature in the tail, e.g., Edwards 2008: Fig. 1d). As can be seen from the data points and the fits of the PL model (solid blue lines), none of the data sets actually appear that straight. This agrees with the lack of support for the

PL model concluded from the Akaike weights. The lack of suitably heavy-tailed data is also evident in the Appendix: Fig. A1, which shows the same plots as Fig. 2 but on non-logarithmic axes.

The gray circles in Fig. 2 show the data values <*a* for each data set. Recall that *a* is set to the value used in each original study. As can be seen, for some data sets
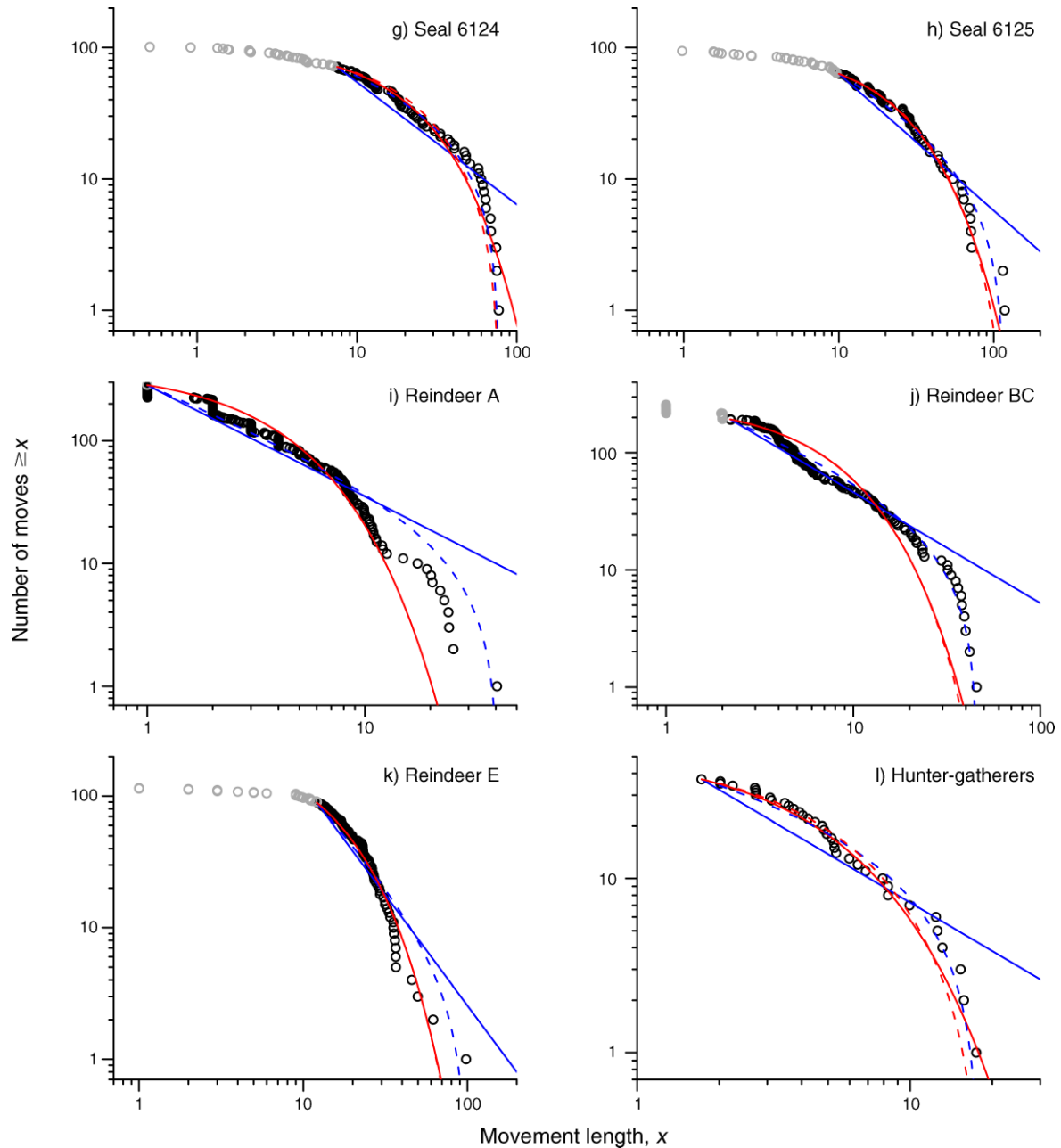
FIG. 2. Continued.

the value of a means that a significant portion of the data was not fitted to in the original study (e.g., for the Peruvian fishing boats, the first bins of the histograms were excluded when fitting the power law). For most cases, the gray circles appear as a somewhat smooth continuation of the curve given by the black circles. This is extremely evident in the Appendix: Fig. A1.

Thus, results in Table 3 give the objective evidence for which model is best supported for each data set, and Fig. 2 gives graphical agreement of those results. For example, for the Dutch boats in May 2001, Fig. 2d

implies that the exponential models (red curves) are most suitable for this data set, as confirmed by the evidence ratios in Table 3.

Microzooplankton data are shown in the Appendix: Fig. A2 (in the LBN form as originally analyzed), together with the curves that represent the maximum likelihood Exp models (using methods described in the Appendix). For Fig. A2b–d, the Exp model is the model that has the most support (although it is not a suitable model as determined by the P values). Even though the fitted PL lines in Fig. A2 might appear suitable, with

respective r^2 values of 0.98, 0.96, 0.94, and 0.96 (Bartumeus et al. 2003), the originally determined values of μ are quite different than the more accurate MLE values (Table 2). For Fig. A2b–d, the Exp model is far more supported by the data than the PL (or PLB) model (Table 3), so a power-law model is not suitable. This further demonstrates how regression-based and binning-based methods of testing for power laws can be misleading (see also Edwards 2008, White et al. 2008).

CONCLUSIONS

I have reanalyzed 17 published data sets that previously had been concluded to show evidence for Lévy flight movement patterns. This conclusion is overturned for all 17 data sets. The μ values computed using the accurate likelihood approach are different than those previously inferred from regression-based approaches, further demonstrating the inadequacy of such approaches.

The only data set for which a power-law model was suitable (albeit the bounded power law, not the conventional unbounded power law), was for gray seal 6124; and for the hunter-gatherers the bounded power law cannot be ruled out. For all other data sets, either the bounded power law was the most supported of the four tested but the data were not consistent with it, or an exponential model was the best model. Thus, these results overturn the previous conclusions that all of these data sets represent evidence of Lévy flight movement patterns.

The value of a was fixed to that assumed in each original study, as the aim was to test the explicit power-law distribution that had previously been concluded. Testing alternative values of a could be done, involving a decision on where the "tail" of the data starts. Yet this then raises the wider question of how useful it is to fit just the tail of the data, rather than the full range. Fitting just the tail is justifiable to test the pure Lévy flight hypothesis of the PL model, but the lack of support for the PL model here is presumably due to the lack of truly heavy-tailed data. If the distribution of movement lengths was desired as input to a movement model to, say, assess likely consequences of a change in habitat, then just knowing the distribution of data only in the tail would not be very useful. Throwing out a substantial portion of the data (e.g., Appendix: Fig. A1a) does not seem to be a useful approach. A compounding problem is that different values of a were generally assumed for different individuals of the same type (Fig. 2; Appendix: Fig. A1 and Table A2).

Of the 17 data sets analyzed, for only five did I find the data to be consistent with one of the four tested distributions (using the criteria of $P > 0.05$). For the remaining 12 cases, could the best of the four models still be useful for characterizing the patterns? Given that the goodness-of-fit results were generally so unfavorable, this seems unlikely (in particular, for the seven out of the remaining 12 data sets for which the PLB model was

most supported, the P values are 0, 0, 10^{-8}, 0.016, 10^{-10}, 10^{-5}, and 0.0081). This rejection of the best of the tested models may be because animals move for a variety of reasons (although the Lévy flight hypothesis relates to foraging only), so other distributions could be more appropriate to capture more of the complexity. Some of the plotted data (e.g., Fig. 2a–c) demonstrate kinks in the curves, suggesting breaks in the distributions. Consequently, slightly more complex models may be required to adequately model such data (e.g., separate distributions for the short and long movements).

There do remain published examples of Lévy flight search patterns that were not reanalyzed here, e.g., spider monkeys *Ateles geoffroyi* (Ramos-Fernández et al. 2004) and honey bees *Apis mellifera* (Reynolds et al. 2009). Spider monkey data were not available for this study, although the inaccurate LT method was used in the original analysis. And Reynolds et al. (2009) did test the gamma distribution as an alternative to the power law, but did not shift it to start from the value of a (see Edwards et al. 2007: Eq. 2). It was therefore unfairly compared to the power-law distribution that was shifted to start from $a = 15$ m (so the gamma distribution was trying to fit nonexistent data <15 m).

An often overlooked element of Lévy flight theory is that of the requirement of random angles between movements (though see Reynolds and Rhodes 2009). This is required to fulfill the assumption of a simple random walk inherent in the definition of a Lévy flight. The original Wandering Albatross (*Diomedea exulans*) data did not have directional information, but the simulated paths in Viswanathan et al. (1996: Fig. 4) did incorporate the required assumption of random angles. Because directional persistence (having a preferred direction of travel rather than angles being random uniform variables) also gives superdiffusion, and would seem to be a more realistic assumption than random angles for foraging animals, the general lack of data or discussion concerning angles would seem to further undermine the idea of Lévy flights as common movement patterns. Other issues include misidentification of movement paths due to discrete data collection processes (Plank and Codling 2009), inferring a process from a pattern (Benhamou 2007), and neglecting that animals use their intelligence and experience to guide them, factors not included in simple random search models (see Travis 2007). Such issues strengthen the conclusion from the results presented here that many foraging animals and fishermen do not, in fact, move using a Lévy flight strategy. Therefore, Lévy flights do not appear to have potential application as marine ecosystem indicators.

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APPENDIX

Likelihood function derivations and further details regarding statistical tests, microzooplankton data, and hunter-gatherer data (*Ecological Archives* E092-104-A1).