Animal behaviour is an endless challenge to mathematical modellers. In the first of two features, **Mark Buchanan** looks at how a mathematical principle from physics might be able to explain patterns of movement. In the second, **Arran Frood** asks what current models can teach us about ecological networks half a billion years old.

THE MATHEMATICAL MIRROR TO ANIMAL NATURE

C. BERRIE

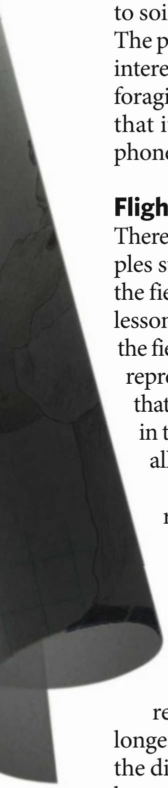
Food is not, in general, spread equally around the world; it comes in lumps. Foragers thus need a strategy for finding those lumps. One appealing option is a Lévy flight — a mathematical concept used in physics. Lévy flights are many-legged journeys in which most of the legs are short, but a few are much longer. They are found in some sorts of diffusion, in fluid turbulence, even in astrophysics. In animal behaviour, the longer the flight, the farther afield a creature will get, offering a way to efficiently exploit food nearby but also to discover sources farther away.

"The pattern captures what biologists often notice," says behavioural ecologist David Sims of the Marine Biological Association Laboratory in Plymouth, UK. "Animals often take lots of short steps in a localized area before making long jumps to new areas."

But just because it makes qualitative sense doesn't mean it is a mathematical key to the real world. Hard evidence is needed to show that the pattern is a real Lévy flight, in which the frequency of steps of given distances is firmly constrained. And this evidence is what physicist Gandhimohan Viswanathan, then a graduate student at Boston University in Massachusetts, and his colleagues seemed to find in 1996.

Albatrosses soar over tremendous distances as they circle the oceans, alighting here or there to feed on squid, fish or krill before heading off again. Observers had thought the foraging was random; but any hidden pattern would be evident only on the scale of seas and oceans. It was this large pattern that Viswanathan, now at the Federal University of Alagoas in Brazil, decided to look for, using electronic logging data gathered by field ecologists at the British Antarctic Survey (BAS) in Cambridge.

Viswanathan and his colleagues found a scale-free fractal-like pattern in the data[1], just what a Lévy flight ought to produce. Three years



later, they seemed to be on the track of a new principle of ecology when they showed that this way of moving is, under some conditions, theoretically the best way for animals to find scarce prey[2]. They and other researchers soon reported the same pattern in the movements of everything from reindeer and bumblebees to soil amoebas and the habits of fishermen[3]. The phenomenon is attracting more and more interest, and it seems to apply to more than just foraging. Research in this week's *Nature* shows that it applies to the movements of mobile-phone users[4] too (see page 779).

Flights of fancy?

There's just one problem. Although other examples stand up to scrutiny, the one that started the field off does not, at least for now. There's a lesson in that. When modellers use data from the field, they have to be sure that the data really represent what they think they represent, and that they fit tightly to their model. The devil is in the detail, when sparse data can put almost all conclusions on shaky ground.

The case for Lévy flights by albatrosses ran into problems in 2004, when physicist Sergey Buldyrev, also of Boston University and one of Viswanathan's co-authors on the original albatross paper, analysed new data on albatross movements. The Lévy pattern didn't turn up. Revisiting the original data collected by the BAS researchers, Buldyrev discovered that the longest flights recorded, which were crucial to the distinctive fractal fingerprint, might have been artefacts of the recording technique.

The original albatross data came from devices called immersion loggers attached to the birds' legs. The devices recorded the proportion of time in each quarter-minute that the birds sat on the sea surface. From these data, the researchers could then infer flights as periods during which the birds remained dry. From five birds, the researchers had obtained a total of 363 flight times, which seemed to show the Lévy pattern.

But Buldyrev wondered whether the longest periods of dry-leggedness — which always seemed to be the first and last in a bout of movement — might in fact record the birds sitting on their nests. The data had not been saying what the team thought they were saying. Finding that the Lévy pattern vanished when these data points were omitted, Buldyrev and his colleagues wrote up a manuscript and sent a draft to ecologist Richard Phillips at the BAS. Phillips, working with ecological modeller Andrew Edwards, also at the BAS, confirmed that there was no support for Lévy flights. Later, when they discovered that some of the albatrosses also had location trackers fitted to them, the BAS team proved that the birds weren't moving during the alleged long flights. "I was disappointed," says Viswanathan, "but also curious, surprised and perplexed."

The Lévy flight notion took another blow last October, when the Boston and Cambridge groups collaborated to publish a comprehensive reanalysis of the original albatross data, including an analysis of a new data set and a reconsideration of earlier studies of deer and bumblebees[5]. They found that the deer and bumblebee data were also ambiguous — the deer data, for example, actually reflected time spent cropping and processing food at a particular feeding site, rather than time spent moving between sites. Using improved statistical techniques, the teams found that none of the data offered strong support for the Lévy flight pattern. The results, they say, "question the strength of the empirical evidence for biological Lévy flights."

"It was wrong, yet it turned out to be fruitful because it led to other ideas that we now think are correct." — Eugene Stanley

It looked like a simple tale of problematic data corrected. But later last year, Sims and his colleagues presented strong evidence for Lévy-like patterns in the foraging of numerous marine predators, including sharks, turtles and penguins[6]. They used what all researchers agree are more sophisticated statistical methods, and much larger data sets. Sims and others now suggest that the data really do point to Lévy flights for a variety of animals, including humans.

Not everyone yet agrees with this position. But they do agree that the episode illustrates the difficulties inherent in identifying statistical patterns with limited data. The difference between a Lévy flight and a more familiar form of random walk, brownian motion, is the distribution of steps of different lengths. In brownian motion, as seen in the jittering of a pollen grain buffeted on all sides by invisible molecules, the distribution of distances follows a bell-shaped curve, so the size of the next step is at least crudely predictable — it is never 10 or 100 times bigger than the average, for example.

Doing the Lévy walk

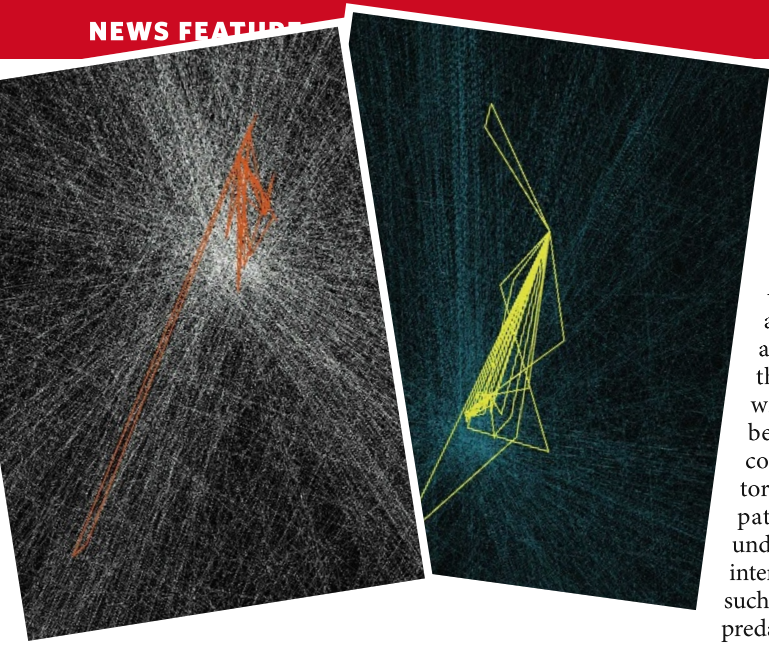
A Lévy flight is a similar sort of random walk — but the distribution of distances is different. For example, the probability of large steps of size D might fall off in proportion to d^{γ}, with γ being a number somewhere between 1 and 3. This distribution, in what is known as a power law, gives more frequent long steps than a bell curve, and produces a pattern characterized by lots of smaller movements broken episodically by long excursions.

Diagnosing a true Lévy flight means showing that the power-law distribution holds. There is a simple statistical approach to this. First 'bin the data': that is, count up the events that fall within each small range of distances to get a measure of the way the probability of differing distances is distributed. If a power law holds, the relationship between the logarithm of this probability distribution and the logarithm of the distance will be linear. Hence, if the log of the first is charted against the log of the second, you'll get a straight line.

As Edwards points out, however, this technique can lead to trouble. "It's well known that log–log axes tend to make relationships look straight." The problem is at its worst when data are in short supply. A more rigorous approach, he says, is to decide mathematically which of two possible distributions, say a power law or an exponential, the data fit better. But such

T. ALLOFS/ZEFA/CORBIS

Dry of foot, but not flying.



Mobile phone records reveal peoples' movements.

C. A. HIDALGO & M. C. GONZALEZ

determinations need a lot of data.

Sims agrees. Inspired by the original albatross paper, he and his colleagues used satellite-linked tags to gather data on plankton-feeding basking sharks. They found horizontal tracks reminiscent of Lévy-like movements, but never obtained enough data to permit a sound statistical analysis. "A lack of data," he says, "means you can fail to detect the pattern even if it's there, or detect an apparently similar pattern even if it is not."

Two years ago, Sims hit on the idea to look at sharks' vertical movements instead. These were recorded at 1-minute intervals for months on end, providing more than 400,000 data points for analysis. Using statistical methods developed in part by Mark Newman of the University of Michigan, Ann Arbor, and similar to those used by Edwards and his team, they found a strong signal of Lévy behaviour. Sims then organized a collaboration of 18 researchers from four countries to gather and test similar data for other marine predators, finding the Lévy pattern for tuna, cod, leatherback turtles and penguins[6].

Sims says that his paper "represents some of the strongest evidence for Lévy-like behaviour in wild predators". "The debate has shifted," says Frederic Bartumeus of Princeton University in New Jersey, who in 2003 found Lévy patterns in the movements of plankton. "The question now isn't whether animals perform Lévy walks, but when they do — and why."

Although welcoming the use of larger data sets, Edwards, now at the Pacific Biological Station in Nanaimo, British Columbia, Canada, doesn't think that these studies end the debate. He says that some scientists have started to use the somewhat softer phrase 'Lévy-like' to describe their results, which may make their claims more defensible, but also introduces some vagueness into the discussion. "How 'non-Lévy-like' do the data have to be for them not to be considered 'Lévy-like' any more?" he says.

The matter is not mere pedantry: getting the pattern right should help researchers to answer meaningful biological questions — which organisms, if any, forage optimally, and why. Yet for Sims, the qualifier 'like' is not without its uses. It could be useful in probing the complex, interacting factors that affect movement patterns. "Animals often undertake other behaviours interspersed with searching, such as social interactions or predator avoidance," he says, which may weaken the Lévy signal.

Man in the mirror

However the debate plays out, analyses of data from one particular animal, humans, are likely to be increasingly important. Over the past decade, technology has transformed researchers' ability to gather quantitative data on human activities, ranging from patterns of e-mail use to consumers' buying habits. People happily carry radio trackers and tags around in the form of mobile phones. "We finally have objective measurements of what people do," says Albert-László Barabási, a researcher studying human dynamics in this way at the Center for Complex Network Research, based at Northeastern University in Boston. "Our observations don't influence them."

This work can be viewed, perhaps, as the beginnings of a natural ecology of human behaviour, for which understanding patterns of physical movement — the crude equivalent of animal foraging — would offer an obvious first goal. Two years ago, physicist Dirk Brockmann of the Max Planck Institute in Göttingen, Germany, took an indirect stab at the issue using the website www.wheresgeorge.com, which facilitates the tracking of dollar notes moving through the United States. People can go to the site and enter the date, their location and the serial numbers of dollar bills in their possession. As the bills move, the site shows their changing locations.

"It's well known that log-log axes tend to make relationships look straight." — Andrew Edwards

Almost 60% of bills starting in New York City were reported 2 weeks later still within 10 kilometres of their starting point. But another 7% had jumped to distances beyond 800 kilometres. If this seems similar to the Lévy pattern, it is. The researchers found that the distribution of distances travelled over a short time follows a power law with a γ equal to about 1.6 (ref. 7).

These data don't directly say anything about the human movements that transport dollar bills. But a team led by Barabási has now gone one step further, using anonymized mobile-phone data to track the movements of more than 100,000 people over a 6-month period. The statistics, they found, again show the Lévy pattern, although with some additional complexity[4].

The team found, overall, that the distribution of the distance moved between two subsequent phone calls follows a power law with an exponential cut-off. The best way to explain this pattern, the researchers argue, is through a combination of two effects — first, a real tendency for individuals to move in a Lévy-like pattern, with many short movements and less frequent long excursions, but also a difference between people in the overall scale on which they move, with some people being inherently longer travellers than others. When the researchers normalized the measurements so that the person-to-person scale factor no longer played a part, the data for all the participants fell onto a single curve. "There are a lot of details that make us different," says Barabási, "but behind it all there's a universal pattern."

And what of the albatrosses? Are they an oddity — an error that nevertheless served as the basis for insights into truth? Perhaps. "I think of it like the Bohr model of the atom," says Eugene Stanley, a physicist from Boston University who was one of the original authors. "It was wrong, yet it turned out to be fruitful. The remarkable fact is that flawed data led to a fascinating idea: a general law governing animal movement."

Or perhaps albatrosses do roam the high seas in the way that Lévy might have anticipated, and we will know that in time with better data and analyses. As Viswanathan points out, he and his colleagues' 1999 paper showing the theoretical optimality of Lévy-style foraging provides a good *a priori* reason to expect that some animals, and quite possibly albatrosses, might exploit this trick.

"Given the power of natural selection," says Viswanathan, "it seems unlikely to me that Lévy walks wouldn't exist somewhere in animal biology. It would be as strange as if vision had never evolved." ■

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