



## Search and navigation in dynamic environments – from individual behaviors to population distributions

Thomas Mueller and William F. Fagan

T. Mueller ([muellert@gmail.com](mailto:muellert@gmail.com)) Graduate Program in Behavior, Ecology, Evolution, and Systematics, Univ. of Maryland, College Park, MD 20742, USA, and National Zoological Park, Conservation and Research Center, Front Royal, VA 22630, USA. – W. F. Fagan, Dept of Biology, Univ. of Maryland, College Park, MD 20742, USA.

Animal movement receives widespread attention within ecology and behavior. However, much research is restricted within isolated sub-disciplines focusing on single phenomena such as navigation (e.g. homing behavior), search strategies (e.g. Levy flights) or theoretical considerations of optimal population dispersion (e.g. ideal free distribution). To help synthesize existing research, we outline a unifying conceptual framework that integrates individual-level behaviors and population-level spatial distributions with respect to spatio-temporal resource dynamics. We distinguish among (1) non-oriented movements based on diffusion and kinesis in response to proximate stimuli, (2) oriented movements utilizing perceptual cues of distant targets, and (3) memory mechanisms that assume prior knowledge of a target's location. Species' use of these mechanisms depends on life-history traits and resource dynamics, which together shape population-level patterns. Resources with little spatial variability should facilitate sedentary ranges, whereas resources with predictable seasonal variation in spatial distributions should generate migratory patterns. A third pattern, 'nomadism', should emerge when resource distributions are unpredictable in both space and time. We summarize recent advances in analyses of animal trajectories and outline three major components on which future studies should focus: (1) integration across alternative movement mechanisms involving links between state variables and specific mechanisms, (2) consideration of dynamics in resource landscapes or environments that include resource gradients in predictability, variability, scale, and abundance, and finally (3) quantitative methods to distinguish among population distributions. We suggest that combining techniques such as evolutionary programming and pattern oriented modeling will help to build strong links between underlying movement mechanisms and broad-scale population distributions.

Animal movements, such as searching behavior for food, homing navigation to a nest site, or dispersal to find a mate, are important contributors to a species' autecology and geographic distribution. Movements are key elements of the ecology of diverse species and occur across a wide range of spatial and temporal scales (summarised by Estes 1991, Alerstam et al. 2003). Many studies have investigated orientation mechanisms, drivers of movements, and resulting patterns of population distributions (Bell 1991, Turchin 1998, Alerstam 2006). However, ecologists also recognize the need to organize these studies into a cohesive framework to better understand and model animal movements. For example, a recent special feature in *Science* suggested 'movement ecology' as a new subdiscipline within which these efforts can be summarized (Holden 2006); however, the actual organizational structure for movement ecology was left open. Here we contribute to a synthesis of movement ecology by outlining an integrative, conceptual framework encompassing many of the various movement types that animals usually exhibit.

We suggest that traditional approaches to the study of animal movements can be organized in three categories:

- a. Studies of how animals search when they lack or have limited information about potential targets. These studies usually assume random and unpredictable resource environments. Some examples include theoretical models designed to identify optimal search strategies under different conditions (e.g. optimized random searches, Bartumeus et al. 2005; optimal 'tortuosity' for central place foraging, Bovee and Benhamou 1991, or 'foray searches' in fragmented landscapes, Conradt et al. 2003). Other studies seek to reveal the strategy at work by fitting empirical data to alternative hypothesized movement strategies (e.g. fitting 'Levy flights' to movements of sea birds, Viswanathan et al. 1999, or modeling movement of ungulates as mixtures of random walks, Morales et al. 2004).
- b. Studies investigating animals' navigational skills relative to known targets. In this category, resources are predictable, and animals use pre-existing information to locate those resources. In broad terms, the pre-existing information represents memories, with the caveat that those memories may be either genetically inherited (e.g. monarch butterflies *Danaus plexippus*,

Brower 1996) or previously learned by individuals (e.g. honey bees *Apis mellifera*, von Frisch 1967). Studies in this category are chiefly empirical and focus on revealing the underlying means animals use to navigate to their targets. Often the navigational skills are remarkable; examples include the waggle dance of bees (von Frisch 1967, Riley et al. 2005), long distance orientation of migrating birds (Alerstam 2006), and homing capabilities of pigeons *Columba livia* (Gagliardo et al. 1999, Biro et al. 2007) or marine turtles (Bowen et al. 2004).

- c. Studies that consider the optimal spatial distribution of animals in relation to conspecifics and resources as a driver of movement behaviors. Unlike the above two categories, this body of research adopts population-level perspectives that emerge from individual-level decisions. Classic examples are the ideal free distribution (IFD, Fretwell and Lucas 1969) and the marginal value theorem (Charnov 1976), which predict that animals will leave a patch when their fitness drops below the average fitness in all patches, leading to a landscape in which the density of individuals is everywhere proportional to resource density. Also in this category are studies of the scaling relationships between body size and optimal home range sizes (Haskell et al. 2002).

Categories a) and c) often share a common assumption that animal fitness is related to efficiency of foraging behavior and that specific measures, such as energy intake, can be directly linked to fitness (i.e. optimal foraging, Pyke 1984). Consequently, several strong links exist between these two categories. Examples include investigations of how an adaptive search behavior can lead to ideal population distributions and attempts to identify which factors (e.g. different competitive abilities, incomplete knowledge, movement costs, conspecific attraction, site fidelity) explain observed departures from ideal distributions (Farnsworth and Beecham 1999, Gautestad and Myrsetrud 2005, Hancock and Milner-Gulland 2006).

On the other hand, a significant disconnect exists between search-related (group a) and navigational (group b) studies. To see this, consider that two recent syntheses analyzing animal movements and animal navigation have almost no content in common (Turchin 1998, Alerstam 2006). For example, Turchin's (1998) book on movement analysis summarizes diffusion-based random walks and rule-based searching models but does not mention navigational issues described in Alerstam (2006) such as how migration routes are affected by orientation mechanisms (e.g. migration trajectories in relation to sunset azimuths). Despite the weakly developed links between these fundamental areas of research, it is likely that a variety of different search and navigation mechanisms work simultaneously, but at different scales, to determine animals' movements and spatial distributions (see Bailey et al. 1996 for a review in mammalian herbivores or Fritz et al. 2003 for a seabird example). Search and navigation may also be used by animals consecutively for different purposes. For example, seabirds may go on foraging trips searching for prey such as krill or fish that exhibit great spatial variability but later return to a specific nest site, using homing and navigation

techniques (e.g. albatrosses, Bonadonna et al. 2005). We believe that progress can be made towards a synthesis of these disparate categories of research on animal movements. This synthesis will require systematically identifying the underlying mechanisms of different movement strategies and providing a conceptual framework that integrates those mechanisms with landscape dynamics and emergent population patterns.

To build toward such a synthesis, we organize our paper as follows. First, we identify three individual-level mechanisms that animals may employ to search and navigate their resource landscapes. We next outline three common population-level patterns that emerge from individuals' movements. In a third section, we consider alternative resource distributions as critical determinants of the efficiency of individuals' movement mechanisms and population patterns. Also in the third section, we specifically investigate the consequences of the temporal predictability and spatial heterogeneity of resources within a given landscape. In a final fourth section, we provide modeling ideas related to our conceptual framework. We focus on bottom-up approaches assuming that animals' movement decisions are governed by state variables of individuals such as physiological condition or perceptual information. Some of these state variables can be linked to specific individual-level movement mechanisms, and we outline the potential of evolutionary programming to combine these qualitatively different types of information. In presenting this synthetic framework, we focus on resource distributions as a main driver for movements. However, our concepts are sufficiently flexible to include life-history traits (e.g. diet type, Boyle and Conway 2007, or sex, Ruckstuhl and Neuhaus 2002) and other factors such as predator avoidance, conspecific interaction, and mate finding (Fauvergue et al. 1995, Moorcroft et al. 1999, 2006, Fortin et al. 2005, Morrell and Kokko 2005).

## Individual level movement mechanisms

We suggest that all active animal movements (versus passive movements such as dispersal of many freshwater invertebrates etc., Bilton et al. 2001) can be assigned to one of three fundamentally different classes: non-oriented mechanisms, oriented mechanisms, and memory-based mechanisms. We emphasize, however, that no single mechanism in isolation is likely to provide a comprehensive framework for the complex patterns of animal movements observed in nature and that different mechanisms likely act simultaneously at different spatial scales (Bailey et al. 1996).

### Class 1. Non-oriented mechanisms

These involve simple movements, such as diffusion and kinesis that result in a movement decision with random direction. With non-oriented mechanisms, sensory stimuli (e.g. resource availability, habitat type) originating from an animal's current location cause an alteration in an individual's movement parameters, such as speed, the distribution of turning angles, or the frequency of movement (Benhamou and Boveé 1989). Non-oriented mechanisms can

be represented mathematically as correlated random walks (Turchin 1998). For example, habitats that provide an individual with a higher energy intake rate can produce lower velocity and more frequent, less correlated turns leading to an encamped walking pattern. In contrast, lower quality habitats may result in “explorative walks” with higher velocity and correlated turns (Kareiva and Odell 1987). Non-oriented mechanisms have been studied extensively in insect dispersal (Turchin 1998).

## **Class 2. Oriented mechanisms**

These rely on perceptual cues, which unlike stimuli in Class 1, stem from a location beyond the animal’s current position and result in movement in a predictable direction. Oriented mechanisms utilize sensory cues (e.g. visual, olfactory, acoustic) and various forms of taxis in which movements are defined by the organism’s perception of a resource or target location. A few empirical studies have explored perceptual ranges of individuals of different taxa, such as insects (Schooley and Wiens 2003), small mammals (Zollner and Lima 1999), pigs (Croney et al. 2003) or birds (Biro et al. 2004). In addition, some models investigate scaling relationships between body size and perceptual ranges (Mech and Zollner 2002) or study the context-dependence of perceptual ranges (Olden et al. 2004). Overall, however, relatively little empirical research has sought to quantify organisms’ perceptual ranges. Consequently, it often remains unknown whether perceptual ranges of individuals operate at spatial and temporal scales comparable to the scales over which resource availability changes. For example, in open grassland systems, we do not know whether foraging ungulates can identify and move towards rain on the horizon.

## **Class 3. Memory mechanisms**

In this class of mechanisms, previous information about the location of the movement target is available. This previous information may derive from the recollection of an individual’s own history (e.g. large herbivores, Bailey et al. 1996), communication from conspecifics (e.g. bees, von Frisch 1967), or as a genetic inheritance from its ancestors (e.g. monarch butterflies, Brower 1996). Research suggests that individuals using memory-based mechanisms may draw upon two fundamentally different techniques, path integration or compass navigation and cognitive maps (i.e. pilotage via known landmarks; Gagliardo et al. 1999, Vickerstaff and Di Paolo 2005, Biro et al. 2007). These techniques, which may be used simultaneously, are best known from studies of birds and insects. For birds, combinations of celestial and olfactory cues, geomagnetic coordinates, magnetic compasses and landmarks facilitate global navigation and homing (Alerstam 2006, Wiltschko and Wiltschko 2006, Åkesson and Hedenström 2007). Other examples are the waggle dance of bees that allows bees to navigate to food sources via communication with conspecifics (von Frisch 1967). Other taxa exhibit similar memory-based movements, including magnetoreception in turtles and magnetic compasses for path integration in moles (Wiltschko and Wiltschko 2006).

For large mammalian herbivores, research has focused on spatial learning of resource locations (Bailey et al. 1996).

To understand why an individual moves the way it does, ecologists need a systematic approach that compares and integrates across these three classes of mechanisms. Unfortunately, very few studies have attempted to compare alternative movement models to one another. Recent modeling efforts seek to integrate memory (Grünbaum 2000), social information on conspecifics (Hancock and Milner-Gulland 2006), or predator avoidance (Morales et al. 2005) in models of movement decisions, but to our knowledge no movement models have integrated non-oriented, oriented and spatial memory mechanisms within a two-dimensional context. Certainly none have done so in connection with empirical data collected on the movement of a specific organism.

## **Population level distributions**

Here, we build on the approach that Roshier and Reid (2003) developed for birds, which allows for the quantification of spatial patterns by considering the spatial distribution of individuals relative to conspecifics. In this framework, three major population-level distribution strategies emerge. These are sedentary ranges, migration, and nomadism.

### **Distribution 1. Sedentary ranges**

Sedentary ranges comprise resident strategies such as home ranges or territories, and are characterized by distributions in which an individual over its lifetime occupies a relatively small area compared to the population range (Roshier and Reid 2003). Long-distance movements in sedentary animals are usually limited to events of natal dispersal. Depending on the species, single individuals or small groups may occupy a sedentary range. A population of range residents exhibits a spatial distribution wherein individual ranges (or those of small groups) are dispersed from each other (Fig. 1A). Resident ranges are usually found when resources are sufficiently abundant throughout the year across the entire population range. Alternatively, resident ranges emerge if animals are dormant and suspend activity in unfavorable seasons (e.g. many bear species). Several studies have explored environmental determinants leading to different types of range residency (from home ranges to territorialism, reviewed by Mahler and Lott 2000).

### **Distribution 2. Migration**

Migration is generally defined as a regular, long-distance pattern of movement, and is typically observed in systems with regular, seasonal fluctuations in environmental conditions (Sinclair 1983, Dingle and Drake 2007). Migrations are usually periodic in nature: movement occurs consistently to and from spatially disjunct seasonal ranges (Fig. 1B; Roshier and Reid 2003). Migration is a common population-level strategy for animals and occurs in diverse taxa (reviewed by Alerstam et al. 2003, Dingle and Drake 2007). Ramenofsky and Wingfield (2007) make clear that

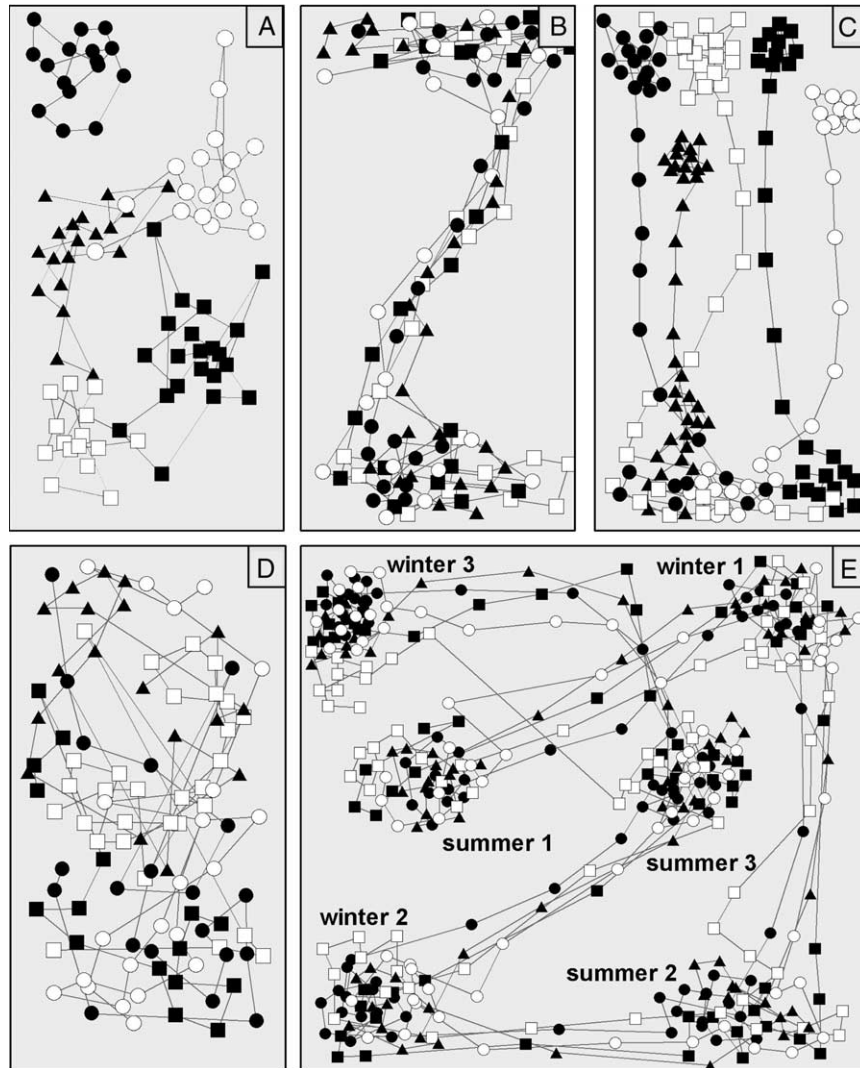


Fig. 1. Theoretical point patterns and trajectories of population distributions. (A) Sedentary ranges, (B) migration, (C) combination from (A) and (B), (D) nomadism type I, (E) nomadism type II. Boundary boxes indicate conceptual population ranges.

an important distinction exists between migration in iteroparous animals (i.e. species that breed multiple times) and semelparous animals (i.e. species that breed once). In iteroparous species, migratory movements usually repeat in adult life history stages (with the possible exception of natal dispersal). For example, individual whales, birds, or caribou migrate to and from breeding grounds multiple times during their lives. In contrast, semelparous animals may migrate during ontogeny but do not repeat their movements (e.g. anadromous Pacific salmon *Oncorhynchus* spp.; see Ramenofsky and Wingfield 2007 for a detailed review of migratory mechanisms). Among semelparous animals, insects are unique in that a single migration event can involve multiple generations (e.g. Monarch butterflies stretch their annual migration across North America over several generations, Brower 1996).

### Distribution 3. Nomadism

Nomadism occurs when animals are neither resident nor migratory, and instead move across the landscape in routes

that do not repeat across years. Such wandering movements occur when resources fluctuate irregularly on a multi-year timeframe over large geographic areas, leading to a) spatial patterns that vary widely among individuals and b) a lack of predictability in where individuals will be from one year to the next.

The term nomadism unfortunately suffers from a lack of or conflicting definitions in the movement literature (Estes 1991, Fahse et al. 1998, Bennetts and Kitchens 2000, Roshier and Reid 2003, Fryxell et al. 2004, Dingle and Drake 2007). Here, we define nomadism as a category of movement patterns on par with sedentary ranges and migration. Nomadism occurs at broad spatial scales, but does not follow the prescribed regular temporal and geographic patterns that characterize migration. These movements lack the inter-year predictability that characterizes both sedentary ranges and migration. In contrast, we suggest that nomadism is characterized by unpredictable movements that vary among individuals for any given year (type I nomadism; Fig. 1D) or among years for any given individual (type II nomadism; Fig. 1E). Compared to sedentary ranges and migration, nomadism has received

extraordinarily little research by ecologists, even though elements of unpredictability are a common feature of movements by many species.

We recognize that these three categories are not always mutually exclusive. For example, many birds occupy territories between migration events (Fig. 1C) and employ a combination of movement strategies that yield resident ranges and migration at different times of the year. Seabirds, such as albatrosses, constitute another exception in that they occupy territories within colonies but show nomadic movements while on foraging trips. In addition, some animal populations simultaneously express different strategies, such as when only a fraction of the population follows regular long distance movements (reviewed by Jahn et al. 2004).

Certainly there are also other frameworks for studying the spatial distribution of populations than just the three part classification we propose. As mentioned above, an obvious one involves ideal free distributions (Sutherland 1983, Hancock and Milner-Gulland 2006, Haugen et al. 2006). The IFD framework is frequently used for testing hypotheses about underlying mechanisms that influence organisms' spatial distributions or activity patterns. For example, researchers have used the IFD framework to study the effects of interference competition or movement costs in studies of oystercatchers and knots (VanderMeer and Ens 1997, van Gils et al. 2006). Likewise, behavioral studies about social organization and spacing among individuals, e.g. grouping behavior due to predation (Fryxell et al. 2007), are ultimately studies about population distributions. Such intra- and interspecific factors may all be at work within each of the three classes of population distributions presented here. For example, variability of density of red knots across intertidal patches may be partly explained by IFD (van Gils et al. 2006), and at the same time, on a broader scale, the movements of these birds can be classified as migratory. We emphasize that the three categories we propose focus on broad scale and long term dynamics, i.e. spatially these categories are based on the landscape ranges of entire populations and functionally these categories are built on effects due to large-scale resource dynamics. Consequently, the three classes we discuss integrate across longer time and consider movement between varying resource landscapes. For example, our use of the term migration is restricted to scenarios involving multiple seasons and years. Although we don't have the space here for a more complete development of the concept, we suggest that the term "ideal free pathway" may be a good descriptor for linking multiple spatial distributions of individuals over time.

## Resource distributions and synthesis

A conceptual framework that links different combinations of individual-level movement mechanisms with patterns of resource dynamics is a key to understanding alternative population-level spatial distributions. Resource environments interact with individual behaviors to influence population-level movement and distribution patterns. Typically, theoreticians explore such linkages by implementing movement models in alternative neutral landscapes

(reviewed by With and King 1997). In these models, change in habitat or resource abundance often only occurs in different realizations of a randomly generated landscape or is due to resource depletion by the consumers themselves. Such approaches ignore temporal environmental variation as a driver of resource abundance and availability. This is an important limitation because the consensus is that large-scale movement patterns such as migration are the result of seasonally changing resource abundance (Fryxell et al. 2004). Some studies do recognize the importance of temporal predictability to species movements. For example, Fryxell et al. (2005) demonstrated that for Thomson's gazelle, *Gazella thomsoni* in the Serengeti Plains, adaptive movements that cause individuals to follow stochastic rainfall events (and thus take advantage of ephemeral food sources) are necessary for population viability. Overall, however, a clear need exists for systematic investigations that explore the performance of alternative movement mechanisms in landscapes with temporal heterogeneity.

Another gap exists between the neutral resource landscapes favored by many theoreticians and the resource distributions evident in empirical landscapes. Though little explored, using empirical landscapes may be advantageous in some modeling studies because model outcomes can be compared with empirical data on organisms' actual distributions via linked GIS and remote sensing databases. This approach allows for predictions about animal movements and distributions in real landscapes, and thus makes results available for conservation and population management (Wiegand et al. 2004, Morales et al. 2005).

We assume that landscape structure is a major driver determining the efficiency of different individual-level movement mechanisms and resulting population-level distributional patterns. We focus on the general case of gradients in resource distributions, which includes but is not limited to a patchy structure divided into habitat and matrix (Bowler and Benton 2005). We suggest that resource gradients can principally change across four axes: 1) resource abundance 2) spatial configuration of resources (e.g. degree of spatial heterogeneity of resource distributions), 3) temporal variability of resource locations, and 4) temporal predictability of resources. It is important to differentiate between temporal variability and temporal predictability of resources. If resources are distributed differently in summer and winter, but those distributional changes occur every year, the resources would be variable but predictable. In contrast, if resource availability changed over time but the spatial patterns were not consistent, the resources would be variable and unpredictable.

We further suggest that the four gradients follow a hierarchical order. For example, spatial configuration (gradient 2) matters only if some resources are present (gradient 1). Likewise, temporal variability (gradient 3) depends on resources being heterogeneously distributed in space (gradient 2). Lastly, predictability of resources (gradient 4) is only relevant with resource variability (gradient 3) as a pre-requisite. Note also, that within a particular landscape, the strengths of the four gradients may themselves vary over time. Conceptualizing resource variation in terms of gradients in total amount, spatial configuration, and degrees of variability and predictability

is especially advantageous because such quantification facilitates modeling of resource dynamics.

Different combinations of these gradients should affect the relative efficacy of different individual-level mechanisms and should result in alternative population-level distributions.

First, for landscapes with little resource variability, memory should generally play an important role. An individual's previous moves are important sources of information for decisions about future movement as the previous moves provide information about where resources might be expected. Home ranges cannot be understood with simple diffusion or low order Markovian random walk models (Turchin 1998) but need to consider the individual history of an organism (Gautestad and Mysterud 2005). However, not only resources alone but also social factors may help configure resident ranges (e.g. intra-specific scent marks may constrain home ranges: Moorcroft et al. 1999, 2006). Discrimination between known neighbors and strangers may be an important mechanism for conflict avoidance and is believed to favor the establishment of territoriality. For example, in some songbird species, individuals can discriminate not just con-specifics but individual neighbors (Lovell and Lein 2004). Social factors may also play a role in cases where populations are resident even though resources are temporally variable and unpredictable provided the resources are sufficiently abundant and fine-grained to ensure long term survival within a consistent range (Fig. 2). Movement mechanisms at work in this scenario should be twofold: memory to recognize neighbors and boundaries of territories plus oriented foraging moves to obtain resources within an organism's perceptual range. Non-oriented movement will be a less beneficial strategy under these conditions: altering turning angles based on food intake will not increase an animal's chances of relocating into good habitat when resources are rather homogeneously distributed.

Second, for landscapes that vary at increasingly longer temporal and broader spatial scales, average (spatiotemporal) distances between high resource areas will increase,

and animals will be required to travel increasingly larger (spatiotemporal) distances between resource patches. Under these conditions, distributional patterns such as resident ranges will break up and transform to migration provided there is sufficient repetition to the seasonal changes. Landscapes exhibiting regular and predictable temporal dynamics should enhance the relative success of movement strategies requiring memory (e.g. it would be beneficial for organisms to remember where and when conditions would be favorable for reproduction and wintering).

Third, if changes between seasons become unpredictable, our framework predicts that migration or sedentary ranges would switch to nomadism as individuals sought resources whose availability was not dependable. In this case, the efficiency of memory would decrease as resources became more unpredictable and the environment changed on scales vastly larger than an individual's perceptual range. Under these conditions, non-oriented movements may constitute the most effective strategy as they would allow an animal to locate resources beyond its perceptual range and successful movements would not depend on the predictability of resources (Fig. 2). On the population level, we suggest that two different types of nomadic patterns can emerge (Fig. 1D–E). In type I nomadism, individuals move between and within years in ways that cannot be predicted and will differ among individuals. We expect this movement strategy will appear in landscapes featuring multiple rich resource areas. In type II nomadism, we envision the case that, at any one time, only very few resource patches exist and that the spatial location of those patches is unpredictable in time. If animals search for these patches they will eventually aggregate in the same locations/patches even if their search paths towards these patches are independent. Consequently, on larger spatial scales individuals' movements may be correlated with each other as in migration but, unlike migration, individual paths will not repeat across years. While both migration and sedentary strategies could transform to nomadism I (and vice versa), it seems plausible that nomadism II is particularly linked to migration.

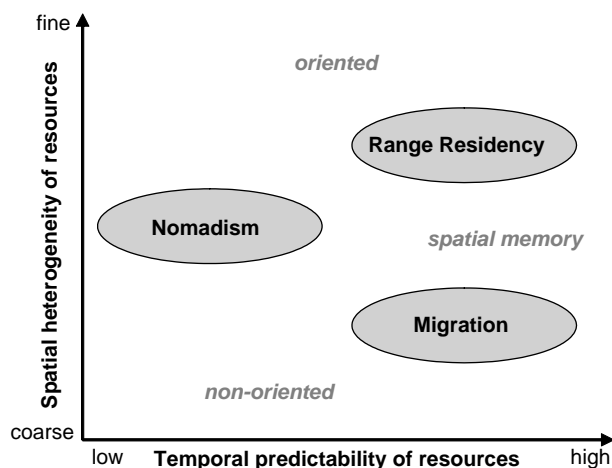


Fig. 2. Effects of gradients in resource distribution and predictability on hypothesized most effective individual-level movement mechanisms (in italics) and the hypothesized emergent population-level movement patterns (gray ellipses) for dynamic landscapes that exhibit resource variability.

## Modeling concepts

### Recent approaches

Any attempt to gain a mechanistic understanding of animal movement faces the challenge that it is generally not feasible to measure the entire suite of relevant low-level parameters (and their interactions) that are hypothesized to determine an animal's movement decisions under field conditions. For some mechanisms, experimental manipulations may allow one to alter a 'normal' movement behavior to demonstrate the relevance of a particular behavior. For example, experimental control of food intake may identify a non-oriented movement mechanism (e.g. 'preytaxis' Kareiva and Odell 1987) and measurements of perceptual ranges in small mammals may demonstrate an oriented mechanism (Zollner and Lima 1999). Likewise, clock-shifting experiments that generate internal conflicts between sun-compass and landmark information may help uncover spatial memory mechanisms, such as whether memorized landmarks or compass navigation are at work (Biro et al. 2007).

While such experiments do elucidate the importance of certain behaviors in specific cases, for many organisms such techniques are unlikely to be practical or transferable to field settings. This is certainly true when movement decisions may be context-specific, may depend on the interaction of several mechanisms, and/or may depend on interactions with conspecifics.

A more powerful approach to understand empirical movements may entail statistical analyses of relocation data, which recently has become an increasingly viable option, particularly for large mammals. For example, coupled GPS-ARGOS systems use satellite-linked collars to provide relocation data that can be acquired independent of field observers. Such data are now precise to within a few meters, meaning that the movement trajectories of individual animals can be captured in great detail. The high spatiotemporal resolution of relocation data emerging from modern tracking technologies has facilitated research on movements at multiple scales and has spawned a new body of literature concerning quantitative analysis of movement paths (Fauchald and Tveraa 2003, Morales et al. 2004, 2005, Jonsen et al. 2005). These approaches identify and parameterize statistics such as estimates of first passage time or shape parameters for distributions of velocity or turning angles that characterize movements in a context-specific fashion. Among many approaches tried, hierarchical state space models based on animal movements have been particularly revealing (Morales et al. 2004, Jonsen et al. 2005). Coupled with field-based relocation data, these models can be used to identify alternative movement states (e.g. feeding or relocating) or environmental covariates that trigger switches between movement states (Morales et al. 2004).

While these probabilistic models do not necessarily allow one to reveal and disentangle the mechanistic underpinnings of movement directly, the statistics they provide could serve as assessment criteria for simulation models that do implement and combine different movement mechanisms. Multiple assessment criteria can provide a framework that allows the parameterization of high dimensional models where not all lower level parameters (e.g. estimates for the spatial extent of perceptual ranges or the temporal duration of detailed memory) can be known from empirical data (Reynolds and Ford 1999). The idea is that a bottom-up individual-based model that reproduces not just one, but multiple characteristic movement statistics as emergent patterns, is likely to be a structurally realistic representation of the processes underlying a species movement. This is termed 'pattern oriented modeling' (Wiegand et al. 2003, 2004, Grimm et al. 2005, Grimm and Railsback 2005) and several studies have parameterized high dimensional individual-based models of movement or animal dispersal in this fashion (Revilla et al. 2004, Morales et al. 2005, Aumann et al. 2006). However, what is missing to date are individual based models that systematically implement the underlying movement mechanisms (oriented, non-oriented and spatial memory) with regard to variability in resources and population patterns.

## Future directions

Here we provide a final overview of three essential components that will be critical to future studies of movement that seek to integrate individual-level mechanisms, resource variability, and population-level movement patterns. We synthesize ideas from the recent literature with our own suggestions. First, it will be necessary to combine the qualitatively different underlying individual-level movement mechanisms (oriented, non-oriented and spatial memory) into a single quantitative framework. Second, models are needed that allow for the manipulation and study of resource gradients in abundance, spatial heterogeneity, temporal variability, and predictability. Third, we make suggestions how model outcomes as well as empirical animal tracking data could be measured at the emergent population level (sedentary ranges, migration, nomadism) to take advantage of pattern oriented modeling techniques (Fig. 3). We now discuss each of these three modeling components in turn.

### *Combining movement mechanisms*

A particular challenge in modeling animal movement is that each of the mechanisms (oriented, non-oriented and memory) represents a qualitatively different method by which an animal can search or navigate, yet the effects of each mechanism need to be linked into a single response – namely, a new location for an individual in space and time. Here we suggest one way of dealing with this complex issue. Our key idea is that each of the three types of individual-level movement mechanisms relies on type-specific input parameters. For example, stimuli such as the current movement angle and velocity are specific to non-oriented mechanisms. Likewise, specified perceptual ranges are unique to oriented movement mechanisms, and memory mechanisms require constraints on how much temporal and spatial information an individual can 'remember'.

Excellent examples of how movement can be modeled by updating velocity and direction based on a suite of dynamic states have been achieved using artificial intelligence approaches to navigate autonomous driving robots (Thrun et al. 2006). Meanwhile in ecology, evolutionary programming techniques such as genetic algorithms (GA) and artificial neural networks (ANN), have been used to model complex animal movements (Morales et al. 2005, Bennet and Tang 2006, Boone et al. 2006, Hancock and Milner-Gulland 2006). Combining GAs and ANNs in individual-based models yields so-called individual-based neural network genetic algorithms (ING models), which were first used in ecology to study one-dimensional movements in fish (Huse et al. 1999, Strand et al. 2002). The ING technique is generally advantageous because it integrates qualitatively different input information but is not contingent on ecologists' abilities to discern or define the rules that govern animal behavioral decisions. This is an especially important consideration in that behavioral rules in the real world may not be transparent, simple, or context-independent, making them difficult to identify from empirical datasets (Morales et al. 2005). However,

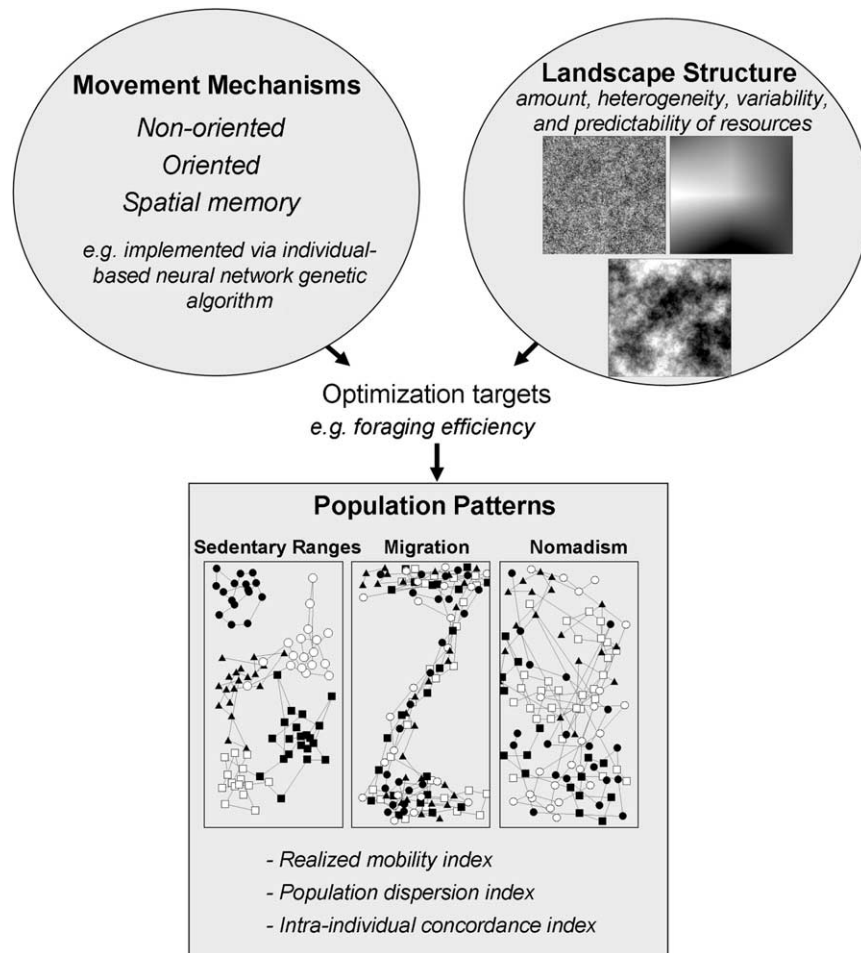


Fig. 3. Conceptual overview about a modeling framework linking movement mechanism with dynamic landscape structures and emergent population level distributions.

these techniques have not yet been used to systematically explore alternative movement mechanisms. We suggest that certain variables in the input layer of an ANN may be mechanism-specific (Fig. 4), and by adding or removing mechanism-specific stimuli from an ANN, it might be possible to test the effects of those variables (and their interactions) with regard to a fitness criterion such as foraging success under different landscape scenarios.

#### **Dynamic resources**

Modeling variability in resource distributions is just as critical for a synthetic understanding of animal movement as is modeling of the movements themselves. For theoretical investigations, several established methods exist by which artificial landscapes may be generated (e.g. as spectral representations; Keitt 2000, Csillag and Kabos 2002). To produce temporal landscape dynamics, a series of such landscapes may be used to simulate seasonal change within years. To represent periodicity across years, landscape series may be repeated in sequence, with varying degrees of 'error' introduced to generate temporal unpredictability. In this way temporal heterogeneity could be introduced within years (simulating seasonal changes in resource availability) as well as between years (varying predictability of resource

landscapes). A more challenging task relates to measuring and modeling of empirical resource landscapes that capture, in detail, how the availability of resources changes over space and time. With ground methods, such data are almost impossible to acquire at high temporal resolutions and across broad spatial scales. Nevertheless, for some ecosystems such as grasslands, remote sensing techniques have provided a partial solution to this problem via indices of vegetation productivity that capture dynamics of landscapes (Pettoelli et al. 2005, Boone et al. 2006, Mueller et al. 2007). These indices of vegetation dynamics constitute an important advance because remote sensing techniques have traditionally focused on static, rather than dynamic, habitat or habitat suitability maps.

#### **Quantifying population-level distributional patterns**

The third critical component in a comprehensive modeling framework for animal movement would be to evaluate and quantify emergent dispersion patterns at the population level (e.g. sedentary ranges, migration, nomadism). Several metrics are possible that can be applied equally well to empirical distributions and the outcomes of simulation models, and each can be used to gain insight into the connections between individual level movements and



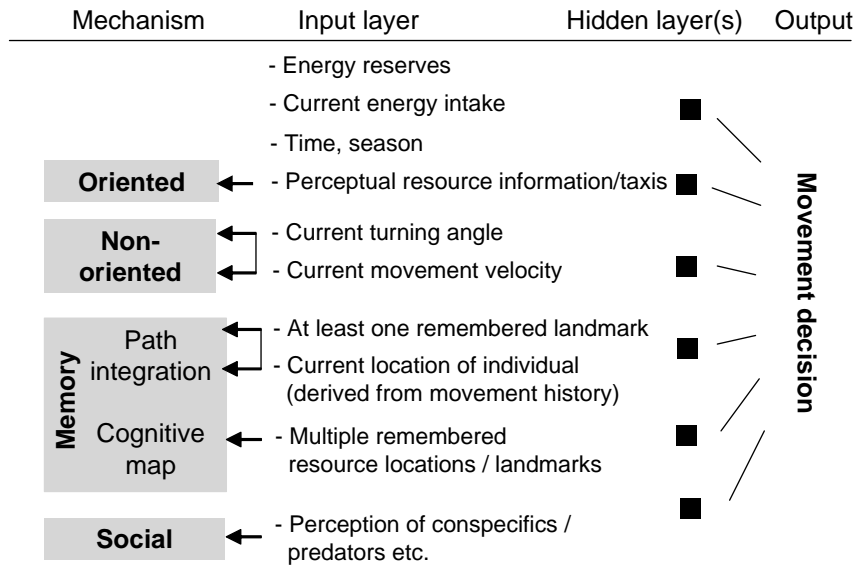


Fig. 4. Simplified scheme of an artificial neural network governing movement decisions. Certain state variables (Input layer) refer to specific movement mechanisms and result in a single behavioral response (i.e. a movement decision such as direction or correlation angle).

population level distributions (Table 1). For example, one might calculate a modified ‘realized mobility index’ (Roshier and Reid 2003) as the ratio of an individual’s yearly range to the entire population’s yearly range. In addition, we suggest that if telemetry data are available for several individuals of a single population, methods of multivariate point pattern analysis (reviewed by Fortin and Dale 2005) may be applied to the relocation data to quantify the spatial relationships of locations between different individuals or between different time periods within the same individuals. More specifically, a ‘population dispersion index’, could determine independence, clustering or dispersion of relocation patterns among individuals. If inter-individual relocation patterns of a population are dispersed, it would indicate sedentary ranges whereas clustering would indicate migration or type II nomadism. A third possible metric is an ‘intra-individual concordance index’ that could measure independence, clustering or dispersion of point patterns within individuals and between years for a given season. If relocations from the same season and different years are spatially clustered it would indicate that an individual has a high fidelity to the same area every year, whereas a dispersed or independent distribution would indicate nomadism. Taken together, these three indices should allow one to distinguish

among the three emergent population-level distributional patterns (Table 1).

## Conclusions

We suggest that combinations of individual-level state variables can be used to represent specific movement mechanisms, and that those mechanisms can be implemented and integrated in individual based models. Integrating different types of movement ranging from search to navigation with dynamic landscapes that vary in predictability and heterogeneity may provide a better understanding of emergent, population-level spatial patterns such as sedentary ranges, migration, and nomadism.

That said, we feel that another strength of the approaches we outlined may lie in their capability to serve as a tool for ecological forecasting. Population dynamics of many species – and specifically long-distance migrants – rely critically on their movement behaviors. To understand better how human activities affect animal movements in real landscapes, we suggest that structurally realistic movement models operating on empirically derived landscapes may provide a valuable tool for resource planning. Such an approach would allow ecologists to predict how individuals’

Table 1. Indices quantifying and distinguishing population level distributional patterns.

	Migration	Sedentary ranges	Nomadism I	Nomadism II
Realized mobility index (quantifies the ratio individual range vs population range)	Large	Small	Large	Large
Population dispersion index (quantifies spatial relation among individuals)	Clustered	Dispersed	Independent	Clustered
Intra-individual concordance index (quantifies spatial relation of relocations for specific individuals among years)	Clustered	Clustered	Dispersed	Dispersed

movements and species' spatiotemporal population dynamics could respond to landscape changes.

*Acknowledgements* – We thank Peter Leimgruber, Todd Fuller, Kirk Olson, Tamara Münkemüller, Heather Lessig, the Fagan lab, Volker Grimm and John Fryxell for helpful comments and discussions. This research was funded in part by grants from the National Science Foundation to TM and WF (DEB-0608224, DEB-0743557), and a Smithsonian Predoctoral Fellowship to TM.

## References

- Åkesson, S. and Hedenström, A. 2007. How migrants get there: migratory performance and orientation. – *Bioscience* 57: 123–133.
- Alerstam, T. 2006. Conflicting evidence about long-distance animal navigation. – *Science* 313: 791–794.
- Alerstam, T. et al. 2003. Long-distance migration: evolution and determinants. – *Oikos* 103: 247–260.
- Aumann, C. A. et al. 2006. How transient patches affect population dynamics: the case of hypoxia and blue crabs. – *Ecol. Monogr.* 76: 415–438.
- Bailey, D. W. et al. 1996. Mechanisms that result in large herbivore grazing distribution patterns. – *J. Range Manage.* 49: 386–400.
- Bartumeus, F. et al. 2005. Animal search strategies: a quantitative random-walk analysis. – *Ecology* 86: 3078–3087.
- Bell, W. J. 1991. Searching behaviour: the behavioural ecology of finding resources. – Chapman and Hall.
- Benhamou, S. and Bovet, P. 1989. How animals use their environment – a new look at kinesis. – *Anim. Behav.* 38: 375–383.
- Bennett, D. A. and Tang, W. 2006. Modelling adaptive, spatially aware, and mobile agents: elk migration in Yellowstone. – *Int. J. Geogr. Inf. Sci.* 20: 1039–1066.
- Bennetts, R. E. and Kitchens, W. M. 2000. Factors influencing movement probabilities of a nomadic food specialist: proximate foraging benefits or ultimate gains from exploration? – *Oikos* 91: 459–467.
- Bilton, D. T. et al. 2001. Dispersal in freshwater invertebrates. – *Annu. Rev. Ecol. Syst.* 32: 159–181.
- Biro, D. et al. 2004. Familiar route loyalty implies visual pilotage in the homing pigeon. – *Proc. Natl Acad. Sci. USA.* 101: 17440–17443.
- Biro, D. et al. 2007. Pigeons combine compass and landmark guidance in familiar route navigation. – *Proc. Natl Acad. Sci. USA.* 104: 7471–7476.
- Bonadonna, F. et al. 2005. Orientation in the wandering albatross: interfering with magnetic perception does not affect orientation performance. – *Proc. R. Soc. Lond. B.* 272: 489–495.
- Boone, R. B. et al. 2006. Serengeti wildebeest migratory patterns modeled from rainfall and new vegetation growth. – *Ecology* 87: 1987–1994.
- Bovet, P. and Benhamou, S. 1991. Optimal sinuosity in central place foraging movements. – *Anim. Behav.* 42: 57–62.
- Bowen, B. W. et al. 2004. Natal homing in juvenile loggerhead turtles (*Caretta caretta*). – *Mol. Ecol.* 13: 3797–3808.
- Bowler, D. E. and Benton, T. G. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. – *Biol. Rev.* 80: 205–225.
- Boyle, W. A. and Conway, C. J. 2007. Why migrate? A test of the evolutionary precursor hypothesis. – *Am. Nat.* 169: 344–359.
- Brower, L. P. 1996. Monarch butterfly orientation: missing pieces of a magnificent puzzle. – *J. Exp. Biol.* 199: 93–103.
- Charnov, E. L. 1976. Optimal foraging, marginal value theorem. – *Theor. Popul. Biol.* 9: 129–136.
- Conradt, L. et al. 2003. Foray search: an effective systematic dispersal strategy in fragmented landscapes. – *Am. Nat.* 161: 905–915.
- Cronev, C. C. et al. 2003. A note on visual, olfactory and spatial cue use in foraging behavior of pigs: indirectly assessing cognitive abilities. – *Appl. Anim. Behav. Sci.* 83: 303–308.
- Csillag, F. and Kabos, S. 2002. Wavelets, boundaries, and the spatial analysis of landscape pattern. – *Ecoscience* 9: 177–190.
- Dingle, H. and Drake, V. A. 2007. What is migration? – *Bioscience* 57: 113–121.
- Estes, R. D. 1991. The behavior guide to African mammals, including hoofed mammals, carnivores, primates. – Univ. of California Press.
- Fahse, L. et al. 1998. Reconciling classical and individual-based approaches in theoretical population ecology: a protocol for extracting population parameters from individual-based models. – *Am. Nat.* 152: 838–852.
- Farnsworth, K. D. and Beecham, J. A. 1999. How do grazers achieve their distribution? A continuum of models from random diffusion to the ideal free distribution using biased random walks. – *Am. Nat.* 153: 509–526.
- Fauchald, P. and Tveraa, T. 2003. Using first-passage time in the analysis of area-restricted search and habitat selection. – *Ecology* 84: 282–288.
- Fauvergue, X. et al. 1995. Mate finding via a trail sex-pheromone by a parasitoid wasp. – *Proc. Natl Acad. Sci. USA* 92: 900–904.
- Fretwell, S. D. and Lucas, H. L. 1969. On territorial behavior and other factors influencing habitat distribution in birds. – *Acta Biotheor.* 19: 16–36.
- Fortin, D. et al. 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. – *Ecology* 86: 1320–1330.
- Fortin, M.-J. and Dale, M. R. T. 2005. Spatial analysis: a guide for ecologists. – Cambridge Univ. Press.
- Fritz, H. et al. 2003. Scale-dependent hierarchical adjustments of movement patterns in a long-range foraging seabird. – *Proc. R. Soc. Lond. B.* 270: 1143–1148.
- Fryxell, J. M. et al. 2004. Predictive models of movement by Serengeti grazers. – *Ecology* 85: 2429–2435.
- Fryxell, J. M. et al. 2005. Landscape scale, heterogeneity, and the viability of Serengeti grazers. – *Ecol. Lett.* 8: 328–335.
- Fryxell, J. M. et al. 2007. Group formation stabilizes predator–prey dynamics. – *Nature* 449: 1041–1043.
- Gagliardo, A. et al. 1999. Homing in pigeons: the role of the hippocampal formation in the representation of landmarks used for navigation. – *J. Neurosci.* 19: 311–315.
- Gautestad, A. O. and Mysterud, I. 2005. Intrinsic scaling complexity in animal dispersion and abundance. – *Am. Nat.* 165: 44–55.
- Grimm, V. and Railsback, S. F. 2005. Individual-based modeling and ecology. – Princeton Univ. Press.
- Grimm, V. et al. 2005. Pattern-oriented modeling of agent-based complex systems: lessons from ecology. – *Science* 310: 987–991.
- Grünbaum, D. 2000. Advection-diffusion equations for internal state-mediated random walks. – *Siam J. Appl. Math.* 61: 43–73.
- Hancock, P. A. and Milner-Gulland, E. J. 2006. Optimal movement strategies for social foragers in unpredictable environments. – *Ecology* 87: 2094–2102.
- Haskell, J. P. et al. 2002. Fractal geometry predicts varying body size scaling relationships for mammal and bird home ranges. – *Nature* 418: 527–530.

- Haugen, T. O. et al. 2006. The ideal free pike: 50 years of fitness-maximizing dispersal in Windermere. – *Proc. R. Soc. Lond. B.* 273: 2917–2924.
- Holden, C. 2006. Inching toward movement ecology. – *Science* 313: 779.
- Huse, G. et al. 1999. Implementing behaviour in individual-based models using neural networks and genetic algorithms. – *Evol. Ecol.* 13: 469–483.
- Jahn, A. E. et al. 2004. Reflections across hemispheres: a system-wide approach to new world bird migration. – *Auk* 121: 1005–1013.
- Jonsen, I. D. et al. 2005. Robust state-space modeling of animal movement data. – *Ecology* 86: 2874–2880.
- Kareiva, P. and Odell, G. 1987. Swarms of predators exhibit preytaxis if individual predators use area-restricted search. – *Am. Nat.* 130: 233–270.
- Keitt, T. H. 2000. Spectral representation of neutral landscapes. – *Landscape Ecol.* 15: 479–493.
- Lovell, S. F. and Lein, M. R. 2004. Neighbor-stranger discrimination by song in a suboscine bird, the alder flycatcher, *Empidonax alnorum*. – *Behav. Ecol.* 15: 799–804.
- Mahler, C. R. and Lott, D. F. 2000. A review of ecological determinants of territoriality within vertebrate species. – *Am. Midl. Nat.* 143: 1–29.
- Mech, S. G. and Zollner, P. A. 2002. Using body size to predict perceptual range. – *Oikos* 98: 47–52.
- Moorcroft, P. R. et al. 1999. Home range analysis using a mechanistic home range model. – *Ecology* 80: 1656–1665.
- Moorcroft, P. R. et al. 2006. Mechanistic home range models capture spatial patterns and dynamics of coyote territories in Yellowstone. – *Proc. R. Soc. B* 273: 1651–1659.
- Morales, J. M. et al. 2004. Extracting more out of relocation data: building movement models as mixtures of random walks. – *Ecology* 85: 2436–2445.
- Morales, J. M. et al. 2005. Adaptive models for large herbivore movements in heterogeneous landscapes. – *Landscape Ecol.* 20: 301–316.
- Morrell, L. J. and Kokko, H. 2005. Bridging the gap between mechanistic and adaptive explanations of territory formation. – *Behav. Ecol. Sociobiol.* 57: 381–390.
- Olden, J. D. et al. 2004. Context-dependent perceptual ranges and their relevance to animal movements in landscapes. – *J. Anim. Ecol.* 73: 1190–1194.
- Mueller, T. et al. 2007. In search of forage: predicting dynamic habitats of Mongolian gazelles using satellite-based estimates of vegetation productivity. – *J. Appl. Ecol.* doi: 10.1111/j.1365-2664.2007.01371.x
- Pettorelli, N. et al. 2005. Using the satellite-derived NDVI to assess ecological responses to environmental change. – *Trends Ecol. Evol.* 20: 503–510.
- Pyke, G. H. 1984. Optimal foraging theory – a critical review. – *Annu. Rev. Ecol. Syst.* 15: 523–575.
- Ramenofsky, M. and Wingfield, J. C. 2007. Regulation of migration. – *Bioscience* 57: 135–143.
- Revilla, E. et al. 2004. Effects of matrix heterogeneity on animal dispersal: from individual behavior to metapopulation-level parameters. – *Am. Nat.* 164: E130–E153.
- Reynolds, J. H. and Ford, E. D. 1999. Multi-criteria assessment of ecological process models. – *Ecology* 80: 538–553.
- Riley, J. R. et al. 2005. The flight paths of honeybees recruited by the waggle dance. – *Nature* 435: 205–207.
- Roshier, D. A. and Reid, J. R. W. 2003. On animal distributions in dynamic landscapes. – *Ecography* 26: 539–544.
- Ruckstuhl, K. E. and Neuhaus, P. 2002. Sexual segregation in ungulates: a comparative test of three hypotheses. – *Biol. Rev.* 77: 77–96.
- Schooley, R. L. and Wiens, J. A. 2003. Finding habitat patches and directional connectivity. – *Oikos* 102: 559–570.
- Sinclair, A. R. E. 1983. The function of distance movements in vertebrates. – In: Swingland, I. R. and Greenwood, P. J. (eds), *The ecology of animal movement*. Clarendon Press, pp. 248–258.
- Strand, E. et al. 2002. Artificial evolution of life history and behavior. – *Am. Nat.* 159: 624–644.
- Sutherland, W. J. 1983. Aggregation and the ideal free distribution. – *J. Anim. Ecol.* 52: 821–828.
- Thrun, S. et al. 2006. Stanley: the robot that won the DARPA grand challenge. – *J. Field Robotics* 23: 661–692.
- Turchin, P. 1998. *Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants*. – Sinauer Associates.
- van Gils, J. A. et al. 2006. Foraging in a tidally structured environment by red knots (*Calidris canutus*): ideal, but not free. – *Ecology* 87: 1189–1202.
- VanderMeer, J. and Ens, B. J. 1997. Models of interference and their consequences for the spatial distribution of ideal and free predators. – *J. Anim. Ecol.* 66: 846–858.
- Vickerstaff, R. J. and Di Paolo, E. A. 2005. Evolving neural models of path integration. – *J. Exp. Biol.* 208: 3349–3366.
- Viswanathan, G. M. et al. 1999. Optimizing the success of random searches. – *Nature* 401: 911–914.
- von Frisch, K. 1967. *Dance language and orientation of the honey bee*. – Harvard Univ. Press.
- Wiegand, T. et al. 2003. Using pattern-oriented modeling for revealing hidden information: a key for reconciling ecological theory and application. – *Oikos* 100: 209–222.
- Wiegand, T. et al. 2004. Dealing with uncertainty in spatially explicit population models. – *Biodiv. Conserv.* 13: 53–78.
- Wiltschko, R. and Wiltschko, W. 2006. Magnetoreception. – *Bioessays* 28: 157–168.
- With, K. A. and King, A. W. 1997. The use and misuse of neutral landscape models in ecology. – *Oikos* 79: 219–229.
- Zollner, P. A. and Lima, S. L. 1999. Orientational data and perceptual range: real mice aren't blind. – *Oikos* 84: 164–166.