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*Review*

## Stochastic modelling of animal movement

Peter E. Smouse<sup>1,\*</sup>, Stefano Focardi<sup>2</sup>, Paul R. Moorcroft<sup>3</sup>,  
John G. Kie<sup>4</sup>, James D. Forester<sup>3</sup> and Juan M. Morales<sup>5</sup>

<sup>1</sup>*Department of Ecology, Evolution and Natural Resources, Rutgers University,  
New Brunswick, NJ 08901-8551, USA*

<sup>2</sup>*Istituto Superiore per la Protezione e la Ricerca Ambientale, via Ca' Fornacetta 9,  
40064 Ozzano dell'Emilia, Italy*

<sup>3</sup>*Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA 02138, USA*

<sup>4</sup>*Department of Biological Sciences, Idaho State University, Pocatello, ID 83208, USA*

<sup>5</sup>*Laboratorio Ecotono, Centro Regional Universitario Bariloche, Universidad Nacional del Comahue,  
Comahue 8400, Argentina*

Modern animal movement modelling derives from two traditions. Lagrangian models, based on random walk behaviour, are useful for multi-step trajectories of single animals. Continuous Eulerian models describe expected behaviour, averaged over stochastic realizations, and are usefully applied to ensembles of individuals. We illustrate three modern research arenas. (i) Models of home-range formation describe the process of an animal 'settling down', accomplished by including one or more focal points that attract the animal's movements. (ii) Memory-based models are used to predict how accumulated experience translates into biased movement choices, employing reinforced random walk behaviour, with previous visitation increasing or decreasing the probability of repetition. (iii) Lévy movement involves a step-length distribution that is over-dispersed, relative to standard probability distributions, and adaptive in exploring new environments or searching for rare targets. Each of these modelling arenas implies more detail in the movement pattern than general models of movement can accommodate, but realistic empiric evaluation of their predictions requires dense locational data, both in time and space, only available with modern GPS telemetry.

**Keywords:** stochastic movement modelling; Lagrangian models; Eulerian models; home range; memory; Lévy

### 1. INTRODUCTION

Currently in the period of dynamic indeterminism in science, there is hardly a serious piece of research which, if treated realistically, does not involve operations on stochastic processes. The time has arrived for the theory of stochastic processes to become an item of usual equipment of every applied statistician. (Neyman 1960, p. 639)

Half a century after Neyman's comment, the study of organism movement is largely focused on explaining predictable patterns that typify movement in deterministic and (sometimes) even in mechanistic fashion (cf. Nathan *et al.* 2008, and accompanying articles). Theory provides us with predictions, but our understanding remains incomplete, and we inevitably find ourselves testing observable movements against theoretical predictions. The fit is never perfect, and, regardless of whether the failure of the movement data to fit our theory is a statement about our still-imperfect understanding or our lack of the necessary

information about the processes in question, or whether they have an intrinsic stochastic component, we find ourselves comparing predictive theory (typically cast in stochastic process form) with field data, using modern statistical techniques. Stochastic modelling remains a necessary translational tool in our armamentarium.

This theme issue is devoted to the use of GPS telemetry to collect temporally and spatially dense positional datasets on animal locations, and the translation of those datasets into movement trajectories that are sufficiently detailed to permit statistical evaluation of previously untestable models of animal movement (Cagnacci *et al.* 2010). To be useful for comparison of field data with predictive theory, our movement models must be predictive of positional field data and amenable to modern statistical analysis. The object of this paper is to provide some indication of the stochastic process models that provide that connection.

The modelling of animal movement has taken two classic approaches: Lagrangian and Eulerian. The Lagrangian approach involves discrete steps and time segments, and is particularly useful for tracking the detailed movements of single individuals across a landscape; the Eulerian approach describes the expected pattern of space use by an individual or

\* Author for correspondence ([smouse@aesop.rutgers.edu](mailto:smouse@aesop.rutgers.edu)).

One contribution of 15 to a Theme Issue 'Challenges and opportunities of using GPS-based location data in animal ecology'.

population (Okubo 1980). There is also a long tradition of deriving Eulerian models from Lagrangian descriptions, and the theoretical interface between the two approaches continues to yield advances in our ability to model. We have two objectives for this paper: (i) to recap the essentials of both Lagrangian and Eulerian approaches, establishing a base from which to launch the models that will follow; and (ii) to review three modelling arenas that represent emerging growth points for the theory of movement (namely (a) home-range formation, (b) memory-based movement and (c) Lévy movement), which is intended to extend the sorts of questions that we can address and improve our comprehension of how and why animals move as they do. All three of these modelling arenas require dense positional data for empiric evaluation, now becoming increasingly obtainable with GPS telemetry methods, and their evaluation can be expected to profit from it.

## 2. STOCHASTIC STARTING POINTS

### (a) *The Lagrangian approach*

The classic approach to using stochastic differential equations (SDEs) to model animal movements is to assume no *a priori* knowledge about resource distributions or animal preferences. This classic Lagrangian approach is described conveniently in the work of Brillinger *et al.* (2004) and Preisler *et al.* (2004), who used SDEs to describe the incremental step of an animal at time ( $t$ ), located at coordinates  $\mathbf{r}(t) = (x, y, t)$ . These models are formulated as combinations of drift (directional) and diffusion (random, in the simplest case) terms in two-dimensional ( $x, y$ ) space. Preisler *et al.* (2004) defined

$$\begin{bmatrix} dx(t) \\ dy(t) \end{bmatrix} = \begin{bmatrix} \mu_x\{\mathbf{r}(t), t\} \\ \mu_y\{\mathbf{r}(t), t\} \end{bmatrix} dt + \mathbf{D}\{\mathbf{r}(t), t\} \cdot \begin{bmatrix} d\Psi_x(t) \\ d\Psi_y(t) \end{bmatrix}, \quad (2.1)$$

where  $dx(t)$  and  $dy(t)$  are the incremental step sizes along the  $x$ - and  $y$ -axes; the vector  $\boldsymbol{\mu} = (\mu_x, \mu_y)'$  contains the drift parameters;  $\mathbf{D}$ —the diffusion matrix—is a function of both time and position at that time; and  $\Psi_x$  and  $\Psi_y$  are random processes for which expected values = 0. If the drivers of the diffusion terms in ( $x, y$ ) space are independent Brownian processes and the drift terms are continuous in time, we obtain a Markovian diffusion process with continuous sample paths. The drift and diffusion parameter set and the random processes control the direction and speed of the motion.

A number of special cases of interest arise from the general model. If the drift term is zero and the diffusion terms along  $x$ - and  $y$ -axes are completely independent, then the model becomes an *uncorrelated random walk*, where individuals travel at random, with no drift in any particular direction. If drift terms are not independent, then the model yields a *correlated random walk*, where consecutive moves are correlated (Preisler *et al.* 2004). If the drift terms are non-zero and diffusion terms are independent, then the model becomes a *biased random walk*, where individuals drift in a particular direction. Finally, in the special case where the individual is attracted to a particular point, such as a den, a nest site or the centre of its home range, the model becomes a mean-reverting

*Ornstein–Uhlenbeck* (O–U) process, with individuals drifting randomly, but attracted to an average point. Note that in a biased random walk process, the individual's consecutive moves persist in a given direction, whereas in the mean-reverting O–U case, movement is biased towards a focal point, such as a food patch or the centre of the home range (Preisler *et al.* 2004).

Other models may be obtained by making the process non-Markovian, by introducing time lags into the drift term. One advantage to such a general formulation is that it incorporates uncorrelated, correlated and biased random walk (including mean-reverting O–U process) models into a single framework. The approach yields rich modelling possibilities, but requires no *a priori* knowledge of habitat features or organism responses to those features. One may use empirically derived movement segments as difference equations to approximate differential equations in a straightforward fashion, resulting in temporally and spatially explicit gradient vector fields. These alone are useful for examining animal movements in response to habitat and landscape features (Kie *et al.* 2005). One can extend the model by treating the drift term as a potential function, highlighting areas of strong attraction at a given time (Brillinger *et al.* 2004; Preisler *et al.* 2004); calculating that function is mathematically complex.

Lagrangian approaches are particularly well suited to field studies, where individual positional data are typically collected at discrete time intervals, projected onto landscape maps. The movements may often be continuous, but the data are not. State–space models seem to be the most powerful and promising way to handle such data, because they can handle both measurement error and process stochasticity (Patterson *et al.* 2008; Schick *et al.* 2008), though they are computationally demanding. Most treatments require the use of sophisticated model fitting techniques such as Markov Chain Monte Carlo (MCMC) or sequential importance sampling.

Recent application of MCMC methods, coupled with Bayesian analysis, have used Lagrangian movement models, with steps and turning angles modelled via flexible probability distributions (e.g. Jonsen *et al.* 2003, 2005; Morales *et al.* 2004). It is possible and useful to partition movement paths into different movement phases (or behaviours), such as exploratory or resident, each characterized by a particular combination of parameters describing the probability distributions of step sizes and turning angles. Switches between sequential behaviour modes can be modelled as transition probabilities or as functions of current habitat type or distance to a particular habitat type (Morales *et al.* 2004).

Lagrangian approaches are also the usual choice for spatially explicit individual-based models (DeAngelis & Mooij 2005; Grimm & Railsback 2005). In fact, the movement modes fitted to GPS telemetry data can easily form the building blocks for stochastic simulation models. Haydon *et al.* (2008) have elaborated movement models for Canadian elk (*Cervus canadensis*) reintroduced to Ontario, emphasizing social factors affecting the switch between exploratory and encamped behaviour. These movement models were then

combined with mortality and fecundity analysis to build a spatially explicit, individual-based model for the dynamics of this reintroduced population. Their analysis showed that elk moved further when they were solitary than when they were grouped, and that their mortality rate increased as they moved progressively away from the release area. The simulation model showed how the spatial distribution and growth rate of the population depended on the balance of fission and fusion processes governing group structure.

### (b) The Eulerian approach

Studying movement from the Lagrangian perspective is appealing because a movement path is a direct signature of an animal's behavioural process. However, this process is necessarily stochastic, and individual-based approaches are therefore difficult to apply directly to research questions focused on expected patterns of space use. Eulerian approaches, on the other hand, can be used to predict these patterns, because they focus on how the probability of an individual's occurrence (or, if studying a population, the density of animals) can be expected to change through time at any given point in space. The models thus become 'place-based'.

Eulerian approaches typically involve the mathematical analysis of diffusion models, and Skellam (1951) showed that diffusion is a useful approximation of classic random walk models. In this influential paper, Skellam (1951) examined how diffusion and population growth would affect the dispersal of two species of organisms competing in heterogeneous space. This led to many studies of organism movement (e.g. Keller & Segel 1971; Kareiva & Shigesada 1983; Turchin 1998), although the focus tended to be on taxa that were expected to have relatively simple behaviours, such as invertebrates and micro-organisms. Diffusion approaches have been applied to vertebrates, but usually in the context of dispersing individuals or spreading populations (e.g. Skalski & Gilliam 2000). When the focus of study was on the stable rather than dispersing portion of the population, more traditional statistical methods have been applied (e.g. kernel density estimators; Worton 1989).

Seton (1909, p. 23) observed that 'No wild animal roams at random over the country; each has a home-region, even if it has not an actual home.' This home-region, typically called a home range, is defined as the area that an animal uses while taking care of young and searching for food and mates (Burt 1943). Home-range analysis has evolved from early attempts to determine the home-range area via minimum convex polygons (Blair 1940; Odum & Kuenzler 1955) to methods that describe the animal's home range as a utilization distribution (UD)—that is, a two-dimensional relative frequency distribution of animal locations (Jennrich & Turner 1969; Van Winkle 1975; Worton 1989; Getz & Wilmers 2004) that may change through time (Keating & Cherry 2009).

The key link between individual-based and place-based analysis is translating the random and directed

components of movement into diffusion and advection processes, respectively. By assuming that movement can be described by distributions of movement rates and directions, variations of random walk models can be expressed as diffusion approximations via the Fokker–Planck equation for space use. This approach was developed by Patlak (1953) to describe the movement of particles (specifically long-chain polymers) but has subsequently been applied to animal movement (Okubo 1980; Doucet & Wilschut 1987; Turchin 1991). These models provide an intuitive way to link patterns of space use with the process of individual movement, thus allowing for the development of a mechanistic basis for home-range models.

### 3. MOVEMENT IN HOME-RANGE CONTEXT

The home range is often represented by a UD, and, while there are subtle differences in the definitions of home range and UD, we will use the terms interchangeably here. For an alternative approach, see Kie *et al.* (2010). We treat the UD as the probability of observing an animal at any given location and time, given a known starting location at time  $t = 0$ —basically the equilibrium density at all locations, given the underlying movement process—which may include a temporal component, in which case the resulting UDs will also depend on time (Keating & Cherry 2009).

This process can be thought of as a redistribution kernel that describes, for a time interval  $\tau$ , the probability of moving from a starting point  $\mathbf{a}$  to an ending point  $\mathbf{b}$ , where  $\mathbf{a}$  and  $\mathbf{b}$  are vectors representing the  $x$  and  $y$  map coordinates at the respective locations. This redistribution kernel may be arbitrarily complex, but in its simplest form is a joint probability distribution of movement distance (step length) and direction (bearing):

$$\phi(\mathbf{b}, \mathbf{a}, \boldsymbol{\theta}) = v(\mathbf{b}, \mathbf{a}, \boldsymbol{\theta}_v) \times d(\mathbf{b}, \mathbf{a}, \boldsymbol{\theta}_d), \quad (3.1)$$

where  $\boldsymbol{\theta}$  is a vector of parameters, partitioned as a subvector of step-length parameters ( $\boldsymbol{\theta}_v$ ) and a subvector of compass-bearing parameters ( $\boldsymbol{\theta}_d$ ). The distribution  $\phi(\cdot)$  is the product of independent probability density functions of step lengths,  $v(\cdot)$ , and compass directions,  $d(\cdot)$ , each with its own parameter subvector ( $\boldsymbol{\theta}_v$  and  $\boldsymbol{\theta}_d$ , respectively).

When there is no bias in the distribution of movement directions (i.e.  $d(\cdot)$  is a two-dimensional uniform distribution) and the parameters of  $v(\cdot)$  are fixed with respect to position,  $\phi(\cdot)$  represents a simple uncorrelated random walk. Animals moving in such a fashion will diffuse over the whole plane, rather than develop home ranges. Many models have been proposed to account for animal home ranges (see Börger *et al.* 2008 for a recent review). Animals that exhibit this behaviour are altering the rate and bias of their movement in response to some feature of the landscape, either within their immediate perceptual range or within their memory. The spatial and temporal grain and scale of landscape features affect animal movement, and are the key factors underlying the specification of mechanistic home-range models.



Viewing movement models as hypotheses, we build various landscape features into the models in such a way as to yield the ‘localization’ actually observed as ‘home-range’ behaviour. There are various ways to do this, and comparison of predictions with real data elucidates the phenomenon, suggesting which factors and assumptions are likely to be informative and which are not. The most basic model that will lead to home-range formation is a random walk with a constant bias towards some focal point such as a nest, den or roost. Originally proposed by Holgate (1971) and updated by Okubo (1980), this localizing model alters the probability distribution of movement direction in response to an animal’s location, relative to its home-range centre. The random and directed components of this movement process can be described as an advection diffusion model, a partial differential equation (PDE) describing how the probability density function of an animal’s location changes through time. The steady-state solution of the PDE represents the expected pattern of space use by an individual (i.e. the UD). Because this model describes how an animal will return to a known focal point in its home range, it is essentially describing a simple memory process, where the location and strength of the memory landscape are constant through time. A limitation of this model is that it leads to unimodal, circular UDs, whereas most animal UDs are multimodal and non-circular.

One modelling approach that will allow for heterogeneous UDs is to incorporate multiple areas of attraction within the home range. Blackwell (1997, 2003) generalized a model originally proposed by Dunn & Gipson (1977), in which an animal’s redistribution kernel is a multivariate Gaussian (specifically, Ornstein–Uhlenbeck) process, with the characteristics of that process determined by the animal’s ‘state’. Each state (corresponding to a behavioural mode, such as resting, moving or feeding) has its own set of parameters governing movement rate and the strength of attraction to an arbitrary number of home-range ‘nuclei’ (*sensu* Don & Rennolls 1983). This approach may be promising if mechanisms governing the location and number of nuclei are developed along with those of the state-switching probabilities.

Moorcroft *et al.* (1999) applied an extension of the Holgate–Okubo model proposed by Lewis & Murray (1993) to show that accounting for some of the mechanisms known to affect the movement of carnivores can provide additional insight into the home-range patterns of coyotes (*Canis latrans*). The model consisted of a series of PDEs and ordinary differential equations (ODEs) that described how adjacent packs used scent marks to demarcate their territories and how individuals responded to conspecific scent marks. Inter-pack interaction was based on animals increasing their rate of scent marking in the presence of foreign scent marks and simultaneously biasing their movement towards their own home-range centre. The resulting UDs were unimodal, but their contours (and effective boundaries of the home ranges) were dependent on the locations of the neighbouring packs.

Moorcroft & Lewis (2006) showed that conspecific avoidance was not sufficient to explain the home-range patterns of coyotes in Yellowstone National Park. They extended the underlying movement model to include an additional response to prey availability. As in the previous model, conspecific avoidance governed the rate of scent marking and bias in movement direction (advection), but the movement rate decreased in areas of high prey densities. Including both components in the model resulted in multimodal UDs and also allowed successful prediction of how adjacent coyote packs would adjust their home-range locations after the break-up of one of the packs in the study area.

Including resource or habitat selection in the model is important, because animals have energetic and anatomical limitations on their movement rates that interact with the distribution of resources to affect movement patterns and, subsequently, the UD. Arthur *et al.* (1996) suggested that habitat selection occurred within an ‘availability radius’, and this idea was extended by Hjermmann (2000) to allow for availability to decline as a continuous function of distance. Rhodes *et al.* (2005) built upon these approaches to account for home-range behaviour by describing a resource selection model that was a function of distance from current location, distance from home-range centre and resource preference:

$$P(\mathbf{a} \rightarrow \mathbf{b}) = k(\mathbf{a}, \mathbf{b}, \tau) = \frac{\phi(\mathbf{a}, \mathbf{b}, \boldsymbol{\theta}) \times w(\mathbf{b}, \mathbf{Z}, \boldsymbol{\beta})}{\int_{\mathbf{c} \in D_{\tau}} \phi(\mathbf{a}, \mathbf{c}, \boldsymbol{\theta}) \times w(\mathbf{c}, \mathbf{Z}, \boldsymbol{\beta}) d\mathbf{c}}, \quad (3.2)$$

where  $D_{\tau}$  is the domain available to the individual during the time interval  $\tau$ ,  $\phi(\cdot)$  is a probability distribution describing two-dimensional movement in the absence of selection and  $w(\cdot)$  is the selection function calculated at a given location. Landscape resources (including distance to home-range centre) are described by the matrix  $\mathbf{Z}$ , and the strength of the animal’s selection for these resources is described by the vector  $\boldsymbol{\beta}$ . Overall, this selection function serves to bias the animal towards preferred areas (i.e. preferred habitat close to the home-range centre).

Moorcroft & Barnett (2008) showed that equation (3.2) constitutes a mechanistic movement model (*sensu* Moorcroft *et al.* 1999) and results in the relative intensity of space use at any location being equal to the square of the preference function  $w(\cdot)$  at that location (Barnett & Moorcroft 2008). However, in order for this parameterization to result in a characteristic home range, an advection term representing bias towards the home-range centre is required. Without such a term, the expected pattern of space use for an individual is spread across the entire domain, albeit varying in the level of preference for different habitat types.

All of the examples presented thus far require the presupposition of some home-range centre or other attractive nuclei. While this formulation works well for animals that have fixed centres of attraction, other approaches are required for animals without such concrete home-range features. Briscoe *et al.* (2002) showed that if animals are attracted to their own scent marks and if proximity to those scent

marks causes their marking rate to increase, stable home ranges will develop in the absence of any focal point attraction. This occurs because of an orthokinetic process in which the animals reduce their movement rate in areas with high densities of their own scent marks. However, while this model appears to work well mathematically, it is not clear that it arises from realistic fine-scale movement behaviour. A more plausible rule is that animals bias movement towards areas with high densities of scent marks within their olfactory range (i.e. including a  $\beta$  term for scent mark density in equation (3.2)), or towards familiar areas beyond that radius of perception (Wolf *et al.* 2009; see §4 for additional discussion).

The models discussed above are extremely simplistic relative to the actual interactions between an animal's internal state, memory and external environment. The result from these models is often thought of as a predictive surface (i.e. the researchers' best guess at where an animal is likely to be at any given time). An important question to ask is what these models are able to predict. For example, the home-range model developed by Moorcroft & Lewis (2006) was able to predict the shape of the UD and how the UDs of adjacent packs of coyotes would respond when one of the packs dissolved, but that model relied upon a prior designation of the home-range centres of each pack. It does not predict where home ranges will be found elsewhere on the landscape; only what UD will be expected, given a prescribed home-range centre. The location and sizes of home ranges are likely to depend on the needs of the individual animal and the distribution of resources across the landscape (e.g. Mitchell & Powell 2004; Anderson *et al.* 2005). If an animal leaves its established home range, what combination of landscape features and conspecific territories determines where it will choose to 'settle down'? That clearly leads to an entirely different class of modelling problems.

One of the challenges facing wildlife ecologists is to understand how animals will adapt to changing landscapes. Thus, it is increasingly important for us to collect data on animals that are in some way pushed outside of their current equilibrium setting and then use these data to challenge predictive models of animal movement. The PDE approaches do allow for temporal variability in selection, although this adds complexity to the equations. The power of these approaches is that once the mechanisms underlying the genesis of a UD are understood, they can be used to predict how the UD will change in response to a changing landscape (Moorcroft *et al.* 2006).

Empiric evaluation of any of these models against densely packed, GPS-derived field data involves the assumption of independence of sequential animal locations, and, though they clearly elucidate the processes of deeper interest, such sequences are obviously not independent. Recent work, however, has shown that most testing procedures are robust with respect to this assumption, and thinning datasets to ensure independence by throwing out large quantities of valuable data is generally counter-productive (deSolla *et al.* 1999; Fieberg 2007; Fieberg *et al.* 2010).

#### 4. MEMORY-BASED MOVEMENT

Most animals are capable of acquiring, storing and using information about the landscapes they inhabit. Knowledge of the environment can potentially reduce uncertainty about the location and availability of resources, and even allow for the anticipation of danger. Although little is known about how animals actually store and use spatial information (e.g. landmark-based versus geometric cognitive maps; Etienne *et al.* 1996; Menzel *et al.* 2000; Vlasak 2006; Janson & Byrne 2007), there is evidence that wild animals are capable of navigating adaptively through familiar landscapes (e.g. Gallistel 1990; Shettleworth 1998).

Detailed navigation models can be built using artificial neural networks. These are quite useful for integrating several sources of information and in simulating sensible decision-making (e.g. Folse *et al.* 1989; Voicu & Schmajuk 2002; Morales *et al.* 2005; Dalziel *et al.* 2008), but random walk formulations are better suited to analytical treatment and for translating behavioural rules into UDs. Using the behavioural minimalist approach (Lima & Zollner 1996), we will deal here with a simple random walk that includes some form of memory, as opposed to the traditional first-order Markov treatment of correlated random walks (Morales *et al.* 2010).

Random walk models and their diffusion approximations have been used to model animal reactions to landscape heterogeneity by changing movement speed (distance moved) and/or the distribution of turning angles (Kareiva & Odell 1987; Turchin 1991; Grünbaum 1999; Morales *et al.* 2004), as well as to include movement biases at habitat boundaries (Ovaskainen 2004; Ovaskainen *et al.* 2008). Even though some features of animal movements can be captured by such models, and might be all that is needed for certain species at certain temporal scales, they will fail to retain individuals realistically within a particular sector of the landscape and/or to mimic revisitation rates to certain areas. Given enough time, individuals moving according to these models will spread over the entire area being considered. Whether this is acceptable will, of course, depend on the species under consideration and the time scale of interest. In cases where home ranges form, animals probably deviate from pure random walks by altering their movement biases in response to a combination of the landscape composition in their immediate vicinity and their long-term memory.

More generally, random walks where the movement of a particle is affected by its history are called reinforced walks (Davis 1990; Pemantle 2007). These are walks on a lattice or a graph that preferentially revisit neighbouring locations that have been visited before. In the majority of these theoretical studies, the probability of using a particular edge (link) or vertex (node) in a graph depends on its 'weight', which increases as a function of the number of previous visits. Important mathematical differences have been found, depending on whether the reinforcement occurs at edges or nodes of a graph. For example, edge-reinforced walks are recurrent on

finite graphs, meaning that every edge is traversed many times at large time scales. In contrast, node reinforcement results in random walkers becoming trapped between just a few vertices (Volkov 2006). Sometimes a clear phase transition between these two possible behaviours has been identified through extensive simulation (Foster *et al.* 2009).

In reinforced random walks, memory effects that modify habitat choice probabilities are inserted into the model; as certain links or nodes in a graph are used, they become more likely to be used in the future. These habitat-based memory effects can be used to model the effect of previous use, not only on the individual performing the changes, but also on other individuals. For example, Othmer & Stevens (1997) studied movement and aggregation in slime-producing myxobacteria. These organisms leave a slime track that facilitates subsequent movement by the same or other bacteria, conforming to a reinforced random walk. The authors used PDEs to approximate the behaviour of many individuals performing such walks and show that the local reinforcement owing to slime produced stable aggregations of bacteria (without the need for long-distance signalling between cells). Such path reinforcement may also play a role in movement of vertebrates, as many animals readily follow a network of footpaths engraved in the landscape by previous use, in some cases by other species and previous generations. We suspect that these models could be suitably modified to deal with landscape use reinforcement.

Even though these models can be useful in developing our intuition about the effects of past history on movement decisions, it is important to note that they use local conditions to model movement. This contrasts with how animals' long-term memory may affect movement decisions (e.g. Janson & Byrne 2007; Healy *et al.* 2009), because it introduces a form of perceptual distance that precludes purposeful returns to distant places. Perhaps a more realistic form or reinforced model for animal movement would allow the possibility of returning to any previously visited place even if such locales are outside the current perception area. Recently, Gautestad & Mysterud (2006) proposed what they called a 'Lévy flight with strategic returns' (or multi-scaled random walk), where movement steps follow a truncated Lévy flight (long steps, but not beyond a certain distance), though the walker is allowed to return to previous locations every so often. This model is aimed at describing the result of animals mixing local (tactical) movements with less frequent (strategic) far-ranging commutes. The authors showed that various patterns of space use can arise, depending on model parameterization. In particular, a simple random walk with strategic returns leads to a unimodal distribution of space use, while the truncated Lévy flight version produces multi-modality.

Van Moorter *et al.* (2009) simulated a forager's movement as biased correlated random walk in an area with randomly placed foraging patches, where bias was a function of past patch use. They assumed that long-term (reference) memory motivated animals

to return to previously visited patches, while short-term memory encouraged them to move away from recently visited patches. Their simulations showed that by using both types of memory, foragers made more efficient use of resources. Also, the rate of increase in the area covered by animals slowed with time, but more extensive simulations or theoretical analyses are needed to determine whether these processes can lead to stable home ranges.

While there is little doubt that memory can affect movement processes in many ways, there remains much to do in model development and data analysis. We anticipate that future work will contrast observed animal trajectories with alternative random walk models that include memory. Reinforced random walks (RRWs) seem to be a good starting point, especially where individual movement modifies the habitat by leaving chemical signals or physically facilitating further displacements. However, classical RRWs should be extended to allow for movement biases towards distant remembered locations. Because we do not know *a priori* which of the possible cognitive processes are involved in the movement decisions of a given species, some observed spatial trajectories could be consistent with a large number of processes, ranging from simple undirected search processes to strategic goal-oriented travel. Given what we do know about animal cognition in general, we expect animals to be motivated to explore and update their knowledge of the environment they inhabit. Realistic movement models that include memory should consider both exploratory behaviour and the use of past experience in movement decisions. Blackwell (1997, 2003) and Morales *et al.* (2004) modelled changes in behavioural states that resulted in different movement patterns, including what they called 'exploration', but they did not use these explorations to update future movement biases. Future work might include the possibility of exploratory movement, leading to new home-range nuclei.

How well our models predict movement choices in the field can only be evaluated with dense GPS telemetry. Memory reinforcement may well require repetition, of course, so if we are to evaluate changes in either point-specific or track-specific probability array in response to accumulating experience, we will almost surely require GPS records over an extended time track to allow for repeated visits to a substantial number of locations. Moreover, to elucidate deeper (probably neuronal) causation, we will also have to monitor the animal's internal state, using evolving biosensor technology, now rapidly developing (Tomkiewicz *et al.* 2010).

## 5. LÉVY MOVEMENT

The traditional statistical treatment of single-step movement distances involves a pdf,  $p(z)$ , that is Poisson, normal or some exponential function of distance  $z$  with finite mean and variance and decaying gradually with increasing distance. Recently, attention has been shifting towards distributions that drop off quickly but that have a long, fat tail (Metzler & Klafter 2004). In some cases, organism movement is so



generally heavy-tailed that the moments of the pdf may not be finite (Mandelbrot 1983).

Lévy flights and walks (see Metzler *et al.* 2007 for the distinction) have received particular attention in this regard. Our interest here is in the size distribution of single steps, and we will concentrate on Lévy walks. Lévy walks exhibit tail probabilities that are proportional to inverse power functions of the distance,  $z$ , described as  $z^{-\mu}$  ( $1 < \mu \leq 3$ ). Beyond some minimal step size  $z_{\min}$ , one can model such distributions as a pdf (cf. Edwards 2008),

$$p(z, \mu) = (\mu - 1)z_{\min}^{\mu-1}(z^{-\mu}) = cz^{-\mu}, \quad (5.1)$$

where  $z$  is the straight-line distance traversed,  $z_{\min}$  is the minimal distance moved, and  $c$  is the normalization constant required of a proper pdf. The parameter  $\mu$  has the remarkable property of being independent of measurement units, so direct comparison can be made across studies. Note that for  $1 < \mu \leq 3$ , the distribution is Lévy, and the sum of moves is also Lévy; for  $\mu > 3$ , the sum of moves converges to a Gaussian distribution and is Brownian. For  $\mu \leq 3$ , the distribution is characterized by unbounded moments, while for values of  $\mu > 3$ , the moments are finite.

Theoretical work shows that a Lévy movement strategy can maximize a consumer's encounter rate with sparse and unknown food resources. Bartumeus *et al.* (2008) evaluated the impact of Lévy searching on the efficiency  $\eta$  (the number of target sites encountered per total distance traversed), incorporating the dimension of the system for still or mobile targets, and for both destructive and non-destructive resource utilization. Conforming to previous results (Rapooso *et al.* 2003), efficiency is maximum at  $\mu = 2$  for the non-destructive case, an emergent compromise between revisiting nearby targets (i.e. resampling paths already traversed) and leaving a visited area to find new targets. For destructive scenarios, encounter rates were highest as  $1 \leftarrow \mu$ , because path resampling is penalized under this scenario. Theoretical considerations suggest that we should encounter widespread Lévy search strategies for targets (food, potential mates or preferred shelter). Lomholt *et al.* (2008) showed that Lévy searching significantly outperforms Brownian searching, because it reduces oversampling. By optimizing an intermittent search strategy for critical and rare targets, a Lévy searcher is much less sensitive to target density. These results were obtained in the one-dimensional case, but Bartumeus *et al.* (2008) have shown that the advantage of Lévy search becomes smaller with increasing dimensionality, though it persists.

Lévy movement might either (i) be an emergent property of the interaction between the searcher and its landscape, or (ii) represent an adaptive behaviour. Benhamou (2007) showed that Brownian walk by a predator searching for random prey items in a patchy environment generates composite search patterns that mimic those generated by Lévy movement. Boyer *et al.* (2006), studying spider monkeys searching among trees of different sizes, have shown that a particular tree-size frequency distribution induces

Lévy movement patterns, while Sims *et al.* (2008) showed that both pelagic predator movements and prey distribution exhibited a Lévy-like pattern, and that the predator movements were an optimal search strategy for prey items that were distributed in Lévy-like fashion. Bartumeus & Levin (2008) postulate the presence of a 'fractal re-orientation clock', a neuronal mechanism that produces a Lévy distribution at times of predator turning, enabling maximal search success.

It is noteworthy that for Brownian movement the mean squared displacement from the initial point of departure is proportional to the first power of time, while for Lévy movement the dependence on time is super-linear, characteristic of super-diffusion. One might be tempted to use dispersion patterns over longer time scales, measured via discrete sampling and conventional VHF telemetry, to detect Lévy patterns, as done by Ramos-Fernández *et al.* (2004) for spider monkeys, but other mechanisms (e.g. fractional Brownian motion) can also yield that outcome. Moreover, Petrovsky *et al.* (2008) and Petrovsky & Morozov (2009) have shown that aggregating mixtures of Brownian moves, where there is parametric variation among either different animals or different situations, can yield a composite distribution that is collectively super-diffusive in its tail behaviour. Thus, hard evidence of super-diffusion does not automatically translate into hard evidence for Lévy movement (Viswanathan *et al.* 2008).

It is thus necessary to rely on high-resolution trajectories to document the presence of Lévy movements. Considerable work has been invested in analysing whether movements do or do not conform to a Lévy pattern. In an oft-cited paper, Viswanathan *et al.* (1999; see also Weimerskirch *et al.* 2005) claimed that wandering albatrosses performed Lévy walks while foraging. Further claims have been published for side-striped jackals (Atkinson *et al.* 2002), reindeer (Mårell *et al.* 2002), zooplankton (Bartumeus *et al.* 2003), grey seals (Austin *et al.* 2004), goats (de Knecht *et al.* 2007), elephants (Dai *et al.* 2007), honeybees (Reynolds *et al.* 2007) and solitary fallow deer (Focardi *et al.* 2009). Lévy movement has also been claimed for fungal spores (Wingen *et al.* 2007) and at least for the tail of the distribution for dispersing plant propagules (e.g. Harper 1977; Okubo & Levin 1989; Portnoy & Willson 1993; Levin *et al.* 2003). One can then use step-length 'survival distributions' to discriminate between Lévy and composite Brownian movement (Benhamou 2007). If movement is Lévy, the relationship should be log-linear, but a log-curvilinear relationship would be indicative of composite Brownian movement. This is the same method described by Newman (2005) and Edwards (2008), though they refer to it as a 'rank-frequency plot'.

The presence of Lévy movements under natural conditions has been severely challenged by a number of independent studies (Benhamou 2007; Edwards *et al.* 2007; James & Plank 2007; Sims *et al.* 2007; Edwards 2008). The debate has consequences (Trevis 2007), because a failure to optimize search behaviour would challenge standard theory, which is



normally based on the idea that active searching is adaptive for organisms that are capable of doing it. Edwards *et al.* (2007) used unbiased likelihood estimates of  $\mu$  to re-analyse Viswanathan *et al.*'s (1999) albatross study and questioned the strength of the empirical evidence for Lévy movement. Other methods yielded under-estimates of  $\mu$ , possibly indicating Lévy movement ( $\mu \leq 3$ ) in cases where motion was actually Brownian ( $\mu > 3$ ; Edwards 2008).

In summary, the evidence for Lévy movements in nature is equivocal, and the ecological conditions under which we should expect it are still not entirely clear. Examples are scattered from unicellular organisms to plant propagules to marine organisms to terrestrial mammals, and the ecological commonalities that tie those cases together are not entirely obvious. It is evident that high-resolution GPS tracking of animal movements will be necessary to obtain the required step-size distribution (see review in Fieberg *et al.* 2010), and we still need to move from testing step-size distributions to a more mechanistic analysis of animal movements. It thus seems appropriate to close with the caution (Bartumeus & Levin 2008) that even a high-resolution trajectory will not be enough for causal analysis, since locations where reorientation occurs during Lévy movements should be defined with other sorts of information, such as changes in the animal's physiological or behavioural state. Dense positional information will be necessary but not sufficient. New developments in biosensor technology show some promise of providing that needed information (see reviews in Cooke *et al.* 2004; Rutz & Hays 2009).

## 6. CONCLUDING REMARK

In spite of our growing concentration on deterministic and mechanistic explanation, we are still, half a century after Neyman's 'paean' to stochastic processes, engaged in modelling organism movement in stochastic process terms. Our biological understanding of 'why they do it' and our physical understanding of 'how they do it' has improved over that period, but whether we ascribe the (still considerable) unpredictable element of movement to our residual process ignorance or inadequate information on the critical factors influencing the animal's movement choices, or to intrinsically probabilistic processes, our reliance on stochastic modelling will continue unabated. Coupled with continuing improvements in GPS and biosensor technology, along with more sophisticated statistical analysis of densely packed data on the landscape across which the animals move, stochastic modelling will continue to contribute to our understanding.

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## REFERENCES

- Anderson, D. P., Forester, J. D., Turner, M. G., Frair, J. L., Merrill, E. H., Fortin, D., Mao, J. S. & Boyce, M. S. 2005 Factors influencing female home range sizes in elk (*Cervus elaphus*) in North American landscapes. *Landscape Ecol.* **20**, 257–271. (doi:10.1007/s10980-005-0062-8)
- Arthur, S. M., Manly, B. F. J., McDonald, L. L. & Garner, G. W. 1996 Assessing habitat selection when availability changes. *Ecology* **77**, 215–227. (doi:10.2307/2265671)
- Atkinson, R. P. D., Rhodes, C. J., Macdonald, D. W. & Anderson, R. M. 2002 Scale-free dynamics in the movement patterns of jackals. *Oikos* **98**, 134–140. (doi:10.1034/j.1600-0706.2002.980114.x)
- Austin, D., Bowen, W. D. & McMillan, J. I. 2004 Intraspecific variation in movement patterns: modeling individual behaviour in a large marine predator. *Oikos* **105**, 15–30. (doi:10.1111/j.0030-1299.1999.12730.x)
- Barnett, A. H. & Moorcroft, P. R. 2008 Analytic steady-state space use patterns and rapid computations in mechanistic home range analysis. *J. Math. Biol.* **57**, 139–159. (doi:10.1007/s00285-007-0149-8)
- Bartumeus, F. & Levin, S. A. 2008 Fractal reorientation clocks: linking animal behaviour to statistical patterns of search. *Proc. Natl Acad. Sci. USA* **105**, 19 072–19 077. (doi:10.1073/pnas.0801926105)
- Bartumeus, F., Peters, F., Pueyo, S., Marrase, C. & Catalan, J. 2003 Helical Lévy walks: adjusting searching statistics to resource availability in microzooplankton. *Proc. Natl Acad. Sci. USA* **100**, 12 771–12 775. (doi:10.1073/pnas.2137243100)
- Bartumeus, F., Fernández, P., da Luz, M. G. E., Catalan, J., Solé, R. V. & Levin, S. A. 2008 Superdiffusion and encounter rates in diluted, low dimensional worlds. *Eur. Phys. J. Spec. Top.* **157**, 157–166. (doi:10.1140/epjst/e2008-00638-6)
- Benhamou, S. 2007 How many animals really do the Lévy walk? *Ecology* **88**, 1962–1969. (doi:10.1890/06-1769.1)
- Blackwell, P. G. 1997 Random diffusion models for animal movement. *Ecol. Model.* **100**, 87–102. (doi:10.1016/S0304-3800(97)00153-1)
- Blackwell, P. G. 2003 Bayesian inference for Markov processes with diffusion and discrete components. *Biometrika* **90**, 613–627. (doi:10.1093/biomet/90.3.613)
- Blair, W. F. 1940 Notes on home ranges and populations of the short-tailed shrew. *Ecology* **21**, 284–288. (doi:10.2307/1930504)
- Börger, L., Dalziel, B. D. & Fryxell, J. M. 2008 Are there general mechanisms of animal home range behaviour? A review and prospects for future research. *Ecol. Lett.* **11**, 637–650. (doi:10.1111/j.1461-0248.2008.01182.x)
- Boyer, D., Ramos-Fernández, G., Miramontes, O., Mateos, J. L., Cocho, G., Larralde, H., Ramos, H. & Rojas, F. 2006 Scale-free foraging by primates emerges from their interaction with a complex environment. *Proc. R. Soc. B* **273**, 1743–1750. (doi:10.1098/rspb.2005.3462)
- Brillinger, D. R., Preisler, H. K., Ager, A. A. & Kie, J. G. 2004 An exploratory data analysis (EDA) of the paths of moving animals. *J. Stat. Plan. Infer.* **122**, 43–63. (doi:10.1016/j.jspi.2003.06.016)
- Briscoe, B., Lewis, M. A. & Parrish, S. 2002 Home range formation in wolves. *Bull. Math. Biol.* **64**, 261–284. (doi:10.1006/bulm.2001.0273)
- Burt, W. H. 1943 Territoriality and home range concepts as applied to mammals. *J. Mammal.* **24**, 346–352. (doi:10.2307/1374834)

- Cagnacci, F., Boitani, L., Powell, R. A. & Boyce, M. S. 2010 Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challenges. *Phil. Trans. R. Soc. B* **365**, 2157–2162. (doi:10.1098/rstb.2010.0107)
- Cooke, S. J., Hinch, S. G., Wikelski, M., Andrews, R. D., Kuchel, L. J., Wolcott, T. G. & Butler, P. J. 2004 Biotelemetry: a mechanistic approach to ecology. *Trends Ecol. Evol.* **19**, 334–343. (doi:10.1016/j.tree.2004.04.003)
- Dai, X. H., Shannon, G., Slotow, R., Page, B. & Duffy, K. J. 2007 Short-duration daytime movements of a cow herd of African elephants. *J. Mammal.* **88**, 151–157. (doi:10.1644/06-MAMM-A-035R1.1)
- Dalziel, B. D., Morales, J. M. & Fryxell, J. M. 2008 Fitting probability distributions to animal movement trajectories: Using artificial neural networks to link distance, resources, and memory. *Am. Nat.* **172**, 248–258. (doi:10.1086/589448)
- Davis, B. 1990 Reinforced random walk. *Probab. Theory Relat. Fields* **84**, 203–229. (doi:10.1007/BF01197845)
- DeAngelis, D. L. & Mooij, W. M. 2005 Individual-based modelling of ecological and evolutionary processes. *Annu. Rev. Ecol. Evol. Syst.* **36**, 147–168. (doi:10.1146/annurev.ecolsys.36.102003.152644)
- de Knegt, H. J., Hengeveld, G. M., van Langevelde, F., de Boer, W. F. & Kirkman, K. P. 2007 Patch density determines movement patterns and foraging efficiency of large herbivores. *Behav. Ecol.* **18**, 1065–1072. (doi:10.1093/beheco/arm080)
- deSolla, S. R., Bonduriansky, R. & Brooks, R. J. 1999 Eliminating autocorrelation reduces biological relevance of home range estimates. *J. Anim. Ecol.* **68**, 221–234. (doi:10.1046/j.1365-2656.1999.00279.x)
- Don, B. A. C. & Rennolls, K. 1983 A home range model incorporating biological attraction points. *J. Anim. Ecol.* **52**, 69–81. (doi:10.2307/4588)
- Doucet, P. G. & Wilschut, A. N. 1987 Theoretical studies of animal orientation. III. A model for kinesis. *J. Theor. Biol.* **127**, 111–125. (doi:10.1016/S0022-5193(87)80164-9)
- Dunn, J. E. & Gipson, P. S. 1977 Analysis of radio telemetry data in studies of home range. *Biometrics* **33**, 85–101. (doi:10.2307/2529305)
- Edwards, A. M. 2008 Using likelihood to test for Lévy flight search patterns and for general power-law distributions in nature. *J. Anim. Ecol.* **77**, 1212–1222. (doi:10.1111/j.1365-2656.2008.01428.x)
- Edwards, A. M. *et al.* 2007 Revisiting Lévy flight search patterns of wandering albatrosses, bumblebees and deer. *Nature* **449**, 1044–1048. (doi:10.1038/nature06199)
- Etienne, A. S., Maurer, R. & Seguinot, V. 1996 Path integration in mammals and its interaction with visual landmarks. *J. Exp. Biol.* **199**, 201–209.
- Fieberg, J. 2007 Kernel density estimators of home range: smoothing and the autocorrelation red herring. *Ecology* **88**, 1059–1066. (doi:10.1890/06-0930)
- Fieberg, J., Matthiopoulos, J., Hebblewhite, M., Boyce, M. S. & Frair, J. L. 2010 Correlation and studies of habitat selection: problem, red herring, or opportunity? *Phil. Trans. R. Soc. B* **365**, 2233–2244. (doi:10.1098/rstb.2010.0079)
- Focardi, S., Montanaro, P. & Pecchioli, E. 2009 Adaptive Lévy walks in foraging fallow deer. *PLoS ONE* **4**, e6587. (doi:10.1371/journal.pone.0006587)
- Folse, L. J., Packard, J. M. & Grant, W. E. 1989 AI modelling of animal movements in a heterogeneous habitat. *Ecol. Model.* **46**, 57–72. (doi:10.1016/0304-3800(89)90069-0)
- Foster, J. G., Grassberger, P. & Paczuski, M. 2009 Reinforced walks in two and three dimensions. *New J. Phys.* **11**, 023009. (doi:10.1088/1367-2630/11/2/023009)
- Gallistel, C. R. 1990 *The organization of learning*. Cambridge, MA: MIT Press.
- Gautestad, A. O. & Mysterud, I. 2006 Complex animal distribution and abundance from memory-dependent kinetics. *Ecol. Complex.* **3**, 44–55. (doi:10.1016/j.ecocom.2005.05.007)
- Getz, W. M. & Wilmers, C. C. 2004 A local nearest-neighbor convex-hull construction of home ranges and utilization distributions. *Ecography* **27**, 489–505. (doi:10.1111/j.0906-7590.2004.03835.x)
- Grimm, V. & Railsback, S. F. 2005 *Individual based modeling and ecology*. Princeton, NJ: Princeton University Press.
- Grünbaum, D. 1999 Advection-diffusion equations for generalized tactic searching behaviors. *J. Math. Biol.* **38**, 169–194. (doi:10.1007/s002850050145)
- Harper, J. L. 1977 *Population biology of plants*. New York, NY: Academic Press.
- Haydon, D. T., Morales, J. M., Yott, A., Jenkins, D. A., Rosatte, R. & Fryxell, J. M. 2008 Socially informed random walks: incorporating group dynamics into models of population spread and growth. *Proc. R. Soc. B* **275**, 1101–1109. (doi:10.1098/rspb.2007.1688)
- Healy, S. D., Bacon, I. E., Haggis, O., Harris, A. P. & Kelley, L. A. 2009 Explanations for variation in cognitive ability: behavioural ecology meets comparative cognition. *Processes* **80**, 288–294. (doi:10.1016/j.beproc.2008.10.002)
- Hjermann, D. Ø. 2000 Analyzing habitat selection in animals without well-defined home ranges. *Ecology* **81**, 1462–1468. (doi:10.1890/0012-9658(2000)081[1462:AHSAIW]2.0.CO;2)
- Holgate, P. 1971 Random walk models for animal behavior. In *Statistical ecology: sampling and modeling biological populations and population dynamics*, vol. 2 (eds G. Patil, E. Pielou & W. Walters), pp. 1–12. University Park, PA: Penn State University Press.
- James, A. & Plank, M. J. 2007 On fitting power laws to ecological data. (<http://arxiv.org/abs/0712.0613v1>).
- Janson, C. H. & Byrne, R. 2007 What wild primates know about resources: opening up the black box. *Anim. Cogn.* **10**, 357–367. (doi:10.1007/s10071-007-0080-9)
- Jennrich, R. I. & Turner, F. B. 1969 Measurement of non-circular home range. *J. Theor. Biol.* **22**, 227–237. (doi:10.1016/0022-5193(69)90002-2)
- Jonsen, I. D., Myers, R. A. & Flemming, J. M. 2003 Meta-analysis of animal movement using state-space models. *Ecology* **84**, 3055–3063. (doi:10.1890/02-0670)
- Jonsen, I. D., Flemming, J. M. & Myers, R. A. 2005 Robust state-space modeling of animal movement data. *Ecology* **86**, 2874–2880. (doi:10.1890/04-1852)
- Kareiva, P. & Odell, G. 1987 Swarms of predators exhibit ‘preytaxis’ if individual predators use area-restricted search. *Am. Nat.* **130**, 233–270. (doi:10.1086/284707)
- Kareiva, P. M. & Shigesada, N. 1983 Analyzing insect movement as a correlated random walk. *Oecologia* **56**, 234–238. (doi:10.1007/BF00379695)
- Keating, K. & Cherry, S. 2009 Utilization distributions in space and time. *Ecology* **90**, 1971–1980. (doi:10.1890/08-1131.1)
- Keller, E. F. & Segel, L. A. 1971 A model for chemotaxis. *J. Theor. Biol.* **30**, 225–234. (doi:10.1016/0022-5193(71)90050-6)
- Kie, J. G., Ager, A. A. & Bowyer, R. T. 2005 Landscape-level movements of North American elk (*Cervus elaphus*): effects of habitat patch structure and topography. *Landscape Ecol.* **20**, 289–300. (doi:10.1007/s10980-005-3165-3)

- Kie, J. G., Matthiopoulos, J., Fieberg, J., Powell, R. A., Cagnacci, F., Mitchell, M. S., Gaillard, J.-M. & Moorcroft, P. R. 2010 The home-range concept: are traditional estimators still relevant with modern telemetry technology? *Phil. Trans. R. Soc. B* **365**, 2221–2231. (doi:10.1098/rstb.2010.0093)
- Levin, S. A., Muller-Laundau, H. C., Nathan, R. & Chave, J. 2003 The ecology and evolution of seed dispersal: a theoretical perspective. *Annu. Rev. Ecol. Evol. Syst.* **34**, 575–604. (doi:10.1146/annurev.ecolsys.34.011802.132428)
- Lewis, M. A. & Murray, J. D. 1993 Modeling territoriality and wolf–deer interactions. *Nature* **366**, 738–740. (doi:10.1038/366738a0)
- Lima, S. L. & Zollner, P. A. 1996 Towards a behavioral ecology of ecological landscapes. *Trends Ecol. Evol.* **11**, 131–135. (doi:10.1016/0169-5347(96)81094-9)
- Lomholt, M. A., Koren, T., Metzler, R. & Klafter, J. 2008 Lévy strategies in intermittent search processes are advantageous. *Proc. Natl Acad. Sci. USA* **105**, 11 055–11 059. (doi:10.1073/pnas.0803117105)
- Mandelbrot, B. B. 1983 *The fractal geometry of nature*. San Francisco, CA: Freeman.
- Mårell, A., Ball, J. P. & Hofgaard, A. 2002 Foraging and movement paths of female reindeer: insights from fractal analysis, correlated random walks, and Lévy flights. *Can. J. Zool.* **80**, 854–865. (doi:10.1139/z02-061)
- Menzel, R., Brandt, R., Gumbert, A., Komischke, B. & Kunze, J. 2000 Two spatial memories for honeybee navigation. *Proc. R. Soc. Lond. B* **267**, 961–968. (doi:10.1098/rspb.2000.1097)
- Metzler, R. & Klafter, J. 2004 The restaurant at the end of the random walk: recent developments in the description of anomalous transport by fractional dynamics. *J. Phys. A* **37**, R161–R208. (doi:10.1088/0305-4470/37/31/R01)
- Metzler, R., Chechkin, A. V. & Klafter, J. 2007 Lévy statistics and anomalous transport: Lévy flights and subdiffusion. (<http://arxiv.org/abs/0706.3553v1>).
- Mitchell, M. S. & Powell, R. A. 2004 A mechanistic home range model for optimal use of spatially distributed resources. *Ecol. Model.* **177**, 209–232. (doi:10.1016/j.ecolmodel.2004.01.015)
- Moorcroft, P. R. & Barnett, A. H. 2008 Resource selection analysis and mechanistic home range models: a reconciliation and unification. *Ecology* **89**, 1112–1119. (doi:10.1890/06-1985.1)
- Moorcroft, P. R. & Lewis, M. A. 2006 *Mechanistic home range analysis*. Monographs in Population Biology. Princeton, NJ: Princeton University Press.
- Moorcroft, P. R., Lewis, M. A. & Crabtree, R. L. 1999 Home range analysis using a mechanistic home range model. *Ecology* **80**, 1656–1665. (doi:10.1890/0012-9658(1999)080[1656:HRAUAM]2.0.CO;2)
- Moorcroft, P. R., Lewis, M. A. & Crabtree, R. L. 2006 Mechanistic home range models predict spatial patterns and dynamics of coyote territories in Yellowstone. *Proc. R. Soc. B* **273**, 1651–1659. (doi:10.1098/rspb.2005.3439)
- Morales, J. M., Haydon, D. T., Frair, J., Holsinger, K. E. & Fryxell, J. M. 2004 Extracting more out of relocation data: building movement models as mixtures of random walks. *Ecology* **85**, 2436–2445. (doi:10.1890/03-0269)
- Morales, J. M., Fortin, D., Frair, J. L. & Merrill, E. H. 2005 Adaptive models for large herbivore movements in heterogeneous landscapes. *Landscape Ecol.* **20**, 301–316. (doi:10.1007/s10980-005-0061-9)
- Morales, J. M., Moorcroft, P. R., Matthiopoulos, J., Frair, J. L., Kie, J. G., Powell, R. A., Merrill, E. H. & Haydon, D. T. 2010 Building the bridge between animal movement and population dynamics. *Phil. Trans. R. Soc. B* **365**, 2289–2301. (doi:10.1098/rstb.2010.0082)
- Nathan, R., Getz, W. M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D. & Smouse, P. E. 2008 A movement ecology paradigm for unifying organismal movement research. *Proc. Natl Acad. Sci. USA* **105**, 19 052–19 059. (doi:10.1073/pnas.0800375105)
- Newman, M. E. J. 2005 Power laws, Pareto distributions and Zipf's law. *Contemp. Phys.* **46**, 323–351. (doi:10.1080/00107510500052444)
- Neyman, J. 1960 Indeterminism in science and new demands on statisticians. *J. Am. Stat. Assoc.* **55**, 625–639. (doi:10.2307/2281586)
- Odum, E. P. & Kuenzler, E. J. 1955 Measurement of territory and home range size in birds. *Auk* **72**, 128–137.
- Okubo, A. 1980 *Diffusion and ecological problems: mathematical models*. Biomathematics, vol. 10. Basel, Switzerland: Springer.
- Okubo, A. & Levin, S. A. 1989 Theoretical approach for data analysis of wind-dispersal of seeds and pollen. *Ecology* **70**, 329–338. (doi:10.2307/1937537)
- Othmer, H. G. & Stevens, A. 1997 Aggregation, blowup, and collapse: the ABC's of taxis in reinforced random walks. *SIAM J. Appl. Math.* **57**, 1044–1081. (doi:10.1137/S0036139995288976)
- Ovaskainen, O. 2004 Habitat-specific movement parameters estimated using mark-recapture data and a diffusion model. *Ecology* **85**, 242–257. (doi:10.1890/02-0706)
- Ovaskainen, O., Luoto, M., Ikonen, I., Rekola, H., Meyke, E. & Kuussaari, M. 2008 An empirical test of a diffusion model: predicting clouded Apollo movements in a novel environment. *Am. Nat.* **171**, 610–619. (doi:10.1086/587070)
- Patlak, C. S. 1953 Random walk with persistence and external bias. *Bull. Math. Biophys.* **15**, 311–338. (doi:10.1007/BF02476407)
- Patterson, T. A., Thomas, L., Wilcox, C., Ovaskainen, O. & Matthiopoulos, J. 2008 State-space models of individual animal movement. *Trends Ecol. Evol.* **23**, 87–94. (doi:10.1016/j.tree.2007.10.009)
- Pemantle, R. 2007 A survey of random processes with reinforcement. *Probab. Surv.* **4**, 1–79. (doi:10.1214/07-PS094)
- Petrovsky, S. & Morozov, A. 2009 Dispersal in a statistically structured population: fat tails revisited. *Am. Nat.* **173**, 278–289. (doi:10.1086/595755)
- Petrovsky, S., Morozov, A. & Li, G. L. 2008 On the possible origin of fat tailed dispersal in population dynamics. *Ecol. Complex.* **5**, 146–150. (doi:10.1016/j.ecocom.2007.10.002)
- Portnoy, S. & Willson, M. F. 1993 Seed dispersal curves: behavior of the tail of the distribution. *Evol. Ecol.* **7**, 25–44. (doi:10.1007/BF01237733)
- Preisler, H. K., Ager, A. A., Johnson, B. K. & Kie, J. G. 2004 Modeling wildlife movements using stochastic differential equations. *Environmetrics* **15**, 643–657. (doi:10.1002/env.636)
- Ramos-Fernández, G., Mateos, J. L., Miramontes, O., Cocho, G., Larralde, H. & Ayala-Orozco, B. 2004 Lévy walk patterns in the foraging movements of spider monkeys (*Ateles geoffroyi*). *Behav. Ecol. Sociobiol.* **55**, 223–230. (doi:10.1007/s00265-003-0700-6)
- Raposo, E. P., Buldyrev, S. V., da Luz, M. G. E., Santos, M. C., Stanley, H. E. & Viswanathan, G. M. 2003 Dynamical robustness of Lévy search strategies. *Phys. Rev. Lett.* **91**, 240 601. (doi:10.1103/PhysRevLett.91.240601)
- Reynolds, A. M., Smith, A. D., Reynolds, D. R., Carreck, N. L. & Osborne, J. L. 2007 Honeybees perform optimal scale-free searching flights when attempting to locate a



- food source. *J. Exp. Biol.* **210**, 3763–3770. (doi:10.1242/jeb.009563)
- Rhodes, J. R., McAlpine, C. A., Lunney, D. & Possingham, H. P. 2005 A spatially explicit habitat selection model incorporating home range behavior. *Ecology* **86**, 1199–1205. (doi:10.1890/04-0912)
- Rutz, C. & Hays, G. C. 2009 New frontiers in biologging science. *Biol. Lett.* **5**, 289–292. (doi:10.1098/rsbl.2009.0089)
- Schick, R. S. *et al.* 2008 Understanding movement data and movement processes: current and emerging directions. *Ecol. Lett.* **11**, 1338–1350. (doi:10.1111/j.1461-0248.2008.01249.x)
- Seton, E. T. 1909 *Life-histories of Northern animals: an account of the mammals of Manitoba*. New York, NY: Charles Scribner's Sons.
- Shettleworth, S. J. 1998 *Cognition, evolution, and behavior*. New York, NY: Oxford University Press.
- Sims, D. W., Righton, D. & Pitchford, J. W. 2007 Minimizing errors in identifying Lévy flight behaviour of organisms. *J. Anim. Ecol.* **76**, 222–229. (doi:10.1111/j.1365-2656.2006.01208.x)
- Sims, D. W. *et al.* 2008 Scaling laws of marine predator search behaviour. *Nature* **451**, 1098–1102. (doi:10.1038/nature06518)
- Skalski, G. T. & Gilliam, J. F. 2000 Modeling diffusive spread in a heterogeneous population: a movement study with stream fish. *Ecology* **81**, 1685–1700. (doi:10.1890/0012-9658(2000)081[1685:MDSIAH]2.0.CO;2)
- Skellam, J. 1951 Random dispersal in theoretical populations. *Biometrika* **38**, 196–218.
- Tomkiewicz, S. M., Fuller, M. R., Kie, J. G. & Bates, K. K. 2010 Global positioning system and associated technologies in animal behaviour and ecological research. *Phil. Trans. R. Soc. B* **365**, 2163–2176. (doi:10.1098/rstb.2010.0090)
- Travis, J. 2007 Do wandering albatrosses care about math? *Science* **318**, 742–743. (doi:10.1126/science.318.5851.742)
- Turchin, P. 1991 Translating foraging movements in heterogeneous environments into the spatial distribution of foragers. *Ecology* **72**, 1253–1266. (doi:10.2307/1941099)
- Turchin, P. 1998 *Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants*. Sunderland, MA: Sinauer Press.
- Van Moorter, B., Visscher, D., Benhamou, S., Borger, L., Boyce, M. S. & Gaillard, J. M. 2009 Memory keeps you at home: a mechanistic model for home range emergence. *Oikos* **118**, 641–652. (doi:10.1111/j.1600-0706.2008.17003.x)
- Van Winkle, W. 1975 Comparison of several probabilistic home-range models. *J. Wildl. Manage.* **39**, 118–123. (doi:10.2307/3800474)
- Viswanathan, G. M., Buldyrev, S. V., Havlin, S., da Luz, M. G. E., Raposo, E. P. & Stanley, H. E. 1999 Optimizing the success of random searches. *Nature* **401**, 911–914. (doi:10.1038/44831)
- Viswanathan, G. M., Raposo, E. P. & da Luz, M. G. E. 2008 Lévy flights and superdiffusion in the context of biological encounters and random searches. *Phys. Life Rev.* **5**, 133–150. (doi:10.1016/j.plrev.2008.03.002)
- Vlasak, A. N. 2006 Global and local spatial landmarks: their role during foraging by Columbian ground squirrels (*Spermophilus columbianus*). *Anim. Cogn.* **9**, 71–80. (doi:10.1007/s10071-005-0006-3)
- Voicu, H. & Schmajuk, N. 2002 Latent learning, shortcuts and detours: a computational model. *Behav. Process.* **59**, 67–86. (doi:10.1016/S0376-6357(02)00060-8)
- Volkov, S. 2006 Phase transition in vertex-reinforced random walks on  $\mathbb{Z}$  with non-linear reinforcement. *J. Theor. Probab.* **19**, 691–700. (doi:10.1007/s10959-006-0033-2)
- Weimerskirch, H., Gault, A. & Chérel, Y. 2005 Prey distribution and patchiness: factors in foraging success and efficiency of wandering albatrosses. *Ecology* **86**, 2611–2622. (doi:10.1890/04-1866)
- Wingen, L. U., Brown, J. K. M. & Shaw, M. W. 2007 The population genetic structure of clonal organisms generated by exponentially bounded and fat-tailed dispersal. *Genetics* **177**, 435–448. (doi:10.1534/genetics.107.077206)
- Wolf, M., Frair, J., Merrill, E. & Turchin, P. 2009 The attraction of the known: the importance of spatial familiarity in habitat selection in wapiti *Cervus elaphus*. *Ecography* **32**, 401–410. (doi:10.1111/j.1600-0587.2008.05626.x)
- Worton, B. J. 1989 Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* **70**, 164–168. (doi:10.2307/1938423)