Evidence for biological Lévy flights stands

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Analyses of movement patterns are crucial to elucidate the mechanisms explaining animal foraging strategies. Scale-free frequency distributions of foraging flights or displacements are usually regarded as underlying complex behaviours, in contrast to Poisson processes. Edwards et al.\textsuperscript{1} revisited well-known studies reporting power-laws in the foraging patterns of albatrosses\textsuperscript{2,3}, and concluded that no Lévy process\textsuperscript{4,5} could model recent observations of higher resolution. Here we show that this re-analysis\textsuperscript{1} suffers from a conceptual misunderstanding, and that the new albatross data remain consistent with a biological Lévy flight.

Edwards et al. interpret the results of their analysis by focusing on the tails of the frequency distributions of foraging movements (or their rank/frequency plots (RFP)). The exponential law, not the power-law, dominates the 2004 high resolution albatross data at large scales, indicating a Poisson process\textsuperscript{1}. Edwards et al. have underestimated the crucial fact that all foraging processes are subject to finite size constraints. Exponential tails are actually an essential outcome (although overlooked so far) of Lévy random search theory\textsuperscript{3}: they stem from target detection, a foraging issue by excellence. A forager with a perception radius $r_v$ and deciding to move a distance $x$ on a plane containing randomly distributed targets in number density $\rho$ has a probability $e^{-xld}$ of not
finding any target, with $d=(2r, \rho)^{-1}$. We derive the actual step length distribution for the model of ref. 3:

$$P(x) = P_0(x)e^{-x/d} + d^{-1} e^{-x/d} \int_x^\infty du P_0(u)$$

with $P_0(x) = Cx^{-\mu}$ ($\mu > 1$) being the choice distribution, and $C$ a normalization constant. The first term in (1) is the probability of making a trip of length $x$ and not finding any target, the second the probability of finding a target at a distance $x$ (implying that the chosen length $u$ is $>x$). $P$ takes two limiting forms: (i) $P(x) \approx C x^{-\mu}$ if $x \ll d(\mu - 1)$, a wide interval only if resources are scarce; (ii) $P(x) \sim x^{1-\mu} e^{-x/d} \neq P_0(x)$ if $x \gg d(\mu - 1)$.

Formula (1) has sounder biological and physical grounds than the ad hoc gamma function introduced in ref. 1 to fit the 2004 albatross data. It should also be preferred to the simple power-law model for testing biological Lévy flights. With $\mu=1.18$ and $d=1.89$ hours, Eq. (1) describes the albatross data very well (Fig.1). The data can not be fitted by a pure random Poisson process ($P(x)=d^{-1} e^{-x/d}$), which is recovered in Eq. (1) when $\mu \to 1$ (Fig. 1). Although $\mu$ differs from the optimal value 2 for immobile targets$^3$, it remains larger than unity: the flying times can still be interpreted as drawn from a genuine, normalizable power-law distribution, contrary to what is concluded in ref. 1 (where $\mu=0.69$ is reported).

Furthermore, although RFP are used in many contexts$^7$, they should be interpreted with care: truncated-power-law distributed data do not produce RFP with straight lines in log-log, even at small scales, unless the power-law regime of the frequency distribution spans over at least three decades. This is rarely the case in biological data (see e.g. Fig.1). The absence of scaling exponent in a data set cannot be simply concluded by showing the lack of straight lines in a log-log RFP (as in figure 1 and 3c of ref. 1).
Likelihood and goodness-of-fit tests are useful methods to rule out hypotheses, or to notice that several models (e.g. exponential, power-law) are equally likely to describe a given data set of small size, as illustrated by Edwards et al. in the case of bumble-bees\textsuperscript{1}. But in order to improve the understanding of foraging processes, these tests should be applied, whenever possible, to analytical or numerical results of foraging models, rather than to \textit{a priori} given mathematical functions taken out of their biological context.
Figure 1. Cumulative distribution of the duration of the 2004 albatross flights (x, open circles), compared with the cumulative of the probability distribution function predicted by Lévy search theory, Eq. (1), with μ=1.18 and d=1.89h (solid line). Since only the flights larger than 30s were considered in the field study, we have taken the power-law choice distribution $P(x) \neq 0$ if $x>30$ s and 0 otherwise. With this assumption the forager can still perform flights that have $x<30$ s in the model (1); nevertheless, only those with $x>30$ s are represented, like in the albatross data. These data were obtained by digitalizing the histogram of Ref. 1. A log-likelihood ratio test of significance (G-test) was performed with the parameter values above for $\mu$ and $d$ by using a Monte Carlo (MC) procedure generating $10^4$ independent data sets. The obtained $P$ value is 0.21 (meaning that 21% of the artificial data sets drawn from Eq. (1) are further away from this distribution than the albatross data). The two dotted curves are from Eq. (1) with $\mu=1.01$ ($d=1.89h$ and $1h$): at this exponent value, the distribution $P(x)$ is nearly Poisson and cannot fit the data for any $d$ ($P<10^{-4}$). The discrete nature of the albatross data (see Ref. 1, Supplementary Methods 1) was taken into account in the MC calculations and for plotting the theoretical curves.