

REVIEW AND  
SYNTHESIS

## Are there general mechanisms of animal home range behaviour? A review and prospects for future research

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**Abstract**

Home range behaviour is a common pattern of space use, having fundamental consequences for ecological processes. However, a general mechanistic explanation is still lacking. Research is split into three separate areas of inquiry – movement models based on random walks, individual-based models based on optimal foraging theory, and a statistical modelling approach – which have developed without much productive contact. Here we review recent advances in modelling home range behaviour, focusing particularly on the problem of identifying mechanisms that lead to the emergence of stable home ranges from unbounded movement paths. We discuss the issue of spatiotemporal scale, which is rarely considered in modelling studies, as well as highlighting the need to consider more closely the dynamical nature of home ranges. Recent methodological and theoretical advances may soon lead to a unified approach, however, conceptually unifying our understanding of linkages among home range behaviour and ecological or evolutionary processes.

**Keywords**

Diffusion, home range, random walk, site fidelity, spatial ecology.

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**INTRODUCTION**

*(...) it may be here remarked that most animals and plants keep to their proper homes, and do not needlessly wander about; we see this even with migratory birds, which almost always return to the same spot.*

(Darwin 1861)

Darwin (1861) pointed to a fundamental characteristic of animal movement: many animals restrict their movement to specific home ranges (Burt 1943; White & Garrot 1990) that are much smaller than one might expect from observed levels of mobility. Such area-restricted space use behaviour ('site-fidelity') has fundamental consequences for many ecological processes, such as the distribution and abundance of organisms and population regulation (Gautestad & Mysterud 2005; Wang & Grimm 2007), habitat selection (Rhodes *et al.* 2005), predator–prey dynamics (Lewis & Murray 1993), biological transport processes and community structure (Fagan *et al.* 2007), or infection spread (Kenkre *et al.* 2007). Despite many decades of research, however, we still lack a general movement framework that leads to the emergence of

stationary home ranges. Typically, home range research has been split into separate areas of enquiry (Ford 1983) – an analytical modelling approach stemming from the field of statistical physics (Turchin 1998; Okubo & Levin 2001; Moorcroft & Lewis 2006), an individual-based modelling approach developed from optimal foraging theory (Mitchell & Powell 2004), and a statistical modelling approach rooted in behavioural ecology and natural history (Burt 1943; Worton 1987; White & Garrot 1990; Powell 2000; Kernohan *et al.* 2001; Laver & Kelly 2008) – with a unitary treatment never attempted. Thanks to important recent developments emerging in the theoretical and empirical literature of animal movements as well as in statistical mechanics (Gautestad & Mysterud 2005; Börger *et al.* 2006b; da Silva *et al.* 2006; Giuggioli *et al.* 2006; Moorcroft & Lewis 2006; Mitchell & Powell 2007; Dalziel *et al.* 2008; Horne *et al.* 2008; Moorcroft & Barnett 2008), a unified view of home range behaviour is now emerging. We review these developments, showing that they open exciting new research avenues, crucial for the development of a new synthesis of animal movement and space use behaviour.

## DEFINING CHARACTERISTICS OF HOME RANGES AND TERRITORIES

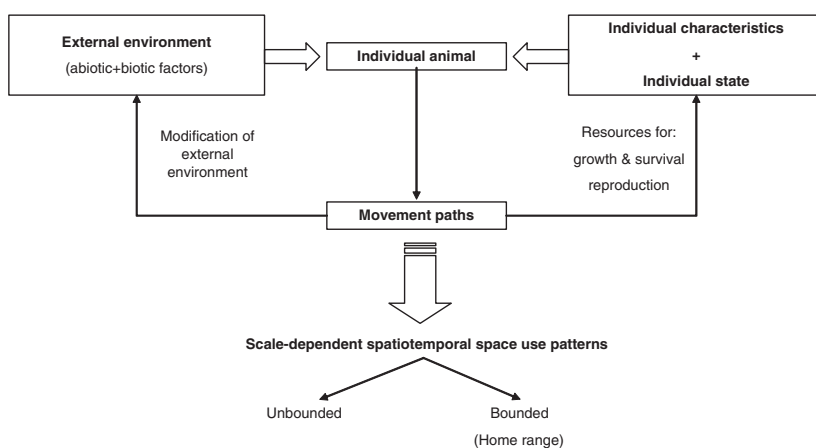
Home ranges are the spatial expression of behaviours animals perform to survive and reproduce (Burt 1943). These macroscopic patterns are determined by a large number of single movement steps (Moorcroft & Lewis 2006), each of which results from the interactions among individual characteristics, individual state, and the external environment, and the moving animal in turn modifies both its individual state and the external environment (Fig. 1). Home ranges are hence the resultant patterns of dynamic processes, which has profound consequences for the population-level effects of home range behaviour (Wang & Grimm 2007), as well as the time scale used for analysis of home ranges (White & Garrot 1990). In other words, home ranges defined over different time scales are not directly comparable. Furthermore, an animal might well show unbounded movement at a small spatiotemporal scale, but still have a well-defined and stable home range at a larger scale (Powell *et al.* 1997; Weimerskirch 2007). Stable home ranges at one age or ontogenetic stage can change due to natal dispersal or spawning migration (Pittman & McAlpine 2003). It is therefore crucial to define the timescales for the analysis of home range behaviour (Cooper 1978; Spencer *et al.* 1990; Laver & Kelly 2008). Similarly, the timing of the sampling period over which location data are collected can have a marked effect on the ability to identify temporal patterns (Börger *et al.* 2006b). To this end a very useful approach can be derived from random walk theory (squared displacement analysis, Spencer *et al.* 1990; Moorcroft & Lewis 2006, chapter 10), which avoids the need to use home range estimation methods. In general, it is important to note that, contrary to a territory (see below), a home range is defined and estimated without reference to defence or advertisement or reaction to intrusion by neighbouring

individuals; only the presence of the individual is required (Brown & Orians 1970).

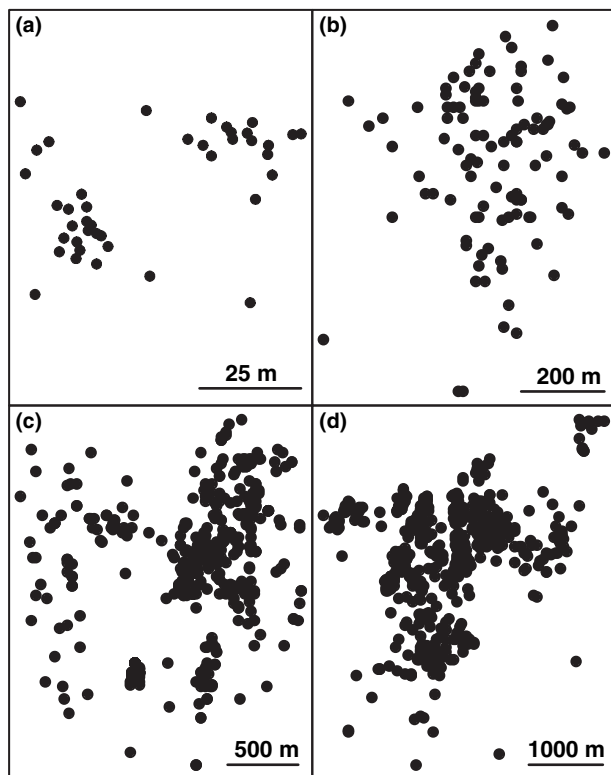
Empirically, home range behaviour has been recorded in both invertebrates and vertebrates (reviewed in White & Garrot 1990; Switzer 1993; Powell 2000; Kernohan *et al.* 2001; Laver & Kelly 2008). The spatial scale may range from a few square metres to several thousand square kilometres and a home range may be occupied for a single season or over many years. A quite common characteristic across spatiotemporal scales is a complex, multimodal internal structure (for examples, see Fig. 2).

Territoriality arises when individuals exhibit spatially oriented aggressive behaviour, i.e. aggressive defence of a space containing limiting resources (Burt 1943; Brown & Orians 1970; Davies & Houston 1984; Maher & Lott 1995; Adams 2001). The essential characteristics of a territory are (i) a fixed area, (ii) presence of territorial defence or keep-out-signals which elicit escape and/or avoidance responses by competitors, and (iii) exclusive use of the territory by its holder (Brown & Orians 1970). Crucially, when territorial defence fails to prevent intrusion by competitors, the area should not be defined as a territory (Burt 1943; Brown & Orians 1970). While a home range is estimated using all available location data, a territory is estimated by delineating the location of defence events, and the location of competing neighbours is needed to define the area of exclusive use (Burt 1943; Brown & Orians 1970).

The territory of an individual may be limited to a circumscribed area within the home range, where specific activities are performed (e.g. mating), or may extend to the whole home range; the latter case is usually called an all-purpose territory (Brown & Orians 1970). All-purpose territories are sometimes called 'defended home ranges', which has led to interchangeable use of the terms 'home range' and 'territory' (Moorcroft *et al.* 1999; Jetz *et al.* 2004). Nonetheless, the processes governing the form and size of



**Figure 1** A graphical model of animal space use processes.



**Figure 2** Examples of empirical home range patterns: location data for (a) a juvenile female brush rabbit (redrawn from Dixon & Chapman 1980); (b) a female roe deer (data from Börger *et al.* 2006b); (c) a female kestrel (data downloaded from <http://www.imperial.ac.uk/litsproject/>); and (d) a female elk (data from Dalziel *et al.* 2008). Notice the change in spatial scale, as well as the complex space use patterns.

most territories may be different from those determining the shape and size of the home range. For a review of the differences between defended and non-defended home ranges see Grant *et al.* (1992).

### MECHANISTIC HOME RANGE MODELS: THE RANDOM WALK APPROACH

*An animal following a random walk in the plane does not have a home range. However, by introducing a closely reflecting boundary or by invoking a return-to-origin rule, it is possible to devise a home range model in which the moving animal spends most of its time following a random walk.*

(Solow 1990)

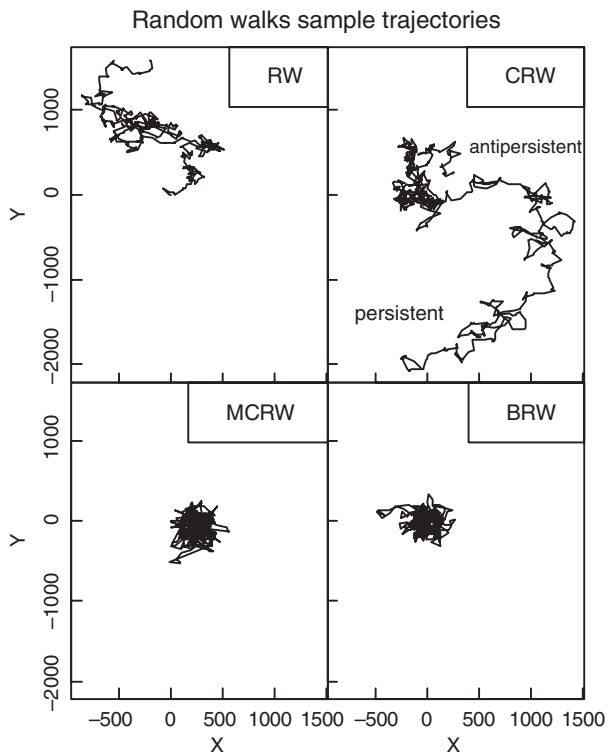
As presciently recognized by Solow (1990), movement models rarely lead to the formation of stationary home ranges. Due to their Markovian nature, random walks continue to slowly expand over time. This raises an important question: which biological features lead to the formation of stable home ranges out of fundamentally

unstable movement paths? A related question: which features lead to the formation of home ranges that have a realistic internal structure? We start by describing the characteristics of unbounded random walks, proceed to discuss model features that lead to the emergence of bounded space use patterns, showing that the available models apply only to a restricted set of taxa, and briefly discuss also novel non-Markovian random walk models of potential utility for modelling animal home ranges.

### Classical random walk and diffusion models

Random walks and the resulting pattern of diffusion are the basic building blocks of most movement models (Turchin 1998). They have been applied to ecological problems for over 50 years (Skellam 1951; Okubo & Levin 2001). A random walk is a mathematical formalization describing a movement path composed of successive steps, each in a random direction (the term was first coined by Pearson 1905; for an example see Fig. 3). When linked with a specified distribution of step lengths, a random walk yields the probability that a particle will occur at a given distance from the starting point after a given period of time. To determine a specific position it is necessary to know the complete history of the steps of a particle, called the trajectory. Usually a single trajectory is of little interest, however, as it is just one of many potential outcomes of a random walk with many steps. Using a statistical approach, we can derive the equations governing the evolution of the probability density function of the position of the random walker. A fundamental statistic for characterizing random walks is the mean squared displacement (MSD), which is the expected squared displacement over time for a certain random walk. The MSD is obtained by taking the average squared displacement over time repeated over many simulations (see Moorcroft & Lewis 2006, chapter 10 for a useful discussion).

Whereas random walk models provide a discrete representation of movements based on a sequence of single movement steps, diffusion models provide analogous representation in continuous time and space. More specifically, diffusion models summarize the dynamics of an ensemble of random walks in a space/time-continuous probability field using partial differential equations. Consequently, diffusion is most often applied to Eulerian (i.e. population-based) approaches to spatial ecology, whereas Lagrangian (i.e. individual-based) approaches are often based on random walk models (Turchin 1998). Diffusion and random walks, however, are closely connected, as the diffusion equations provide a limit approximation (i.e. infinitely small step lengths) for the outcome of many random walks (Turchin 1998). In fact, diffusion equations have been used to model the spread of individual



**Figure 3** Sample trajectories (1000 steps) of an uncorrelated random walk (RW), two correlated random walks (CRW) showing persistence and anti-persistence, respectively (notice, both trajectories are on the same pane), a biased random walk (BRW; biased towards the origin), and a persistent CRW with simple long-term memory (MCRW). Step lengths for all models are distributed as  $r \sim 1/\text{RND}^2$  where RND is a uniform random number between 0 and 1.  $r$  is truncated at  $r_{\max} = 100$ , which is approximately the 99th percentile of the untruncated distribution. The turning angles in the CRW are from wrapped Cauchy distributions with mean vector directions 0 for the persistent model, and  $\pi$  for the anti-persistent model; mean vector length is 0.7 for both. In the BRW, the magnitude and direction of steps are positively correlated with the distance and direction to the origin. This correlation increases linearly with distance from the origin until a precise return is certain. In the MCRW, the walker moves as for the persistent CRW, but at each step there is a chance ( $P = 0.05$ ) that it will instead return to a previously visited location, selected randomly.

animal locations within a home range or territory (Don & Rennolls 1983; Lewis & Murray 1993; Blackwell 1997; Moorcroft *et al.* 1999; Blackwell 2003; Moorcroft & Lewis 2006; Fieberg 2007).

The link between random walks and diffusion can be readily seen for the special case of Brownian motion: the random movement of particles floating in a fluid. It is one of the simplest continuous-time stochastic processes, arising as the limit of many random walk models. In Brownian motion, the displacement of a particle increases with the square root of time (Einstein 1905), implying that the

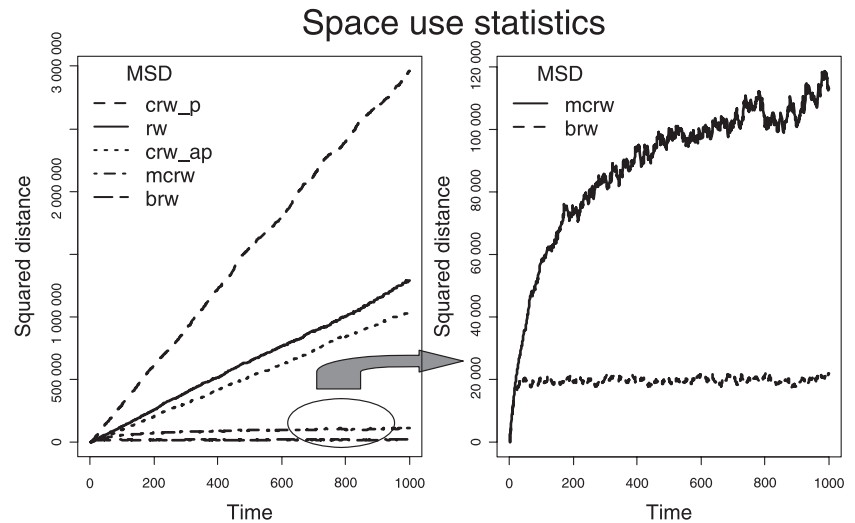
displacement from the point of introduction is initially rapid, but slows down with increasing time span. The parameters of many different varieties of diffusion can be directly estimated by observing sequential changes in the spatial distribution of particles over time (Turchin 1998). The path of a Brownian particle is of infinite length and covers the whole space evenly, giving rise to normal distribution, characterized by a Gaussian distribution of locations whose variance (i.e. the variance of the location coordinates on any arbitrary axes) increases linearly over time. Hence the variance is directly related to the mean-squared displacement (variance =  $\text{MSD}/n$  in  $n$ -dimension space).

Different random walks generally give rise to different forms of diffusion, which can be classified according to the value of the scaling exponent  $\alpha$  relating the mean-squared displacement (MSD) of the random walk to time ( $\text{MSD} \sim t^\alpha$ ). In this context, a scaling exponent  $\alpha = 1$  corresponds to normal diffusion, whereas super diffusion occurs if  $\alpha > 1$ , and sub-diffusion if  $\alpha < 1$ . In the case of localized home range use, however, the mean-squared displacement displays asymptotic behaviour, converging on a stable value (Fig. 4).

On the basis of the observations of animal trajectories and densities, increasingly complex models can be built to mimic more complex movement paths (Turchin 1998). In a correlated random walk (Fig. 3), for instance, the directions of successive moves are correlated up to a specified range, which induces a local directional bias. Specifically, correlated random walks give trajectories that exhibit either directional persistence, in the case of positive autocorrelation, or back track to previously visited sites ('anti-persistence') in the case of negative autocorrelation (in the sense of shuttling back and forth, i.e. without involving a specific spatial memory of some locations; see Fig. 3). In the long-term, however, the distribution of turn angles becomes uniformly distributed as the influence of the initial movement direction disappears (Benhamou 2006). Hence, correlated random walks are useful for modelling the forward persistence propensity characteristic of most animal movements (Patlak 1953a; Bovet & Benhamou 1988).

In a biased random walk (Gillis 1956; Turchin 1998; Benhamou 2006) movement in every direction is no longer of equal probability but is consistently biased by attraction to a fixed point in space. Alternatively, a biased random walk can be built where the turning rate is modified by exposure to some environmental properties experienced since the last direction change (Grunbaum 1999), or both correlation and bias might be combined into a biased correlated random walk model (Patlak 1953b; Turchin 1998). Traditionally, biased random walks have been used to model movement paths with an orientation component, from movement responses of bacteria to concentration gradients up to animal migration, with the location of the goal far from the

**Figure 4** Mean squared displacements (MSD) of five random walk models (1000 steps for 1000 simulations; time and space are in arbitrary units; crw\_p is the MSD of a persistent crw, crw\_ap of an antipersistent crw, see Fig. 3 for further details). The biased random walk (BRW) is the only model converging to a home range (the MSD reaches a stable value), as is evident by comparing the left panel (all five models) to the right panel (BRW and MCRW only, notice the change in scale on the Y-axis).



starting point (Turchin 1998; Benhamou 2006). This can result in close to linear (often termed ‘ballistic’) movement paths that move away from the starting point considerably faster than diffusive movements. If the goal is located close to the starting point instead of a long distance away then it becomes an attraction point around which the random walker moves and a localized space use pattern is obtained (Fig 3). This behaviour forms the basis for one of the simplest home range models: the focal-point attraction model.

Biased random walks (and biased correlated random walks) are related to so-called advection-diffusion models, where ‘advection’ refers to the directional movement and ‘diffusion’ indicates that in such models there usually remains a large random component (i.e. diffusion). Contrary to the case of Brownian motion or correlated random walks, it is usually difficult to derive an advection-diffusion model as the mathematical limit of a biased random walk, because of mathematical difficulties in deriving and solving the partial differential equations. As a consequence, researchers building home range models based on advection-diffusion equations (e.g. Moorcroft *et al.* 2006) often resort to numerical methods for integration. When analysing real animal movement paths it is often also difficult to statistically distinguish correlated and biased random walks (for recent approaches see Challet *et al.* 2005; Benhamou 2006).

Several other classes of random walk models have been introduced for modelling animal movements, such as Lévy walks (Edwards *et al.* 2007) or, more recently, multiphasic random walk models (Morales *et al.* 2004; Schmitt *et al.* 2006; Benichou *et al.* 2007; Zhang *et al.* 2007). After having solved the fundamental problem of finding biological features that lead to the formation of stable home ranges out of fundamentally unstable movement paths – a problem

which applies equally to most random walk models – it should prove worthwhile to explore the usefulness of these recent random walk models to obtain realistic within-home range space use patterns.

In conclusion, random walk models are simple and very effective tools for modelling real systems, i.e. systems subject to disorder, noise, or randomness, and thus can form a general framework for modelling animal movements. However, comparing empirical animal location data with predictions of different random walk models is statistically challenging (Jonsen *et al.* 2003; Morales *et al.* 2004; Coscoy *et al.* 2007) and requires an appropriate choice of sampling interval for discretizing continuous movement paths (Turchin 1998; Benhamou 2006). Finally, to truly unite random walk theory with movement ecology, we must find ways to include processes that lead to the emergence of home ranges in a diversity of taxa and at a wide range of spatiotemporal scales. Our inability to achieve this represents a fundamental problem with the current implementation of random walk models in ecology (Gautestad & Mysterud 2005).

### Focal point attraction

The simplest home range model is the Holgate and Okubo model. It was first developed by Holgate (1971), modified by Okubo (1980), and has recently been newly analysed in detail by Moorcroft & Lewis (2006, chapter 3). Originally, it was a biased random walk model in a square lattice with explicit values for the four transition probabilities to neighbouring cells. More recent versions use a diffusion model composed of two terms: a diffusion term governing the distance moved (and keeping the animal moving), and an advection term influencing the biased directionality of moves. All movements are biased towards the home range centre, with the degree determined by an attraction

parameter (called the 'localizing tendency parameter'). The model produces a circular home range centred on a focal attraction point. The mean and mean-squared distances moved are simple functions of the localizing tendency parameter, levelling off over time (Moorcroft & Lewis 2006).

Benhamou (1989) extended the focal point model by including within-home range scent marking behaviour and olfactory orientation of the animal to its own scent marks as mechanisms to explain within home range orientation behaviour. In a further elaboration (Benhamou 1994) the same author combined a focal point spatial reference orientation mechanism with area-concentrated search, showing that restricting movements to a stationary home range leads to marked improvements in foraging efficiency, compared with area-restricted searching without focal point attraction.

A problem with the simple focal point attraction model is that it always leads to unrealistic circular home ranges. Dunn & Gipson (1977) introduced a new approach, which assumes that animal movement paths follow a bivariate Ornstein–Uhlenbeck diffusion process. The model is described by three parameters: the mean vector and covariance matrix of the bivariate equilibrium distribution of the animal's position, and a matrix that determines the centralizing tendency of the process. An appealing feature of this approach is that the model can be readily fitted to real animal location data. A drawback is that the model still rests on quite restrictive assumptions about animal movements: the animal always moves according to a single diffusion model for which the stationary distribution is always normal and the shape of the home range is always elliptical and unimodal. In reality most animal home ranges are multinuclear. Don & Rennolls (1983) introduced an approach that allows for multinuclear home ranges, but this is obtained by centring separate distribution functions on a set of biological attraction points (e.g. den sites), the locations of which have been estimated independently.

Blackwell (1997) introduced a broad generalization of the Ornstein–Uhlenbeck model, further generalized recently (Blackwell 2003), which addresses many of those criticisms and provides a more flexible approach to the analysis of animal location data. The key feature is that it allows an individual animal to switch between different movement processes (modelled as different diffusion processes), on the basis of changing behavioural state or position within the home range. The models can be fitted to real data using Bayesian methods (Markov Chain Monte Carlo), which makes it possible to include prior information.

Recently, Giuggioli *et al.* (2006) introduced a new approach to estimating home ranges from animal displacement data obtained through mark-recapture methods. It is based on the Fokker–Planck equation, with a diffusion

constant for the movement of the animals and an attraction potential to obtain bounded home ranges. Part of the interest in this approach lies in its ability to estimate home range size using a limited set of recapture data. Yet the mechanisms leading to the emergence of home ranges out of unrestricted movement paths is still based on simple focal point attraction.

Indeed, the main shortcoming of all these focal point models is that the location of the home range centre is imposed *a priori*. The home range is not an emergent property of the movement process *per se*, but rather a built-in statistical property of a fundamentally stationary model. A truly mechanistic home range model should be able to recreate these patterns without fitting *a priori* an outcome of the process itself. A useful application of even simple focal point attraction home range models, however, is that they generate animal space use distributions that can be used to evaluate the performance of empirical home range estimation methods (Fieberg 2007).

### Memory effects

Many animals have the ability to remember previously visited sites and tend to revisit them periodically. Hence, memory effects provide a plausible biological mechanism that could potentially lead to stationary home ranges. Memory effects have been incorporated into random walk models by introducing a function that first attributes value to locations that have already been visited, and then weights these values to yield the relative attraction to previously-visited areas at each time step. Over the past decade, there has been a renewed interest in such non-Brownian random walks with complex memory processes. Depending on the weighting scheme used, these models can give rise to self-avoiding trajectories (self-avoiding random walks, reviewed in Madras & Slade 1993) or paths which are self-attracting (self-attracting random walks, e.g. Tan *et al.* 2001). Self-avoiding random walks are by definition not suitable for modelling animal home ranges, as home ranges are characterized by heavily revisited areas. Conversely, self-attracting random walks lead to the emergence of bounded movement paths and represent a promising approach to modelling home ranges. However, such an approach comes at the cost of assuming very high memory capacity: in some models each step depends on the complete history of all previous steps (Schutz & Trimper 2004; da Silva *et al.* 2006; Paraan & Esguerra 2006). Nonetheless, self-attractive models are being actively developed for other applications, especially in the physical sciences, and we suggest that, with suitable modifications, they might prove useful to model animal space use.

The first home range model incorporating a memory function was published by Siniff & Jessen (1969). It is based

on a biased correlated random walk, where the movements of each individual are biased towards previously visited sites. The correlated random walk component instead keeps the animal moving even when an attractor is reached. The balance between these two opposing processes leads to the emergence of a bounded space use pattern.

Another example is the self-attracting walk model of Sapozhnikov (1994, 1998), later modified by Tan *et al.* (2001). Visited sites are scored by the number of visits obtained (this is called the 'environment parameter'), up to a certain specified maximum saturation value (called the 'environment saturation' parameter). A random walker moves to a neighbouring site, with probability proportional to the number of visits previously received by the site and the value of the attraction towards its own trajectory. At the beginning, and for low attraction values, the walk resembles a random walk. Over time, and with higher attraction values, the balance between random fluctuations and attractive interaction switches towards a self-attracting walk, depending on the pre-defined environment saturation value. For all parameter values, however, the dimension of the cluster continues to increase until it covers all the entire two-dimensional space. Hence, no convergence towards home range behaviour is attained.

Tan *et al.* (2002) modified the self-attracting walk by introducing memory decay, resulting in a random walk model with memory enhancement and decay. Interestingly, introducing memory decay causes the accumulation of remembered sites to cease beyond a certain threshold, as a dynamic balance is reached between forgotten and newly visited sites. Hence, the movement remains fundamentally Brownian, as the cluster of visited (and hence remembered) sites drifts randomly across space, driven by changes in the number of visited sites at the edge sites of the cluster. A roughly constant home range is formed, but the coordinates of the centre of that range drift slowly over time. This is an interesting feature that anticipates an observed tendency for gradual home range drift observed in some animals (Moorhouse & Macdonald 2005).

A similar 'return-to-a-previously visited location' rule has been used by Gautestad & Mysterud (2005) in their multiscaled random walk model (MRW), which combines a multiscaled movement model with a site-fidelity algorithm. The site-fidelity algorithm produces return to previously visited sites (chosen randomly from all visited sites) at fixed time intervals. The model produces complex fractal but non-stationary space use patterns (Gautestad & Mysterud 2005, p. 49). Furthermore, as for the self-attracting walk models, no rational or biological justification is given for the site-fidelity algorithm, which consequently resembles an *ad-hoc* rule (for an example of a similar *ad-hoc* memory function applied to a correlated random walk see Figs 3 and 4).

On the basis of the observation that animals are willing to incur costs to remain in a familiar area, which implies that place-specific experience enhances fitness in that space, Stamps (1995) hypothesized a mechanistic role of motor learning in home range formation. Specifically, home ranges form because individuals learn site-specific serial motor programs that substantially enhance their ability to move in those familiar areas. This is an interesting hypothesis which, to the best of our knowledge, has not yet been incorporated into a movement-based home range model. It might prove useful for representing the space use behaviour of certain taxa (Stamps 1995).

Van Moorter, B., Visscher, D.R., Benhamou, S., Börger, L., Boyce, M. & Gaillard, J.M. (unpublished data) integrate foraging theory into a mechanistic home range model of general applicability. A correlated random walk model is biased by two memory processes that track environmental change, given by resource availability. For certain combinations of memory parameters the movements become restricted to a bounded space use pattern. Intriguingly, these same parameter combinations lead to more efficient resource acquisition than does purely random walk, a finding that extends and generalizes the results of Benhamou (1994) for the case of central place foragers.

Animal movements are the result of complex interactions between an individual animal and the external environment (Forester *et al.* 2007). Dalziel *et al.* (2008) developed a new method for evaluating interactions between physical landscape structure, the distribution of resources, and the memory of previous locations in determining movement trajectories of individual animals. Using non-linear regression with real location and landscape data for elk, the authors show that models based upon interactions among elements of landscape structure and memory are more likely than more traditional models, which rely on successive draws from static probability distributions.

### Habitat and resource distribution

Home ranges link the movement of animals to the distribution of the resources necessary for survival and reproduction. South (1999) developed a space use model, parameterized using data for red squirrels, where individuals move in response to energetic needs, or to build a memory map of food resources, or in response to the distribution of nest sites (used for resting). Individuals interact indirectly by depleting food resources or by occupying nest sites. Starting from a uniform distribution of food resources and naïve foragers, the author investigated the effect of changing food density on the area and overlap of home ranges. At high food densities, home ranges areas were small, similar sized and non-overlapping among individuals. At low food densities, ranges were overlapping, large and of dissimilar

sizes. These emergent space use patterns resulted from changes in food density, the ratio of population density to carrying capacity and the random distribution of nest sites. Most importantly, the results were robust to changes in parameter estimates. It would be most interesting to extend this model to explore the effect of other movement rules on animal space use patterns.

Matthiopoulos (2003) developed a flexible framework for modelling patterns of habitat use by central-place foragers, taking into account the effect of topographical barriers. It could prove very fruitful to extend this modelling framework to animal home ranges, as it provides a very elegant way to model animal space use as a function of the accessibility of spatial locations containing crucial resources, and the preference of individual animals for those resources.

It has been proposed (Moorcroft & Barnett 2008) that a recently developed spatially explicit resource selection model that includes home range behaviour (Rhodes *et al.* 2005) can be included in mechanistic home range models, accounting for preferential movement towards certain habitats. This would constitute an important connection between mechanistic home range models and the rich resource selection literature, as these two areas of enquiry traditionally developed independently without productive contact (Moorcroft & Barnett 2008).

This gap between different methodologies is addressed also by a new modelling approach by Horne *et al.* (2008). It consists of a multivariate approach for modelling the utilization distribution of an animal as an explicit function of environmental and behavioural covariates. This procedure allows to simultaneously couple home range behaviour and resource selection analysis into a single model. We further discuss this work in the section about statistical modelling approaches, as it constitutes an interesting link between statistical and process-based movement approaches to home range modelling.

### Territoriality and other social interactions

Territoriality models are typically based on a redirect-towards-the-centre response to boundary scent marks (Moorcroft & Lewis 2006) or an imposed boundary (Stamps & Krishnan 1999). More specifically, most existing mechanistic models of territoriality are modifications or extensions of Lewis & Murray's (1993) wolf pack territory model. These authors derived a partial differential equation model, in which the movement of wolves is diffusive, but where foreign scent marks elicit an advection-type reflection response towards the home range centre (assumed to correspond to the den site) proportionate to the density of foreign scent marks. Two other sets of equations govern scent marking behaviour: the intensity of marking is proportional to the presence or absence of foreign scent

marks, and scent marks decay over time. If scent marking is absent, the model reduces to simple diffusion and does not lead to the formation of a territory or a stationary home range (Lewis & Murray 1993). If scent marking occurs, however, an interesting feature is that the model predicts scent marking patterns and territories which resemble field data quite well. In subsequent extensions of the basic model (White *et al.* 1996; Lewis *et al.* 1997; Briscoe *et al.* 2002) the authors showed how interactions between neighbouring wolf packs leads to the formation of buffer zones, with low wolf density and high ungulate density (refuge areas). Similarly, the inclusion of an attraction towards the home range centre, irrespective of foreign scent marks, leads to the formation of a stationary home range even for a single pack, as expected from simple focal point models. Conversely, by including a differential response to foreign and familiar scent marks, Briscoe *et al.* (2002) propose a mechanisms by which a stable home range is formed also for a single pack without a den site, in concordance with empirical observations. Other modifications of the wolf model include a dependence of territory size on the number of pack members.

A method for fitting the mechanistic territory model to field data has been developed and applied to data on coyote territories (Moorcroft *et al.* 1999). An interesting feature is that the model fits can be used to obtain predictions for the distribution of locations and scent marks, as well as for the response to a removal or addition of a pack. Similarly, the effects of prey distribution and topography can be evaluated (Moorcroft *et al.* 2006), or predictions can be obtained about interspecific interactions with other carnivore species (Moorcroft & Lewis 2006).

It is not yet clear if these models will prove equally useful for other territorial species. More generally, given that the models break down in the absence of territorial behaviour (i.e. the scent-marking response), it seems unlikely that they will be appropriate for modelling all forms of home range behaviour. Spatially explicit modelling of territorial behaviour based on game theory (see Morrell & Kokko 2005 and references therein) suggests that, under certain conditions, it might be adaptive for animals to avoid fight locations, leading to the formation of well-defined, exclusive territories. This suggests a possible generalization of the scent-marking-based wolf and coyote models, with the advection-type response towards scent marks substituted by an avoidance response towards fight locations.

An as yet unexplored potential mechanism leading to the emergence of home range behaviour might be conspecific attraction. Conspecific attraction is an important mechanism influencing settlement decisions of animals (Fletcher 2007). A recent study (Haydon *et al.* 2008) has shown that a socially informed random walk model, where the movement parameters differ between solitary and grouped individuals,

is better able to capture the dispersal behaviour of a reintroduced elk population. It should be interesting to investigate if, and under which conditions, conspecific attraction might lead to the emergence of home range behaviour.

### **MECHANISTIC HOME RANGE MODELS: THE OPTIMAL FORAGING APPROACH**

Many vertebrate and invertebrate taxa are capable of higher cognitive abilities, such as navigation, homing, and specialized search tactics such as traplining and food caching (Bell 1991; Wehner 1997). When the target locations are perfectly known, the search problems consist of finding the optimal route connecting the resource patches (the travelling salesman problem) and determining how much time to spend harvesting resources in each patch. Classical optimal foraging theory assumes that animals have complete knowledge of the spatio-temporal distribution of resources, allowing predictions of the resource depletion level at which an animal should leave each food patch (the Marginal Value Theorem, reviewed in Stephens & Krebs 1986). It has typically developed rather independently from other diffusion-based modelling approaches to mimic gradient-climbing search behaviour, such as area-restricted search (Grunbaum 1999). Bayesian and risk-sensitive approaches to optimal foraging theory subsequently relaxed the assumption of omniscient animals, as animals are assumed to gather both energetic resources and information about the environment (McNamara & Houston 1985; McNamara *et al.* 2006).

In general, optimal foraging theory is based on an evolutionary approach to behaviour, centred on the functional analysis of trade-offs in the allocation of time and energy to different activities (Cuthill & Houston 1997). This is generally missing in approaches based on statistical mechanics (but see Lewis & Moorcroft 2001). Incorporating the optimal foraging framework into mechanistic home range models will be crucial for developing quantitative movement models based on the proximate or ultimate mechanisms determining animal space use behaviours. Indeed, recent research on the cognitive basis of animal movement (reviewed in Hills 2006) has not only shown that foraging- and feeding-related behaviours share similar molecular mechanisms across eumetazoans, suggesting an early evolution of the foraging behaviour based on area-restricted search, but also that the molecular mechanisms controlling foraging and goal-directed behaviour have been co-opted over evolutionary time to modulate the control of goal-directed cognition. Thus, for the first time there is now an imperative to develop truly mechanistic movement models.

One of the most intensively studied cases in optimal foraging theory is that of central place foragers. It constitutes an interesting example of a spatial constraint

on the organization of animal movements (Bovet & Benhamou 1991). For example, forage selectivity should decrease with distance from the central place (Fryxell & Doucet 1991). Most studies have focused on understanding how the central place constraint affects foraging and optimal diet choice, and not on which processes lead to the formation of bounded space use patterns. For example, Ford (1983) used optimal foraging rules to simulate the home range of a central place forager in a patchy environment. The model predicts that home range size should be inversely related to maximum resource density and renewal rate, positively related to movement rate, and spatiotemporal variation of within home range space use patterns should be driven by changes in maximum resource density or renewal rate.

Mitchell & Powell (2004) also used an optimal foraging approach to develop a mechanistic model to investigate the effect of the spatio-temporal distribution of resources, in relation to the travel costs from the home range centre, on the formation of home ranges. The model assumes that animals optimally choose which patches to include into home ranges based on a trade-off between resource benefits and travel costs. A fundamental difference with random-walk-based models is that Mitchell & Powell (2004) only model the process by which patches are selected for inclusion into the home range. Space use enters only indirectly through its effect on patch profitability, which is discounted for travel costs that are proportional to the distance from the home range centre. Mitchell & Powell (2004) modelled two different strategies: animals that maximize the amount of resources within a home range, within a limit determined by travel costs, or animals that choose the smallest area that includes the minimal amount of necessary resources. Furthermore, the authors explored the effects of resource depression caused by patch use. Overall, the landscape distribution of resources was the main determinant of the home range configuration, along with the amount of resource depression in relation to population density. The model is not based on an explicit movement equation, however, and the algorithm does not always produce stationary home ranges. Mitchell & Powell (2007) recently validated the model using location data collected on female black bears, obtaining a satisfactory fit to model predictions. This work nicely demonstrates that heterogeneous resources, discounted by the travel costs to reach them, might be an important mechanism leading to the emergence of bounded space use patterns.

### **STATISTICAL MODELLING OF ANIMAL HOME RANGES**

Traditionally, mechanistic home range models have attempted to recreate probability density distributions of

animal space use patterns from basic mathematical movement rules. The resultant distribution is then compared with actual movement data. In contrast, modern statistical modelling approaches focus on a different level: location data are used to estimate the most likely probability density function for the home range (e.g. Kernohan *et al.* 2001; Fieberg 2007; Getz *et al.* 2007). This likelihood function is used to evaluate a hypothesized set of possible processes determining its size and shape (Börger *et al.* 2006b). In other words, modern statistical modelling of home ranges focuses on the processes which determine the characteristics of the emergent home range, rather than examining the processes that determine its emergence from unbounded movement *in primis*.

Statistical approaches are based on the understanding that home ranges derive from dynamic scale-dependent processes. Hence home range size, location, and shape may change depending on the state of the individual and the conditions of the external environment. This is fundamentally different from most mechanistic approaches, which mostly consider home ranges in a static landscape. Dynamic home ranges can have an important impact on ecological processes such as population regulation (Wang & Grimm 2007). Analytical and statistical approaches to movement modelling should be complementary. In home range studies, however, these two approaches have had little productive contact (Moorcroft & Lewis 2006). This is unfortunate, as in fact any statistical model of locations reflects a corresponding movement model (Solow 1990), which can be incorporated into mechanistic movement models (Moorcroft & Barnett 2008).

Horne *et al.* (2008) have developed a new statistical modelling approach that promises to combine for the first time these two different levels of analysis. It consists of a multivariate approach that allows the estimation of the probability density function of an individual animal as an explicit function of environmental and behavioural variables in a model comparison framework (see also Horne & Garton 2006). Different sets of covariates represent different hypotheses about the mechanistic processes determining animal space use. Specifically, the approach uses animal location data to compare a null model of space use (e.g. an exponential distribution) with alternative models including environmental or behavioural covariates. It allows one to simultaneously estimate the most likely form of a home range and to evaluate the set of covariates that most likely determine that form. This should facilitate an establishment of links between process-based movement approaches and home range modelling. Historically, this approach can be considered as a generalization of earlier approaches for central place foragers (Getty 1981) based on the concept of an 'elastic disk' used by Huxley (1934) to describe the flexibility of territorial systems.

Statistical studies are fundamental for quantifying movement and space use patterns in relation to the interplay between the internal and external environment of animals (Forester *et al.* 2007). For example, current mechanistic models of territoriality rest on the strong simplifying assumption of a constant environment (Moorcroft & Lewis 2006). This assumption will obviously need to be relaxed at some stage. However, for many taxa it remains uncertain which temporal scales of change are important (Kjellander *et al.* 2004). Similarly, state-dependent differences and individual variability in space use patterns have rarely been considered. New statistical modelling approaches, based on analysing animal home ranges as individual-based time series with complex spatio-temporal autocorrelation structures (Börger *et al.* 2006b), allow one to extract a rich set of detailed information on the underlying state-dependent movement processes and on individual differences. We encourage the use of statistical mechanistic models for analyzing animal home ranges to obtain more refined understanding of the covariates governing animal space use. Given that the major methodological problems related to the estimation of home ranges have been largely solved (Börger *et al.* 2006a; Horne & Garton 2006; Fieberg 2007; Getz *et al.* 2007; Laver & Kelly 2008), it is now possible to address new and important questions: at what spatiotemporal scales do animals exhibit home range behaviour? How does home range behaviour change over large scales, e.g. across a species range or over an individual's lifetime? In the latter case, are home range changes associated with predictable changes in the life-history of the individual? These questions have seldom or often never been addressed, yet an enhanced understanding should also prove crucial for understanding the mechanisms governing home range behaviour.

## HOME RANGE BEHAVIOUR: A SYNTHESIS AND PROSPECTS FOR FUTURE RESEARCH

*It is apparent that many ecological problems have a physical analogue, and that the solution of these problems will require treatments and the use of functions with which we are already very familiar. Unlike most of the particles considered by physicists, however, living organisms reproduce, and members of the same and of different species interact. As a result the equations of mathematical ecology are often of a new and unusual kind (...) and require special treatment*

(Skellam 1951)

Home range behaviour is a very common space use behaviour of animals and has fundamental consequences for ecological processes. However, a general mechanistic understanding of this behaviour is still lacking. Crucially, research is split into three separate areas of inquiry – a mechanistic modelling approach based on the random walk framework,

mechanistic home range models developed based on optimal foraging theory, and a statistical modelling approach – which have developed without much productive contact.

Researchers using the random walk framework have focused on two key modelling issues: (i) choosing appropriate mathematical equations for modelling the movement paths and (ii) developing model features that lead to the emergence of site-restricted movement patterns out of unrestricted and unbounded movement paths. Satisfactory models have been developed so far only for two special cases – central-place foragers and territorial carnivores – and these generally make the restrictive assumption of constant environments and of stable home ranges. Ongoing progress in random walk studies has led to the recent emergence of novel non-Brownian random walks, opening exciting new avenues for modelling animal movement and space use behaviour. This will allow a model comparison framework, for which robust methods have been recently developed (Horne & Garton 2006; Dalziel *et al.* 2008; Horne *et al.* 2008). This is crucially needed, as animal movement data are the result of complex interactions between stochastic generating processes.

Optimal foraging theory is based on an evolutionary approach to behaviour, centred on the functional analysis of trade-offs in the allocation of time and energy to different behaviours, where travel costs are an important trade-off. This predictive element is generally missing in approaches based on statistical mechanics (but see Lewis & Moorcroft 2001). Hence, incorporating the optimal foraging framework into mechanistic home range models will be crucial for developing quantitative movement models based on the proximate or ultimate mechanisms determining animal space use behaviour. Cognition might be a crucial process leading to a higher foraging efficiency for animals showing home range behaviour, when compared with random searches (Benhamou 1994; Van Moorter, B., Visscher, D.R., Benhamou, S., Börger, L., Boyce, M. & Gaillard, J.M. unpublished data). This might lead to studies starting to tackle the exciting question of the evolution and development of spatial cognition involved in home range behaviour. However, a crucial limitation is that we currently know very little about the spatial cognitive abilities of animals at large scales like home ranges (Benhamou 1997), yet even this limitation might not be insurmountable given the rapid progress of research on spatial cognition (e.g. Hills 2006; Byrne *et al.* 2007; Jackson & Redish 2007; Janson & Byrne 2007).

Statistical modelling of animal home ranges has been hampered for a long time by methodological problems related to the estimation and analysis of home ranges. These issues have been solved to a large extent, opening the door for important yet unsolved questions about the dynamical nature of home range behaviour. Examples could include quantifying the spatiotemporal scales of variation of home

range behaviour across environmental conditions, over time, and among individuals, thereby quantifying the degree of consistent individual variation of home range behaviour. Most importantly, any statistical model of locations reflects a corresponding movement model (Solow 1990), hence there should be room for fruitful interchanges between mechanistic and statistical approaches (Horne *et al.* 2008; Moorcroft & Barnett 2008). Adoption of such a unified approach would hasten development of a truly quantitative body of theory for home range behaviour, conceptually unifying our understanding of linkages among home range behaviour and ecological or evolutionary processes.

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