CrossMark

A priority-based queuing process explanation for scale-free foraging behaviours

Andrew M. Reynolds [a, *], Yan Ropert-Coudert [b, c], Akiko Kato [b, c], Andre Chiaradia [d], Andrew J. J. MacIntosh [e, f]

[a] Rothamsted Research, Harpenden, Hertfordshire, U.K.
[b] CNRS, UMR7178, Strasbourg, France
[c] Université de Strasbourg, IPHC, Strasbourg, France
[d] Research Department, Phillip Island Nature Parks, Cowes, Victoria, Australia
[e] Kyoto University Wildlife Research Center, Sakyo, Kyoto, Japan
[f] Kyoto University Primate Research Institute, Inuyama, Aichi, Japan

ARTICLE INFO

Spatial scale-invariant Lévy walk (power-law) patterns seem common among animals that move continually during searching. Scaling laws also describe well the spontaneous patterns of waiting times of sit-and-wait ambush predators, which show random 'burstiness' that appears scale-invariant across a broad set of scales. The occurrence of these scaling laws has been attributed to stochastic decision-based queuing processes. Taken together these various studies suggest that stochastic decision-based queuing processes may apply more generally across taxa with divergent foraging strategies, ranging from highly mobile pursuit predators to the less mobile ambush predators. Here we provide support for this proposition by demonstrating that simple stochastic priority processes capture accurately the timings of dives made by little penguins, *Eudyptula minor*, in their natural habitat, whose use of space and time falls between that of sit-and-wait predators and Lévy walkers.

The decisions that animals make about how long to engage in particular activities (e.g. waiting or moving) have a central influence on the success of behaviours that can affect survival and lifetime reproductive output (Houston & McNamara, 1999; Stephens & Krebs, 1986). For sit-and-wait ambush predators (cephalopods, sharks, skates, teleosts) the distributions of waiting times show random 'burstiness' that appears scale invariant across a broad set of scales (Wearmouth et al., 2014). These temporal (waiting time) scaling laws may represent the parallel in ambush predators of the spatial scale-invariant Lévy walk (power-law) patterns that seem common among animals that move continually during searching (Harris et al., 2012; Hays et al., 2011; Humphries et al., 2010; Humphries, Weimerskirch, Queiroz, Southall, & Sims, 2012; Korobkova, Emonet, Vilar, Shimizu, & Cluzel, 2004; Raichlen et al., 2014; Reynolds et al., 2007; Sims et al., 2014, 2008; Viswanathan, da Luz, Raposo, & Stanley, 2011). Although the occurrence of these statistical laws seems remarkable given

that an animal's behaviour is strongly shaped by its psyche and by complex environmental interactions, they can in fact be attributed to simple stochastic–deterministic decision processes (Reynolds, 2011; Viswanathan et al., 2011; Wearmouth et al., 2014).

Decision-based queuing process models prioritize certain actions over others (e.g. exploration over exploitation), making them appropriate candidate models to examine how simple rules may potentially underlie apparently complex movement patterns. The models capture a tension between two mutually exclusive, competing activities. In the simplest version, two competing behaviours (activities 1 and 2) are given 'priorities' x_1 and $x_2 = 1 - x_1$, which are randomly selected from some distribution $\rho(x)$ (Reynolds, 2011). These priorities are treated as probabilities such that activity 1 is chosen with probability x_1 and activity 2 is chosen with probability x_2. If activity 1 is chosen, then priorities x_1 and x_2 remain unchanged (because the animal's internal state does not change significantly), whereas if activity 2 is chosen the animal actively forages and may feed or become hungrier, affecting its 'state', and thus new priorities are randomly selected from $\rho(x)$.

* Correspondence: A. M. Reynolds, Rothamsted Research, Harpenden, Hertfordshire, AL5 2JQ, U.K.
E-mail address: andy.reynolds@rothamsted.ac.uk (A. M. Reynolds).

Wearmouth et al. (2014) introduced a degree of determinism into the model by replacing x_1 with $x_1' = \frac{1}{1+\left(\frac{x_2}{x_1}\right)^\gamma}$ and x_2 with $x_2' = 1 - x_1'$. This form is chosen because it smoothly interpolates between the aforementioned stochastic protocol (obtained when $\gamma = 1$) and a deterministic protocol (obtained as $\gamma \to \infty$). In the deterministic protocol the highest priority activity is always performed next (i.e. low-priority activities are no longer selected, because $x_1' \to 1$ if $x_1 > x_2$ and $x_1' \to 0$ if $x_2 > x_1$). For intermediate cases ($\gamma > 1$) the highest-priority activity is executed with probability close to unity while the lower-priority activity is rarely executed. The model predicts that the durations of bouts of activity 1 are power-law distributed while those of activity 2 are exponentially distributed. A simple proof of this can be found in Reynolds (2011). The power-law exponent depends upon the degree of determinism (i.e. the value of γ) and ranges between 2 (the purely stochastic case) and 1 (the strongly deterministic case).

The simplest, purely stochastic version of this model may account for some movement patterns in probabilistic foragers that can be approximated by Lévy walks. The scaling behaviours of sit-and-wait predators, which are dependent upon body size and energy content of the prey, are captured by the more general version of the model which incorporates a degree of determinism. None the less, it remains to be seen whether stochastic–deterministic priority processes arise in taxa exploiting alternative foraging strategies. Here, we addressed this by testing whether or not the model captures accurately the foraging patterns of active predators, little penguins, *Eudyptula minor*, in their natural habitat. Our objective was not to refine or develop the model but rather to apply it to a novel subject, that of an active predator, and thereby test the range of its validity.

METHODS

During the 2010 breeding season, we fitted 28 free-living little penguins from the Penguin Parade, Phillip Island (38°31′S, 145°09′E), Victoria, Australia, with time–depth data loggers (ORI400-D3GT, Little Leonardo, 12×45 mm, 9 g) set to record depth to a resolution of 0.1 m with an accuracy of 1 m (range 0–400 m) at 1 s intervals. Dive records were collected during the guard stage of the chick-rearing period when penguins conduct single, 1-day foraging trips. Devices were attached using waterproof Tesa tape (Beiersdorf AG, Hamburg, Germany) along the median line of the lower back feathers to minimize drag and facilitate rapid deployment and easy removal upon recapture. Birds were recaptured after one foraging trip and the logger and tape were removed (MacIntosh, Pelletier, Chiaradia, Kato, & Ropert-Coudert, 2013).

Observed surface time intervals were fitted to the stochastic priority list models described above, which produce mixed bimodal (power-law exponential) distributions (equation (1a) below). We then tested whether the stochastic priority list model provided better fits to our observed surface time intervals than other three competing models: (1b) a power-law model; (1c) an exponential model, indicative of a Poisson process; and (1d) a bi-exponential model. These model distributions are prescribed by:

$$p_1(l) = AN_1 l^{-\mu} + (1 - A)N_2 \exp(-\lambda l) \tag{1a}$$

$$p_2(l) = N_1 l^{-\mu} \tag{1b}$$

$$p_3(l) = N_2 \exp(-\lambda l) \tag{1c}$$

$$p_3(l) = AN_3 \exp(-\lambda_1 l) + (1 - A)N_4 \exp(-\lambda_2 l) \tag{1d}$$

where N_1, N_2, N_3 and N_4 are normalization factors that ensure that the frequency distributions sum correctly to unity when integrated over all time intervals between the lower and upper cutoffs; μ is the power-law exponent (known as the Lévy exponent in the literature on Lévy flight foraging; Sims et al., 2008); λ, λ_1 and λ_2 are the exponential decay rates; and A and $1 - A$ are the relative weights of the two modes in the bimodal distributions. Fits to data were obtained using maximum likelihood methods. The lower cutoff was taken to be 50 s and the upper cutoff was taken to be longest of the intervals under consideration. However, comparable results were obtained when the lower cutoff was taken to be 10 s (data not shown).

Ethical Note

Animal handling during fieldwork was approved by the Phillip Island Animal Experimentation Ethics Committee (2.2010), with a research permit issued by the Department of Sustainability and Environment of Victoria, Australia (number 10006148). Handling of birds was conducted by a team of two trained scientists under the supervision of Dr Chiaradia, a member of staff at the Penguin Parade since 1995. The protocol for deploying loggers has been used since 2003 on an annual basis. Birds are identified using subcutaneous transponders, which are injected when they are juveniles, and are monitored continuously using an automated identification system in place at one of the entrance points of the colony. Birds breed in artificial nestboxes, which have removable lids that allow researchers to easily access the bird upon capture without causing stress during approach. Capture, handling and release of birds was conducted within 5 min, after which the bird was returned to its nestbox. During handling, a hood was kept on the bird's head, preventing it from seeing us. All instrumented birds were recaptured after a single foraging trip and none deserted its nest.

RESULTS

We found that the hallmark of the stochastic priority list model was evident in the diving patterns of free-ranging little penguins,
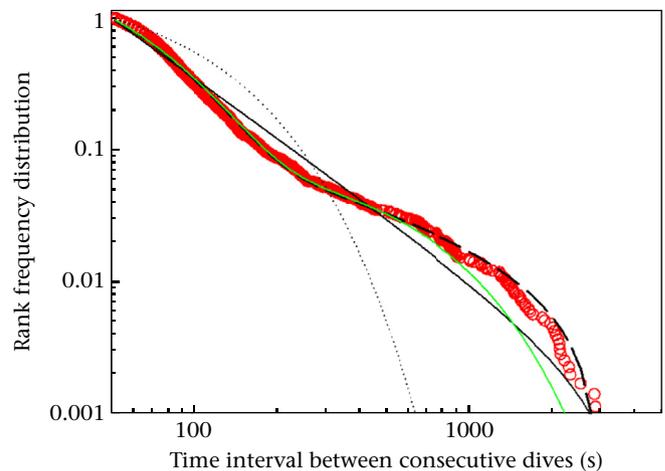

Figure 1. Rank frequency plot showing evidence of bimodal surfacing times between consecutive dives in free-ranging little penguins. Observations (○) pooled over the 28 individuals in the data set are shown together with theoretical expectations for the stochastic priority list model (dashed black line), and the best fit bi-exponential (solid green line), power-law (solid black line) and exponential distributions (dotted).

which are known to have fractal characteristics (MacIntosh et al., 2013). Time intervals between consecutive dives were bimodal (Figs. 1 and 2); they were power-law distributed in one mode and exponentially distributed in the other, albeit with individual-specific parameters (Table 1). This is evident at both population level (Fig. 1) and individual level (Fig. 2). The bimodality cannot be captured by either power law or single exponentials (Fig. 1), and for this reason these distributions are not shown in Fig. 2 and are not
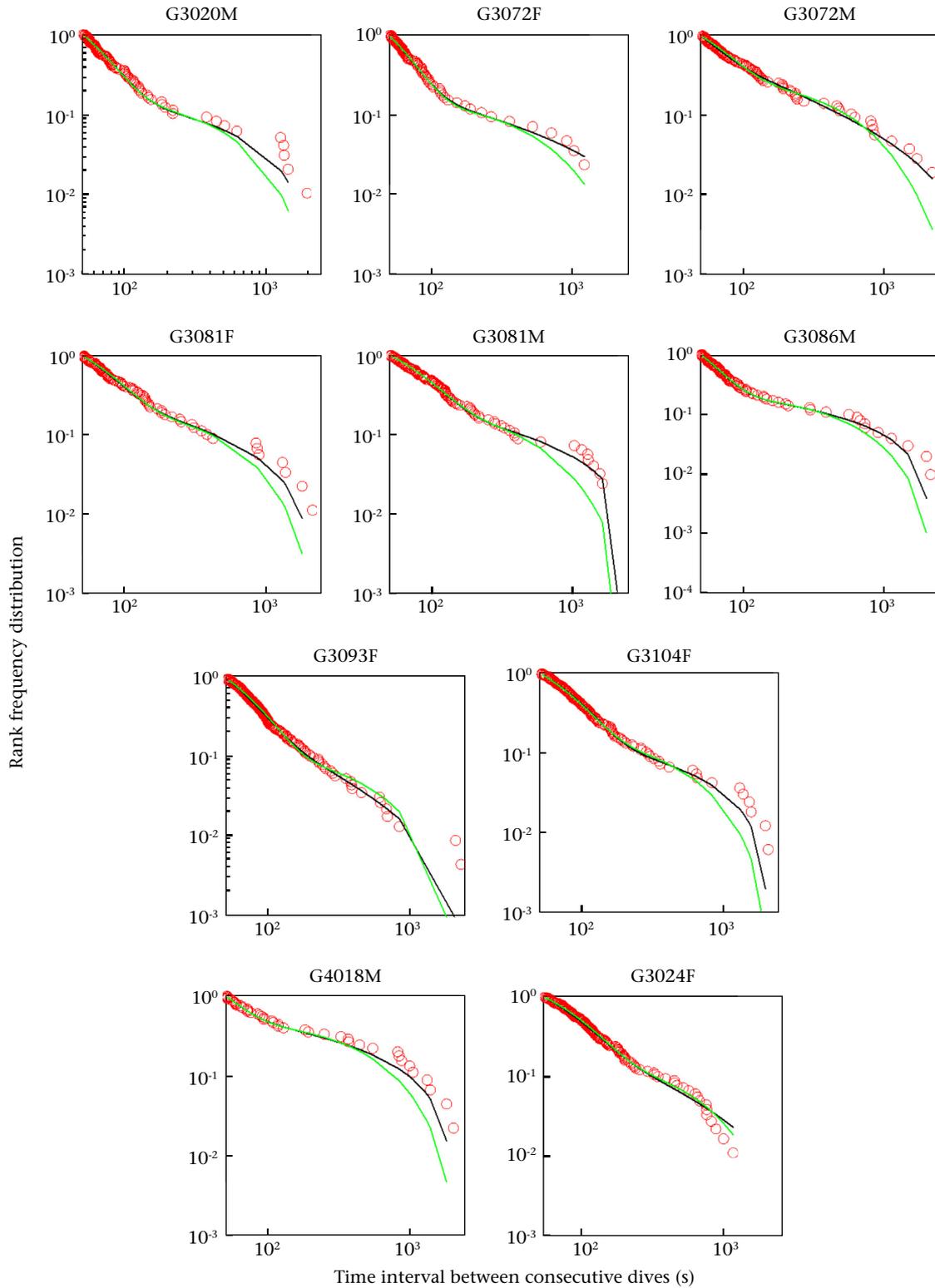

Figure 2. Rank frequency plot showing evidence of bimodal surfacing times between consecutive dives in individual free-ranging little penguins. Observations (○) for 10 individuals randomly sampled from the total of 28 examined in the data set are shown together with theoretical expectations for the stochastic priority list model (solid black line) and the best fit bi-exponentials (solid green lines).

Table 1
Maximum likelihood estimates for model parameters across individuals

Bird	½ log-likelihood bimodal	½ log-likelihood bi-exp	Akaike weight for bimodal	A	λ	μ
3002M	−398.0	−411.7	0.98	0.66	0.044	1.60
3004M	−581.9	−582.8	0.67	0.41	0.040	1.60
3020M	−506.3	−508.4	0.89	0.18	0.034	1.05
3024M	−476.3	−480.3	0.98	0.16	0.020	1.10
3027M	−614.7	−618.4	0.98	0.16	0.043	1.10
3072M	−600.6	−604.3	0.98	0.62	0.048	1.70
3076M	−697.1	−698.7	0.83	0.41	0.026	1.70
3079M	−479.5	−485.4	1.00	0.45	0.050	1.85
3081M	−696.1	−700.7	0.99	0.24	0.022	1.10
3086M	−511.6	−513.5	0.87	0.24	0.049	1.05
3098M	−378.9	−379.0	0.52	0.20	0.042	1.05
3111M	−718.8	−719.8	0.73	0.32	0.040	1.45
4018M	−274.0	−275.9	0.87	0.55	0.049	1.05
4020M	−231.1	−231.4	0.57	0.51	0.050	1.05
3004F	−687.6	−692.7	0.99	0.43	0.050	2.00
3020F	−872.9	−876.6	0.98	0.46	0.027	2.05
3024F	−989.7	−989.1	0.35	0.43	0.022	1.75
3027F	−820.4	−821.0	0.65	0.25	0.034	1.50
3058F	−892.9	−894.1	0.77	0.15	0.024	1.05
3072F	−422.3	−424.9	0.44	0.21	0.043	1.35
3076F	−669.1	−674.1	0.99	0.68	0.046	1.80
3078F	−328.1	−328.2	0.48	0.42	0.050	1.05
3079F	−533.1	−533.9	0.69	0.10	0.048	1.05
3081F	−483.5	−485.5	0.88	0.32	0.029	1.25
3093F	−1090.7	−1093.4	0.94	0.36	0.033	1.90
3098F	−1157.7	−1158.5	0.69	0.92	0.011	2.10
3104F	−890.1	−893.1	0.95	0.17	0.023	1.05
3114F	−914.1	−917.6	0.97	0.21	0.020	1.35

A is the weight of mode 1, λ is the exponential decay rate and μ is the power-law exponent.

presented in the accompanying Table 1. Bi-exponentials are, however, more strongly competing model distributions. The estimates for the characteristic power-law exponents, μ, were typically less than 2 (Table 1), indicating that in most cases decision making was strongly deterministic rather than stochastic, which was previously shown to be the case for Lévy walkers (Sims et al., 2008). For ambush predators, characteristic scaling exponents are species dependent and range between 1.5 and 2 (Wearmouth et al., 2014). The fits of such bimodal distributions to the empirical observations are striking, and are visibly better than those attained by power-law or exponential distributions. Furthermore, comparison of maximum likelihood estimates and Akaike weights clearly demonstrate that the stochastic priority list model provides a significantly better fit to the observed data in the majority of cases than the more strongly competing bi-exponential distributions.

DISCUSSION

In this study, we demonstrate that the stochastic priority list models developed by Reynolds (2011) and applied to sit-and-wait predators by Wearmouth et al. (2014) also accurately describe the behaviour sequences of an active predator, the little penguin. Our results thus provide strong evidence that stochastic priority list models can describe scale-invariant behaviour across taxa with a wider range of foraging strategies than previously acknowledged. Taken together, the results of our study and those of Reynolds (2011) and Wearmouth et al. (2014) may provide a unifying mechanism for scale invariance across ecological contexts. Scale-invariant patterns of switching between two contrasting activities have, after all, been observed in a diverse range of behaviours. The durations of waking episodes during sleep–wake transitions in mammals (mice, rats, cats and humans) are, for example, power-law distributed (Blumberg, Seelje, Lowen, & Karlson, 2005; Lo et al., 2004, 2002). The walking patterns of Drosophila flies in featureless environments are organized into alternating bouts of

activity and inactivity, such that the durations of the bouts of inactivity are power-law distributed across a broad range of scales (Martin, 2004). Scale-invariant patterns of switching between contrasting activities have even been reported in pigs during nest building, when nosing the ground and alertness compete with the need to rest, feed, drink and defecate (Harnos, Horváth, Lawrence, & Vattay, 2000; Reynolds, 2011). But these cases appear to be examples of purely stochastic decision-making processes, as the characteristic power law exponents are close to 2. Decision making in the penguins, however, can be more deterministic (Table 1) and so provides more scope for the testing of model predictions.

Additionally, the observed bimodal distribution of surface times echoes the results of conventional methods used to identify diving bouts, to separate periods of food patch exploitation (within foraging bouts) from between-patch exploration (interbout; Mori, Yoda, & Sato, 2001). Exploitation of food resources is the more heavily constrained of these competing activities because time at the surface is used primarily to replenish oxygen stores, anticipate stores needed for subsequent dives (Wilson, 2003) and remove the lactic acid that accumulates in the blood during diving (Butler, 2006). These physiological constraints prevent penguins from quickly returning to depths where prey are located to optimize prey intake. Between bouts, time at the surface is probably less constrained and birds can thus engage in a range of behaviours including exploring their environment in search of subsequent foraging patches, communicating, preening, etc.

The tensions between competing priorities encapsulated by the model are not necessarily consciously realized by the animal but could instead represent subliminally conflicting behaviours triggered by hormones, neurotransmitters and even body condition. It is known, for example, that corticosterone levels in penguins rise before foraging trips (Angelier et al., 2008), and that low body mass in little penguins triggers longer foraging trips (Saraux, Robinson-Laverick, Le Maho, Ropert-Coudert, & Chiaradia, 2011). Moreover, corticosterone and body mass have been linked to organizational

complexity in penguin dive sequences (Cottin et al., 2014; MacIntosh et al., 2013). In fact, scaling in temporal sequences of animal behaviour is known to be condition dependent, varying significantly in the presence of both endogenous and exogenous stressors (Alados, Escos, & Emlen, 1996; Asher et al., 2009; MacIntosh, Alados, & Huffman, 2011; Rutherford, Haskell, Glasbey, Jones, & Lawrence, 2004), a phenomenon known in the literature on fractal physiology as 'complexity loss' (Goldberger, 1996, 1997; Lipsitz & Goldberger, 1992). Our findings may provide a plausible explanation for this loss of behavioural complexity and incumbent loss of fractal scaling seen in individuals in impaired and distressed states: such individuals may simply dispense with prioritizing competing demands, leading to more deterministic and thus less complex sequences of behaviour.

Our analysis suggests that stochastic decision-making processes are pervasive and underlie scale-free patterns of behaviour seen across taxa. With the discovery of this generative mechanism for scaling in decision making it will become possible to disentangle innate, truly random behaviours from the additional influences of the environment, and so better understand the inherent complexity of natural behaviour patterns. Our results indicate that scale-specific complexity may be the result of environmental cues overriding innate behaviour, and that scale-free movements may be intrinsic and not limited to 'probabilistic' foragers as was previously thought.

Acknowledgments

References

Alados, C. L., Escos, J. M., & Emlen, J. M. (1996). Fractal structure of sequential behaviour patterns: an indicator of stress. *Animal Behaviour, 51*, 437–443. http://dx.doi.org/10.1006/anbe.1996.0040.

Angelier, F., Bost, C.-A., Giraudeau, M., Bouteloup, G., Dano, S., & Chastel, O. (2008). Corticosterone and foraging behavior in a diving seabird: the Adélie penguin, *Pygoscelis adeliae. General and Comparative Endocrinology, 156*, 134–144. http://dx.doi.org/10.1016/j.ygcen.2007.12.001.

Asher, L., Collins, L. M., Ortiz-Pelaez, A., Drewe, J. A., Nicol, C. J., & Pfeiffer, D. U. (2009). Recent advances in the analysis of behavioural organization and interpretation as indicators of animal welfare. *Journal of the Royal Society Interface, 6*, 1103–1119.

Blumberg, M. S., Seelje, A. M. H., Lowen, S. B., & Karlson, K.Æ. (2005). Dynamics of sleep-wake cyclicity in developing rats. *Proceedings of the National Academy of Sciences of the United States of America, 102*, 14680–14864.

Butler, P. J. (2006). Aerobic dive limit. What is it and is it always used appropriately? *Comparative Biochemistry and Physiology A, 145*, 1–6. http://dx.doi.org/10.1016/j.cbpa.2006.06.006.

Cottin, M., MacIntosh, A., Kato, A., Takahashi, A., Debin, M., Raclot, T., et al. (2014). Corticosterone administration leads to a transient alteration of foraging behaviour and complexity in a diving seabird. *Marine Ecology Progress Series, 496*, 249–262. http://dx.doi.org/10.3354/meps10618.

Goldberger, A. L. (1996). Non-linear dynamics for clinicians: chaos theory, fractals, and complexity at the bedside. *The Lancet, 347*, 1312–1314. http://dx.doi.org/10.1016/S0140-6736(96)90948-4.

Goldberger, A. L. (1997). Fractal variability versus pathologic periodicity: complexity loss and stereotypy in disease. *Perspectives in Biology and Medicine, 40*, 543–561. http://dx.doi.org/10.1353/pbm.1997.0063.

Harnos, A., Horváth, G., Lawrence, A. B., & Vattay, G. (2000). Scaling and intermittency in animal behaviour. *Physica A: Statistical Mechanics and its Applications, 286*, 312–320.

Harris, T. H., Banigan, E. J., Christian, D. A., Kondradt, C., Tait Wojno, E. D., Norose, K., et al. (2012). Generalized Lévy walks and the role of chemokines in migration of effector CD8^{+} T cells. *Nature, 486*, 545–548. http://dx.doi.org/10.1038/nature11098.

Hays, G. C., Bastian, T., Doyle, T. K., Fossette, S., Gleiss, A. C., Gravenor, M. B., et al. (2011). High activity and Lévy searches: jellyfish can search the water column like fish. *Proceedings of the Royal Society B: Biological Sciences, 279*, 465–473. http://dx.doi.org/10.1098/rspb.2011.0978.

Houston, A. I., & McNamara, J. M. (1999). *Models of adaptive behaviour.* Oxford, U.K.: Oxford University Press.

Humphries, N. E., Queiroz, N., Dyer, J. R. M., Pade, N. G., Musyl, M. K., Schaefer, K. M., et al. (2010). Environmental context explains Lévy and Brownian movement patterns of marine predators. *Nature, 465*, 1066–1069. http://dx.doi.org/10.1038/nature09116.

Humphries, N. E., Weimerskirch, H., Queiroz, N., Southall, E. J., & Sims, D. W. (2012). Foraging success of biological Lévy flights recorded *in situ. Proceedings of the National Academy of Sciences of the United States of America, 109*, 7169–7174. http://dx.doi.org/10.1073/pnas.1121201109.

Korobkova, E., Emonet, T., Vilar, J. M. G., Shimizu, T. S., & Cluzel, P. (2004). From molecular noise to behavioural variability in a single bacterium. *Nature, 428*, 574–578. http://dx.doi.org/10.1038/nature02404.

Lipsitz, L. A., & Goldberger, A. L. (1992). Loss of 'complexity' and aging: potential applications of fractals and chaos theory to senescence. *Journal of the American Medical Association, 267*, 1806–1809. http://dx.doi.org/10.1001/jama.1992.03480130122036.

Lo, C.-C., Chou, T., Penzel, T., Scammell, T. E., Strecker, R. E., Stanley, H. E., et al. (2004). Common scale-invariant pattern of sleep-wake transitions across mammalian species. *Proceedings of the National Academy of Sciences of the United States of America, 101*, 17545–17548.

Lo, C.-C., Nunes Amaral, L. A., Havlin, S., Ivanov, P. Ch., Penzel, T., Peter, J.-H., et al. (2002). Dynamics of sleep-wake transitions during sleep. *Europhysics Letters, 57*, 625–631.

MacIntosh, A. J., Alados, C. L., & Huffman, M. A. (2011). Fractal analysis of behaviour in a wild primate: behavioural complexity in health and disease. *Journal of the Royal Society Interface, 8*, 1497–1509.

MacIntosh, A. J. J., Pelletier, L., Chiaradia, A., Kato, A., & Ropert-Coudert, Y. (2013). Temporal fractals in seabird foraging behaviour: diving through the scales of time. *Scientific Reports, 3*, 1884. http://dx.doi.org/10.1038/srep01884.

Martin, J.-R. (2004). A portrait of locomotor behaviour in *Drosophila* determined by a video-tracking paradigm. *Behavioural Processes, 67*, 207–219.

Mori, Y., Yoda, K., & Sato, K. (2001). Defining dive bouts using a sequential differences analysis. *Behaviour, 138*, 1451–1466.

Raichlen, D. A., Wood, B. M., Gordon, A. D., Mabulla, A. Z. P., Marlowe, F. W., & Pontzer, H. (2014). Evidence of Lévy walk foraging patterns in human huntergathers. *Proceedings of the National Academy of Sciences of the United States of America, 111*, 728–733.

Reynolds, A. M. (2011). On the origin of bursts and heavy tails in animal dynamics. *Physica A: Statistical Mechanics and its Applications, 390*, 245–249. http://dx.doi.org/10.1016/j.physa.2010.09.020.

Reynolds, A. M., Smith, A. D., Menzel, R., Greggers, U., Reynolds, D. R., & Riley, J. R. (2007). Displaced honeybees perform optimal scale-free search flights. *Ecology, 88*, 1955–1961. http://dx.doi.org/10.1890/06-1916.1.

Rutherford, K. M. D., Haskell, M. J., Glasbey, C., Jones, R. B., & Lawrence, A. B. (2004). Fractal analysis of animal behaviour as an indicator of animal welfare. *Animal Welfare, 13*, S99–S103.

Saraux, C., Robinson-Laverick, S., Le Maho, Y., Ropert-Coudert, Y., & Chiaradia, A. (2011). Plasticity in foraging strategies of inshore birds: how little penguins maintain body reserves while feeding the chicks. *Ecology, 92*, 1909–1916. http://dx.doi.org/10.1890/11-0407.1.

Sims, D. W., Reynolds, A. M., Wearmouth, V. J., Humphries, N. E., Southall, E. J., Metcalfe, B., et al. (2014). Hierarchical random walks in trace fossils and the origin of optimal search behaviour. *Proceedings of the National Academy of Sciences of the United States of America, 111*, 11073–11078. http://dx.doi.org/10.1073/pnas.1405966111.

Sims, D. W., Southall, E. J., Humphries, N. E., Hays, G. C., Bradshaw, C. J. A., Pitchford, J. W., et al. (2008). Scaling laws of marine predator search behaviour. *Nature, 451*, 1098–1102. http://dx.doi.org/10.1038/nature06518.

Stephens, D. W., & Krebs, J. R. (1986). *Foraging theory.* Princeton, U.K.: Princeton University Press.

Viswanathan, G. M., da Luz, M. G. E., Raposo, E. P., & Stanley, H. E. (2011). *The physics of foraging.* Cambridge, U.K.: Cambridge University Press.

Wearmouth, V. J., McHugh, M. J., Humphries, N. E., Naegelen, A., Ahmed, M. Z., Southall, E. J., et al. (2014). Scaling laws of ambush predator 'waiting' behaviour are tuned to a common ecology. *Proceedings of the Royal Society B: Biological Sciences, 281*, 20132997. http://dx.doi.org/10.1098/rspb.2013.2997.

Wilson, R. P. (2003). Penguins predict their performance. *Marine Ecology Progress Series, 249*, 305–310. http://dx.doi.org/10.3354/meps249305.