Lévy flight search patterns of wandering albatrosses

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Lévy flights are a special class of random walks whose step lengths are not constant but rather are chosen from a probability distribution with a power-law tail. Realizations of Lévy flights in physical phenomena are very diverse, examples including fluid dynamics, dynamical systems, and micelles[1,2]. This diversity raises the possibility that Lévy flights may be found in biological systems. A decade ago, it was proposed that Lévy flights may be observed in the behaviour of foraging ants[3]. Recently, it was argued that *Drosophila* might perform Lévy flights[4], but the hypothesis that foraging animals in natural environments perform Lévy flights has not been tested. Here we study the foraging behaviour of the wandering albatross *Diomedea exulans*, and find a power-law distribution of flight-time intervals. We interpret our finding of temporal scale invariance in terms of a scale-invariant spatial distribution of food on the ocean surface. Finally, we examine the significance of our finding in relation to the basis of scale-invariant phenomena observed in biological systems.

We collected data over a three-month summer period as part of a study of the foraging biology of albatrosses in the South Atlantic[5]. Electronic recording devices were attached to the legs of five different adult albatrosses on Bird Island, South Georgia (54° 00′ S, 38° 06′ W), on 19 separate foraging trips. The devices took measurements every 3 s, and recorded $u(t)$, the number of 15-s intervals in each hour t for which the animal was wet for 9 s or more. Each entry in the time series $u(t)$ is therefore a number from 0 to 240, and $t = 1, 2...t_{max}$ is time measured in hours. We thereby obtain 19 time series, one for each of the foraging trips studied. These range in duration from $t_{max} = 77$ h to $t_{max} = 416$ h with a mean of 175 h. The birds do not forage on land, and the wet periods indicate interruptions in their flight paths caused by their alighting on water to eat or rest. As an example of the raw data, see Fig. 1.

First, we analysed the data using 'random walk' methods[6], which can detect the presence of long-range correlations. The net displacement $y(t)$ of the time series $u(t)$ is defined by the running sum $y(t) \equiv \sum_{i=1}^{t} u(i)$. An important statistical quantity characterizing the walk is the root mean square (r.m.s.) fluctuation of the displacement, $F(t) \equiv \sqrt{\langle(\Delta y(t))^2\rangle - \langle\Delta y(t)\rangle^2}$, where $\Delta y(t) \equiv y(t_0 + t) - y(t_0)$. The angular brackets denote expectation values, that is, averaging over all possible times t_0. The calculation of $F(t)$ can distinguish three types of behaviour[7]. Uncorrelated time series give rise to uncorrelated random walks described by

$$F(t) \sim t^{\alpha} \qquad (1)$$

with $\alpha = \frac{1}{2}$, as expected from the central limit theorem. Markov processes also give $\alpha = \frac{1}{2}$ for sufficiently large t. In the presence of long-range correlations with no characteristic time scale, equation (1) holds, but with $\alpha \neq \frac{1}{2}$.

Figure 2*a* shows that long-range correlations exist, because we have an almost perfect power law with $\alpha = 0.84 \pm 0.2 \neq \frac{1}{2}$. (The error is found by estimating α for each time series separately.) When we randomly shuffle the data, the long-range correlations vanish and we recover $\alpha = \frac{1}{2}$ as expected. The power spectrum[8] shown in Fig. 2*b*, *c* and detrended fluctuation analysis (DFA)[7,9] confirm the existence of long-range correlations and scale invariance.

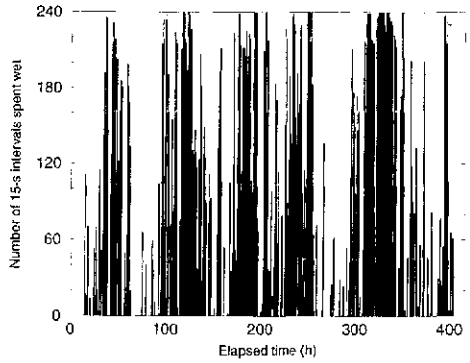


FIG. 1 The longest of the 19 time series, with a length of 416 h. Each point in the time series gives the number of 15-s intervals in each hour for which the animal was wet for 9 s or more.

Having established the existence of scale invariance, we now turn to the question of its origin. Although scale invariance is widely observed in biology[2,10–18], the basis for such scale-invariant behaviour has remained elusive. Scale invariance in complex systems could be caused by nonlinear dynamics, as it is well known that nonlinear dynamics can give rise to intermittency, chaos and scale invariance[19]. However, it has been speculated that scale invariance may confer biological advantages related to adaptability of response; for example, loss of scale invariance for heartbeat intervals corresponds to a diseased state[2,12]. Scale invariance in foraging patterns may reflect the exploitation of highly complex environments which might themselves have fractal properties.[20–22]

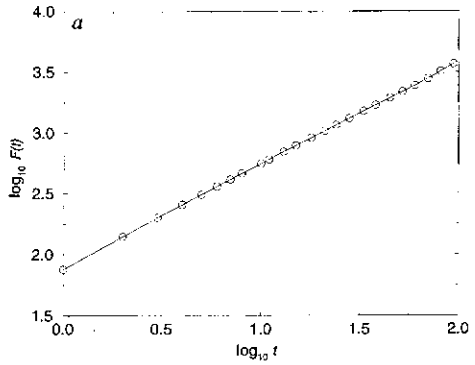
To study the origin of scale invariance found in our data, we plotted the distribution of flight-time intervals (Fig. 3*a*), and found for this distribution approximately a power law. To understand this finding, we developed a one-parameter Lévy flight model of bird foraging in which the probability of flying for a time t_i between landings is

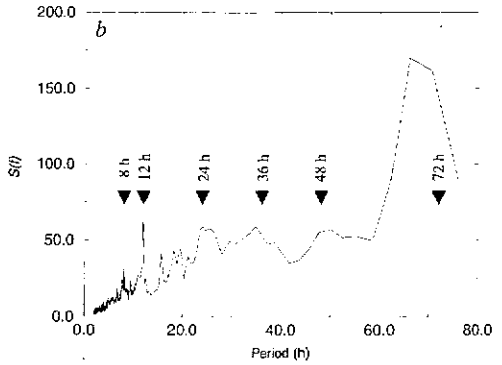
$$P(t_i) \sim (t_i + 1)^{-\mu} \qquad (2)$$

where the '+1 term' arises because the bird spends exactly one unit of time on water for each landing. A power-law distribution of flight-time intervals corresponds to a Lévy walk, not a Lévy flight, but the landing points of the bird correspond to points visited in a Lévy flight (see refs 2,23). We observed a value of $\mu \approx 2$ in the histogram of flight times, so we fixed $\mu = 2$ in our model, and used simulations to find the r.m.s. fluctuation $F(t)$, shown in Fig. 3*b*. The model predicts long-range power-law correlations with $\alpha = 0.8 \pm 0.05$, consistent with the value $\alpha = 0.84 \pm 0.2$ obtained from the data. (It can be shown for the model that α approaches the limit $2 - \mu/2$ asymptotically for sufficiently long sequences.)

Conventional random walks have been used to model the foraging behaviour of bacteria and other organisms[24,25]. However, such models predict not a scale-invariant power law but rather a Poisson distribution, and so cannot explain our experimental findings of temporal scale invariance and Lévy flight behaviour[2,23]. The results of the present quantitative analysis are in conformity with existing qualitative suggestions that this species of seabird specializes in long journeys of 'random foraging'[26], searching for patchily and unpredictably dispersed prey over several million square kilometres. Interruptions to long foraging flight paths, which occur when the birds forage actively on a restricted oceanic area, could conceivably be related to the presence of ships[26]. As there are few ships in this region of the South Atlantic, we are confident that the effects of ships on our data were minimal during the period of our study.

We wondered why the flight times of birds follow a scale-invariant power-law distribution. We next relate the observed





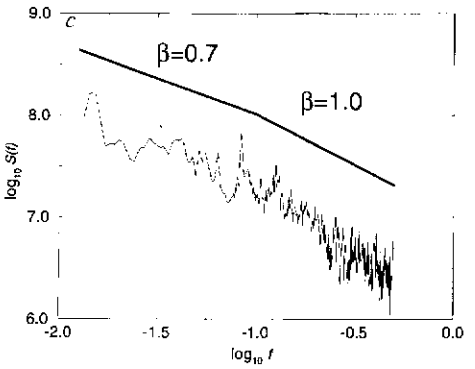
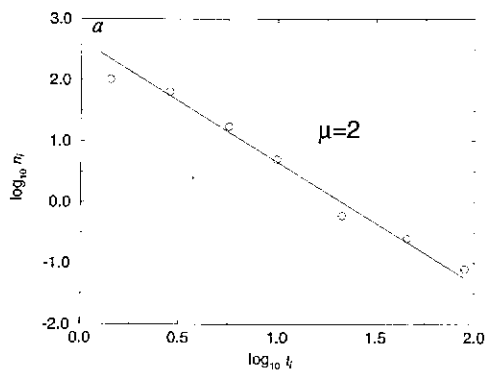


FIG. 2 *a*, Double log plot of the r.m.s. fluctuation $F(t)$. The regression fit gives $\alpha = 0.844 \pm 0.002$ ($F = 159{,}000$). As $\alpha > 0.5$, we conclude that long-range power-law correlations exist in the data. We calculate $F(t)$ by weighting equally all possible configurations of a moving window of length t over the 19 time series. *b*, The sum of the power spectra $S(f)$ of each of the 19 time series in units of 10^6, plotted against the period $1/f$. We find 12-h and 24-h components in the spectrum, consistent with the observation that these birds fly more during daytime than at night[5]. We use only those frequencies corresponding to periods smaller than the length of the smallest time series. That is, $f^{-1} < 77$ h. *c*, Double log plot of the sum of the spectra against frequency f using logarithmic binning. We define the scaling exponent β by $S(f) \sim f^{-\beta}$. The straight lines correspond to $\beta = 1.0$ and $\beta = 0.7$, respectively, showing that the spectrum approximately follows power laws in the two regimes indicated. As $2\alpha = 1 + \beta$ (ref. 7), the low-frequency (large time scale) value $\beta \approx 0.7$ is consistent with the value of $\alpha = 0.84$. In both regimes, the spectrum is not like the white noise ($\beta = 0$) associated with temporally uncorrelated behaviour, but more like the '1/f' spectra associated with long-range correlations in scale-invariant systems.



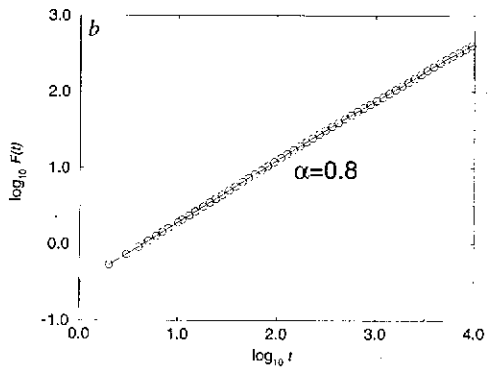


FIG. 3 *a*, Distribution giving the number n_i of intervals in the entire data set with flight-time intervals t_i. We used bin widths of 2^k h for the bin k, and used the geometric midpoints of the bins to plot the results. The Lévy-walk model of foraging fits the data quite well, as can be seen by the agreement of the data with the straight line of slope -2. *b*, Double log plot of the r.m.s. fluctuation $F(t)$ for the model, which gives rise to long-range power-law correlations with $\alpha > 0.5$. Also, the numerical value of α is consistent with the experimental results (Fig. 2a).

temporal behaviour to a possible spatial scale-invariance property in the underlying ecosystem[20]. It is known that the points visited by a Lévy flight form a fractal with dimension $D = \mu - 1$ (refs 2, 23). Figure 4 illustrates typical flight patterns constructed from the data and from the model, assuming that the distance travelled is proportional to the time spent dry, and that the flight directions change randomly after spending time in water. Although the latter assumption is unrealistic, it is nevertheless equally unrealistic for both the model and for the real data. The landing points of the birds have spatially scale-invariant properties, which may indicate that the distribution of food on the ocean surface is also scale invariant[27]. If this is so, then there would be voids on all length scales where there is little or no food, and birds that fail to produce a scale-invariant distribution of flight-time intervals would face a greater difficulty finding food, and hence surviving. It is also not inconceivable that the power-law distribution of flight intervals may be related to the lifetime distribution of the thermals used by the birds to fly[1].

An additional potential advantage of Lévy flights, suggested first for insects (M. F. Shlesinger, personal communication), relates to foragers that operate in swarms or flocks. After t steps, a single brownian walker in two dimensions visits $t/\ln t$ new sites, whereas a single Lévy walker visits t new sites[28]. This is not a large difference: Lévy flights are not much better than brownian motion in terms of reaching new sites. But for a 'swarm' comprised of N walkers, there is a large difference between the brownian walk and the Lévy flight: after t steps, a brownian swarm of N walkers visits only $t\ln(N/\ln t)$ distinct sites until an astronomically large crossover time $t_x \sim e^N$ is reached[28], whereas the swarm of Lévy walkers visits Nt sites. Thus the Lévy flight pattern allows the individual to visit new sites that the swarm has not visited. As some prey can migrate vertically in response to predators, the food at a given site may become unavailable for some time, thereby forcing the birds to find new sites not yet visited. Thus Lévy flight search patterns in animal behaviour may reflect the solution of the biological search problem in complex environments, and it would be interesting to repeat this type of study for birds whose

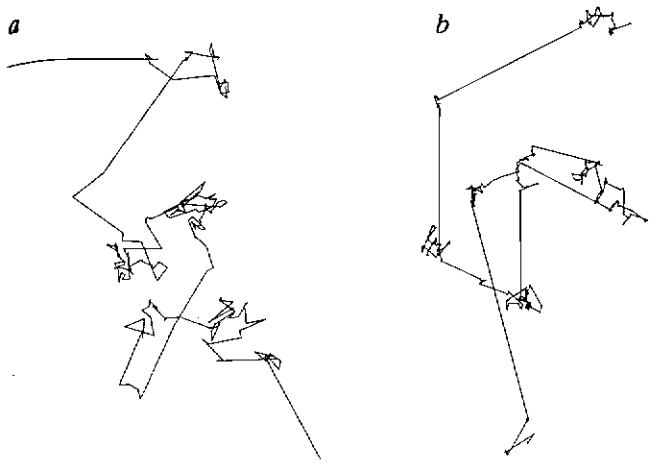


FIG. 4 *a*, Possible flight path of a bird constructed from the longest time series, as described in the text. The time resolution of the data prevents us from considering changes in flight directions which occur more frequently than once per hour. *b*, Possible flight path given by the Lévy-walk model discussed in the text. Both flight paths have scale-invariant 'fractal' properties which may indicate that the distribution of food on the ocean surface is spatially scale invariant.

foraging strategies are different from those of the wandering albatross.

Our findings represent a first attempt at studying Lévy flight search patterns in animal behaviour, and we expect the quality of such studies to improve with better data. So far, only qualitative analyses of data from satellite tracking of the wandering albatross have been presented[26,29,30]. A preliminary analysis of foraging patterns of other species suggests that Lévy flights may be more widespread in nature (see data shown in Fig. 4 of ref. 31). As more data becomes available, quantitative analyses should provide an improved view of the foraging strategies of animals in complex environments. □

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Sensitivity to leptin and susceptibility to seizures of mice lacking neuropeptide Y

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NEUROPEPTIDE Y (NPY), a 36-amino-acid transmitter distributed throughout the nervous system[1,2], is thought to function as a central stimulator of feeding behaviour[1–4]. NPY has also been implicated in the modulation of mood[5], cerebrocortical excitability[6], hypothalamic–pituitary signalling[7], cardiovascular physiology[1,8] and sympathetic function[9,10]. However, the biological significance of NPY has been difficult to establish owing to a lack of pharmacological antagonists. We report here that mice deficient for NPY have normal food intake and body weight, and become hyperphagic following food deprivation. Mutant mice decrease their food intake and lose weight, initially to a greater extent than controls, when treated with recombinant leptin. Occasional, mild seizures occur in NPY-deficient mice and mutants are more susceptible to seizures induced by a GABA (γ-aminobutyric acid) antagonist. These results indicate that NPY is not essential for certain feeding responses or leptin actions but is an important modulator of excitability in the central nervous system.

The NPY gene was disrupted in embryonic stem cells by homologous recombination using a targeting vector in which exon 2, encoding the signal peptide and 35 amino acids of NPY, was replaced by the *lacZ* reporter gene and a neomycin-resistance cassette (Fig. 1*a*). Mice heterozygous for NPY were generated from three correctly targeted clones and bred to create mice of all possible genotypes (Fig. 1*b*). Assaying for β-galactosidase activity with X-gal revealed prominent nuclear staining in neurons of the cerebral cortex, hippocampus, arcuate nucleus of the hypothalamus, and several brainstem nuclei (Fig. 1*d*). X-gal staining was also apparent in paravertebral sympathetic ganglia, dorsal spinal cord, and enteric neurons (not shown). The distribution of X-gal staining corresponded closely to the location of NPY-expressing cells as previously determined by immunostaining and *in situ* hybridization[1].

Mice homozygous for the disrupted allele do not contain detectable NPY messenger RNA in brain or NPY immunoreactivity in brain or adrenal gland (Fig. 1*c*, *e*). Mutant mice are born at approximately the expected frequency, with over 80 NPY-deficient mice produced so far, and are viable through adulthood. Gross and histological examination of brain and other organs revealed no anomalies. Growth of mutant mice occurs at a normal rate and both male and female mutants are fertile, demonstrating that the neuroendocrine systems regulating growth and reproduction as well as the sympathetic innervation to the vas deferens are functional in the absence of NPY.

A subset of young adult NPY-deficient mice had mild seizures, characterized by jerking of the head and body, tail erection and vocalization. Typically, these episodes lasted ~60 s and were witnessed when mice were placed on the cage top. On several occasions, mice fell over and exhibited forelimb clonus, but recovered apparently unharmed. Seizures occurred in 8 of 28 mutants and none of 40 littermate controls over a 10-week period in which each mouse was placed on the cage top for at least 5 min each week. Seizures usually occurred in 6–8-week-old mice and then remitted as they aged, suggesting that NPY exerts an inhibitory influence on neural excitability that is especially critical at that time of development. No other behavioural modifications were obvious in NPY-deficient mice.

Although seizures were not observed in mice older than 9