Geography Compass 4/7 (2010): 682–700, 10.1111/j.1749-8198.2010.00337.x

Agent-based Modeling of Animal Movement: A Review

Wenwu Tang[1]* and David A. Bennett[2]
[1]Department of Geography, National Center for Supercomputing Applications, University of Illinois
[2]Department of Geography, University of Iowa

Abstract

Animal movement is a complex spatiotemporal phenomenon that has intrigued researchers from many disciplines. Interactions among animals, and between animals and the environments that they traverse, play an important role in the development of the complex ecological and social systems in which they are embedded. Agent-based models have been increasingly applied as a computational approach to the study of animal movement across landscapes. In this article, we present a review of agent-based models in which the simulation of animal movement processes and patterns is the central theme. Our discussion of these processes is focused on four key components: internal states, external factors, motion capacities, and navigation capacities. These four components have been identified in the emerging movement ecology research paradigm and are important for modeling animal movement behavior. Because agent-based models allow for an individual-based approach that encapsulates these four components, the underlying processes that drive animal behavior can be deeply explored using this technique. A set of challenges and issues remain, however, for agent-based models of animal movement. In this article, we review the existing literature and identify potential research directions that could help address these challenges.

Introduction

Animal movement, an important theme in biogeography and landscape ecology (Forman 1995; Lomolino et al. 2006; MacDonald 2003; Turner et al. 2001), represents a complex spatiotemporal phenomenon in which the interplay between behavioral patterns and processes is driven by a suite of interacting abiotic and biotic factors (Forman 1995; Nathan 2008; Swingland and Greenwood 1983; Turchin 1998; Turner 1989). This interplay is often critically important to the development and maintenance of complex dynamic landscapes. A set of challenging issues in biogeography and landscape ecology, including species invasion, biodiversity conservation, habitat fragmentation, disease spread, and gene flow (Forman 1995; MacDonald 2003; Quammen 1996; Turner et al. 1994), is intricately related to animal movement. Investigating why, when, where, and how animals move across heterogeneous landscapes (Nathan et al. 2008; Pyke 1983; Turchin 1998) thus presents intriguing research questions and provides insight into the aforementioned issues. As a result, the study of animal movement has received considerable attention from researchers in many disciplines related to biogeography and landscape ecology, including artificial intelligence (Arkin 1998; Bonabeau et al. 1999; Kennedy et al. 2001; Sutton and Barto 1998), biology and ecology (Baker 1978; Nathan et al. 2008; Pyke 1978; Swingland and Greenwood 1983; Turchin 1998), cognitive science (Gallistel 1989; Golledge 1999; Trullier et al. 1997), and geographic information science (Bian 2000; Goodchild et al. 2007; Peuquet 2002; Yuan and Stewart 2008).

Agent-based models (ABM) have been increasingly applied to studies of animal movement, particularly encouraged by their capabilities of integrating with, for example, Geographic Information Systems (GIS), and statistics (Brown et al. 2005b; Gimblett 2002;

Parker et al. 2003). ABM capture in digital form: individuals, interactions among individuals, and interactions between individuals and their environment to simulate the complex dynamics of ecological and social systems (Bousquet and Page 2004; Epstein and Axtell 1996; Grimm et al. 2005; Parker et al. 2003; Railsback 2001). Simulation is a computational approach that has been extensively employed to investigate the movement or dispersal of plants and animals across a landscape (Gardner et al. 1989; Gross et al. 1995; Malanson 1999; Malanson and Armstrong 1996; Siniff and Jessen 1969; Turchin 1998; Turner et al. 2001). Simulation allows for the explicit representation of the underlying processes that guide the production of large-scale animal movement patterns on which conventional studies (e.g. statistical) of animal movement focus. A suite of simulation approaches, including system models, cellular automata, and ABM, have been used to uncover the complex dynamics of animal movement (DeAngelis and Mooij 2005; Folse et al. 1989; Grimm and Railsback 2005; Johnson et al. 1992; Parrott and Kok 2002; Turchin 1998; Turner et al. 2001). Because research focused on individual-level movement patterns and processes (Crist et al. 1992; Nathan 2008; Tischendorf 1997; Turchin 1998) and because computing technology advanced (Armstrong 2000; Atkins et al. 2003; Foster and Kesselman 1999), the interest in the use of ABM for animal movement modeling steadily increased.

Our objectives are to (1) give an introduction to the basics of ABM, (2) identify the alternative approaches used to represent movement processes and patterns of animals in ABM, and (3) discuss challenges and issues associated with ABM for animal movement studies that provide insight into future research directions. We organize the rest of this article as follows. In Sect. 'Agent-based models', we present fundamental concepts associated with ABM. In Sect. 'Agent-based models of animal movement', we discuss in detail the use of ABM for the simulation of animal movement. In Sect. 'Challenges and issues in agent-based models of animal movement', we then illustrate the challenges and issues in ABM of animal movement. Conclusions are presented below.

Agent-based Models

Agent-based models, a disaggregated (or bottom-up) problem-solving approach, are tailored to the study of ecological and social systems (Batty et al. 2003; Benenson and Torrens 2004; Epstein 1999; Gimblett 2002; Matthews et al. 2007; O'Sullivan 2008; Parker et al. 2003). These systems are complex adaptive systems in which emergent, self-organized, non-linear, and adaptive phenomena can be observed (Bennett and Tang 2008; Bousquet and Page 2004; Matthews et al. 2007; Parker et al. 2003; Railsback 2001; Tang et al. 2009). ABM support a wide range of applications by capturing the structural and functional complexity of ecological and social systems (Grimm and Railsback 2005; Parker et al. 2003). The current agent-based modeling paradigm has been developed within the context of four general research streams: individual-based models (IBM) in ecology (see DeAngelis and Gross 1992; DeAngelis and Mooij 2005; Grimm and Railsback 2005; Huston et al. 1988; Shugart et al. 1992), multi-agent systems in computer science and engineering (Ferber 1999; Maes 1994; Russell and Norvig 1995), computational process models in cognitive science (Newell and Simon 1972; Smith et al. 1982), and ABM in social science (Epstein and Axtell 1996; Epstein 1999; Gilbert and Troizsch 1999).

COMPONENTS OF AGENT-BASED MODELS

Agents, environments, and events are fundamental components of ABM and the configuration of these components plays a pivotal role in model design and development.

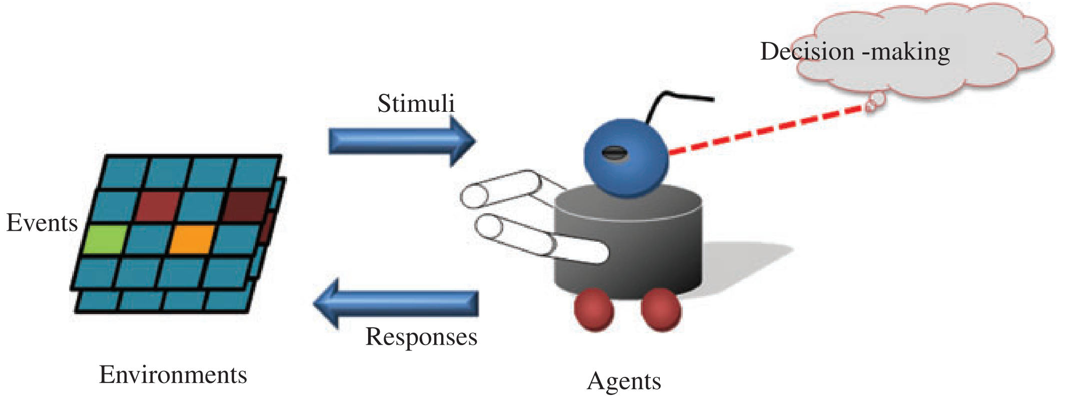

Fig. 1. Illustration of an agent and its environment in an agent-based model.

Agents

Agents are simplified representations of real-world entities and solve problems through sensing and reacting to stimuli from themselves, other agents, and the environment within which they operate (Ferber 1999; Russell and Norvig 1995; Tang 2008; see Figure 1). An agent is characterized by a set of properties (including parameters and state variables) and behaviors (see Figure 2), providing support for modeling the decision-making processes of individuals in response to various situations. The decision-making processes and associated behavior can be described using a set of fixed or learned decision rules (Russell and Norvig 1995). Stimuli perceived by agents can be matched to the condition side of decision rules that, in turn, trigger relevant behavioral responses on

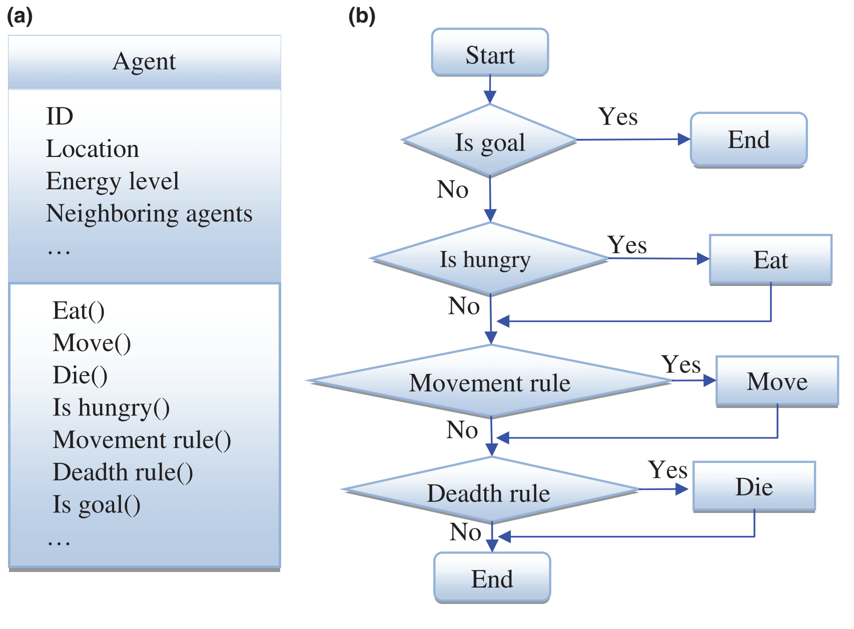

Fig. 2. The structure of an agent and its decision-making rules. (a) UML diagram of agent properties and rules. (b) A flowchart that shows the decision-making processes of an agent within a time step; a conceptual model in which agents move across a landscape was used; UML, unified modeling language; see http://www.uml.org/).

the action side. This stimulus–response couplet drives an agent's interaction with its environment and other agents as they attempt to solve problems.

The decision rules of agents are often associated with a utility function that quantitatively evaluates the performance of agents (Russell and Norvig 1995). Rules with high utility values have high probabilities of being activated. Russell and Norvig (1995) classified agents into four categories: reflexive agents, agents with internal states, goal-based agents, and utility-based agents. These forms of agents are in order of increasing sophistication with respect to their decision-making processes. In particular, goal- and utility-based agents are intelligent agents who possess learning mechanisms that allow them to modify their decision rules in response to system dynamics. These learning mechanisms can be represented using machine learning algorithms (e.g. evolutionary algorithms, neural networks, and reinforcement learning; see Russell and Norvig 1995; cf. Tang 2008).

Environments

Environments constrain the flow of information, energy, and agents across the spatial domain and can be 1, 2, and 3 dimensional. Two dimensional representations have been most thoroughly investigated in the context of ABM. Environments in ABM can be represented using continuous (object-based) or discrete (grid-based) approaches (see Bian 2003; Grimm and Railsback 2005), supported by vector- and raster-based GIS data structures (see Goodchild 1992; Worboys and Duckham 2004). The continuous approach represents an environment based on the set of geometric features (points, polylines, and polygons); the location and shape of entities are defined by continuous coordinates. Topological relationships among spatial features can be established using neighborhood adjacency rules (discussed later).

In this article, we focus our discussion on the grid-based approach. Most ABM use a discrete 2D grid-based approach where the study area of interest is partitioned into a set of regularly shaped grid cells (e.g. square or hexagons) connected by neighborhood adjacency rules. Each cell is associated with a set of environmental state variables and can be occupied by agents. Neighborhood adjacency rules include the von Neumann neighborhood rule, the Moore neighborhood rule, and irregular neighborhood rules (Gilbert and Troizsch 2005). The von Neumann and Moore neighborhood rules with different adjacency orders are commonly used for environmental representation in ABM (see Figure 3). The neighborhood adjacency rule defines the topological relationship of environmental features and is important for characterizing agent-based interactions that rely on relative spatial location to acquire environmental information and build a perceptual window that guides their behavior in space.

The grid-based approach can be extended to 3D environments, in which case each grid cell is represented as a cube or voxel. This approach is useful for models of individuals (e.g. fishes or birds) that interact in high-dimensional environments (Bian 2003). This

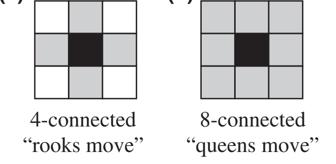

Fig. 3. Illustration of adjacency rules used in agent-based models. (a) A first-order von Neumann neighborhood rule, and (b) a first-order Moore neighborhood rule (gray cells are neighboring ones with respect to the central one in black).

grid-based approach facilitates the explicit representation of environmental dynamics. In particular, it corresponds well to the use of cellular automata models that have utility in the investigation of environmental dynamics (e.g. spatial diffusion processes) through neighborhood interactions (Clarke et al. 1997; Parker et al. 2003; White and Engelen 1997). This correspondence leads to the flexible integration of ABM with cellular automata (Batty 2000; Parker et al. 2003).

Events

Dynamics in real-world systems are modeled through a set of events that update the state of agents and environments in ABM. The importance of events in driving system dynamics has been well-recognized in the study of discrete event-driven simulation (Zeigler et al. 2000), one of the conceptual foundations on which ABM are built. Each iteration of an agent-based model can be viewed as equivalent to a sampling event in a real-world system. Typically, each iteration represents an equal interval of time (i.e. a regular sampling pattern in the temporal dimension). The temporal extent and resolution of ABM need to be appropriately chosen for the representation of dynamics in real-world systems. Bennett and Tang (2006) suggested that the Courant–Friedrichs–Lewy (CFL) criterion (see Courant et al. 1967; cf. Martin 1993), defining the relationship between spatial and temporal resolutions based on the movement rate of information and entities (including agents), is suitable for determining temporal resolutions. Events in ABM, which can be defined using time-stamped empirical or simulated data, are internal (e.g. agent internal state change) or external (e.g. change in environmental conditions). An explicit consideration of events, as Brown et al. (2005b) highlighted, is important for characterizing agent-agent and agent-environment interactions.

MODELING PROTOCOLS, PLATFORMS, AND TEMPLATES

The development of ABM follows the same basic steps as any simulation modeling exercise, including problem definition, model formulation, data preparation, model implementation, validation, experimentation, interpretation, and documentation (see Shannon 1975 for detail). However, specific consideration is often needed for developing ABM. Grimm et al. (2006) designed a high-level standard protocol, ODD (Overview-Design-Details), to facilitate the development of ABM and associated communication tasks. The ODD protocol is comprised of seven components (i.e. purpose, state variables and scales, process overview and scheduling, design concepts, initialization, input, and submodels) that are aggregated into three main categories – overview, design concepts, and details. These components of the ODD protocol allow modelers or users to specify and communicate the modeling procedures of an ABM.

From a software engineering perspective, object-oriented techniques support the design and development of ABM (Tang 2008). UML (Unified Modeling Language) can be used to illustrate agents, environments, and agent-based interactions in a graphical manner (e.g. using class diagrams for agents and environment definition, and sequence diagrams for defining agent-agent and agent-environment interactions). Software packages or libraries, including Swarm (http://www.swarm.org/), NetLogo (http://ccl.northwestern.edu/netlogo/), RePast (http://repast.sourceforge.net/), and MASON (http://www.cs.gmu.edu/~eclab/projects/mason/), have been developed for generic agent-based modeling. These software packages are often implemented using different object-oriented programming languages (e.g. Java, C++, or Objective C) and provide user-friendly GUI (graphic user interface) for different levels of developers and users. These packages are often integrated with other domain-specific functionality, including GIS, spatial statistics, and machine learning algorithms to better support the development of ABM applications. For comparisons of these packages, readers are directed to Railsback et al. (2006). Moreover, a series of templates, represented by Sugarscape (see Epstein and Axtell 1996), StupidModel (see Railsback et al. 2006), and the Schelling Segregation Model (based on Schelling 1969), have been available to support the study, development, and use of ABM.

Agent-based models of animal movement

Agent-based models have been used to simulate the movement of a variety of animals, including birds (Reuter and Breckling 1999; Wolff 1994), fish (e.g. lake and stream fish, tropical pelagic fish; see Huse and Giske 1998; Railsback 1999; Dagorn et al. 2000; Hölker and Breckling 2005), insects (e.g. flies and mosquitoes; see Arrignon et al. 2007; Linard et al. 2009; Shaman 2007), large herbivores (e.g. bison, elk, and sheep; see Bennett and Tang 2006; Dumont and Hill 2004; Morales et al. 2005; Turner et al. 1994), large carnivores (e.g. tiger, and panther; see Ahearn 2001; Comiskey et al. 1997), and large omnivores (e.g. primates; see Hemelrijk 1999; Sellers et al. 2007). In ABM animals and their aggregates (e.g. flocks, herds, schools, and swarms) can be represented as mobile agents that interact with their environments (2D or 3D) or other agents (e.g. predator–prey relationships, conspecific and inter-specific competition). Mobile agents can have multiple sensors that acquire stimulus information and guide movement behavior in response to internal and external drivers. ABM allow us to investigate the complexity of animal movement by linking patterns with processes.

MODELING OF ANIMAL MOVEMENT PROCESSES

In 2008, Nathan et al. (2008) proposed a new movement ecology framework to model the spatial dynamics of individuals. This framework is based on four components inherently linked to the fundamental processes of animal movement: internal state, external factors, motion capacities, and navigation capacities. These four components build on a suite of existing theories that suggest that animal movement can be described by biomechanical, cognitive, random, and optimization processes. These theories provide solid support for ABM of animal movement and the consideration of these components and associated processes facilitates the representation of animal movement behavior (see Figure 4). In this article, we organize our comments on the structure of animal movement models around these four movement components introduced by Nathan et al. (2008). To facilitate this discussion, we focus on those animals identified in Table 1.

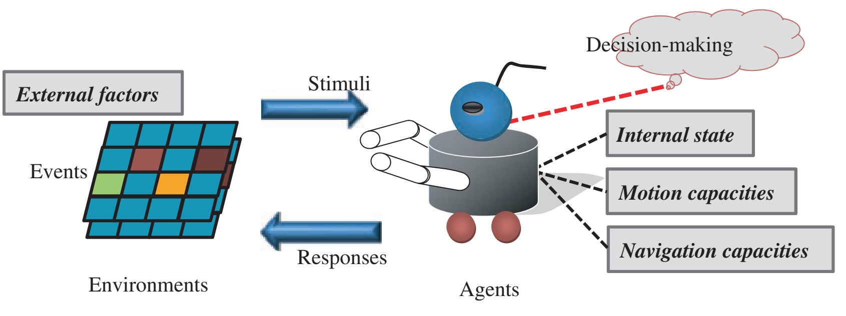

Fig. 4. Key components for agent-based modeling of animal movement.

Table 1. Representative agent-based models of animal movement.

Categories	Citations	Agent	Environment
Birds	Reuter and Breckling (1999); Wolff (1994)	Robin (*Erithacus rubecula*), and wood storks	Food resources (fish or arthropods), temperature, and water depth
Fish	Dagorn et al. (2000); Hölker and Breckling (2005); Huse and Giske (1998); Railsback (1999)	Lake fish (roach), stream fish, and tropical pelagic predatory fish	Food, solar radiation, and temperature
Insects	Arrignon et al. (2007); Linard et al. (2009); Shaman (2007)	Fly (*Episyrphus balteatus*); and mosquitoes	Light, temperature, and food resources
Large carnivore	Ahearn (2001); Comiskey et al. (1997)	Panther, and tiger	Territory, and prey distribution
Large ungulates	Abbott et al. (1997); Bennett and Tang (2006, 2008); Dumont and Hill (2001); Morales et al. (2005); Turner et al. (1994)	Bison, elk, sheep, and white-tailed deer	Biomass, snow, topography, and water
Large omnivores	Hemelrijk (1999); Sellers et al. (2007)	Baboons, and macaques	Habitat types, water, sleeping sites, refuge, or distribution of conspecific neighbors

Modeling the internal state of animals

The internal state of animals plays an essential role in driving movement behavior and can be either physiological or psychological in nature (Bailey et al. 1996; Nathan et al. 2008; Swingland and Greenwood 1983). Physiological traits include body mass, bioenergy flux, and body size; psychological states are mental conditions inherently related to cognitive processes, including perception, memory, learning, and decision-making (Shettleworth 2001). These internal states correspond to different goals (e.g. foraging, mating, risk avoidance, and territory establishment; see Swingland and Greenwood 1983) pursued by animals at multiple spatiotemporal locations (Nathan et al. 2008). These states can be captured as state variables and stored as part of the agent's representation. Changes in these states are simulated through behavioral rules. Information acquired through multiple sensors modifies the state of animals and their associated goals, which in turn guides the acquisition of new stimulus information.

While animal movement can be driven by a range of physiological states and goals, in this article we focus on foraging and bioenergetics to illustrate how the internal states of animals are represented in ABM. Modeling the foraging behavior of animals has a long history (DeAngelis and Mooij 2005; Pyke 1984; Stephens and Krebs 1986). Optimal foraging theory assumes that animals maximize their net energetic intake rate (Emlen 1966; MacArthur and Pianka 1966). This theory can be used to guide an agent's decision on when to begin or end foraging movements and, thus, balance energy gained against energy expended. In their review of ABM of animal foraging, Dumont and Hill (2004) further elucidated the importance of foraging in animal movement. Turner et al. (1994) simulated the wintering behavior of large ungulates (including elk and bison) whose foraging behavior is driven by daily intake requirements and intake rates. Abbott et al. (1997) investigated the response of white-tailed deer to an everglades landscape. The searching and movement behavior of deer is controlled by their maximum daily requirement and the forage level of the cells.

The gain and loss of bioenergy are directly related to the movement behavior of animals (Mace et al. 1983; Parker et al. 1984). Animal movement consumes energy, but can also increase the rate of forage intake and, thus, the rate at which biomass is metabolized into usable energy. Bioenergetic processes have been explicitly represented in ABM of birds (see Reuter and Breckling 1999; Wolff 1994), fish (see Hölker and Breckling 2005; Huse and Giske 1998), large ungulates (see Bennett and Tang 2006; Morales et al. 2005; Turner et al. 1994), and primates (see Sellers et al. 2007). Empirical data and models on bioenergetics can be used to parameterize the bioenergetic variables used to simulate animals. For example, Turner et al. (1994) incorporated an empirically based bioenergetics module in the modeling of winter migration of ungulates.

The psychological state of animals plays a unique role in driving their movement across heterogeneous landscapes (see Bailey et al. 1996; Trullier et al. 1997). ABM are well-suited to representing psychological states and associated cognitive processes, including perception, memory, learning, and decision-making (Shettleworth 2001). As they move animals utilize cognitive capabilities (e.g. sensing and learning) to update their long- and short-term memory (spatial and non-spatial). The representation of memory is often an integral component in ABM of animal movement. For example, Turner et al. (1994) assumed that large herbivores have short-term memory that prevents animals from moving back to the previously visited cell. In their simulation of sheep, Dumont and Hill (2001) examined the impact of spatial memory on the foraging and movement behavior of sheep and found that it guides food searching behavior and is related to landscape characteristics. Bennett and Tang (2006) applied both short and long term memory in their model of elk migration. Individual elk receive stimuli from their immediate environment and store this information as a form of short-term memory. Successful (unsuccessful) movement decisions stored as short-term memory receive positive (negative) reinforcement, captured as long-term spatial knowledge in the form of a cognitive map (O'Keefe and Nadel 1978; see Figure 5). Arrignon et al. (2007) presented an agent-based insect model in which agents use short-term memory to track information gathered from previously visited cells to estimate energy gain and loss. While spatial memory is often regarded as an internal mechanism, some animals, represented by ants, possess external memory mechanisms (e.g. pheromone) to guide their movements. The use of pheromone for movement guidance has been thoroughly investigated in the study of swarm intelligence (see Bonabeau et al. 1999).

Modeling external factors

The external environment, characterized by a combination of abiotic and biotic factors that form and drive complex landscape-level dynamics (Turner et al. 2001), creates significant constraints, threats, and opportunities for animal movement. These external factors may operate across different spatial and temporal scales, and animals must respond and adapt to such environmental gradients as topography, temperature, precipitation, and light intensity during their movements. Different animals respond to different environmental variables. For example, the movement of fish can be driven by temperature, solar radiation, and food (see Hölker and Breckling 2005). The environmental factors that affect large herbivore movements, on the other hand, can be characterized by biomass, snow, topography, and predation (see Bennett and Tang 2006; Morales et al. 2005; Turner et al. 1994).

The environmental factors that influence movement can be categorized into two general classes: resources (e.g. food, shelter) and risks (e.g. climate change and predation), which can be modeled as attractive or repulsive forces that drive animal movement. Resources and risks vary across spatial and temporal dimensions, and are modified by spatiotemporal events (e.g. disturbance). Feedback processes further connect the spatial patterns of resources and risks to animal movement: resource and risk patterns guide

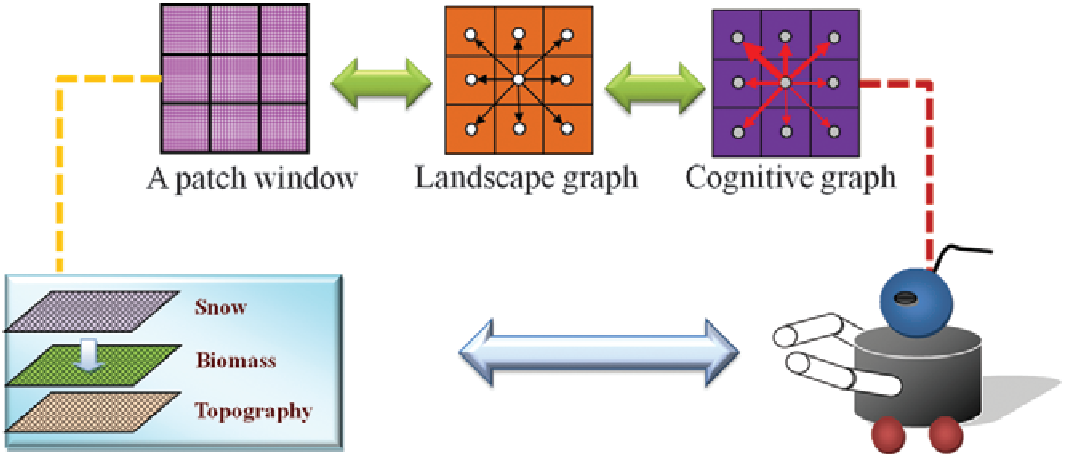

Fig. 5. A graph-based approach for modeling the migratory movement of elk (based on Bennett and Tang (2006); elk modeled as mobile agents interact with landscape factors represented by snow, biomass, and topography; landscape patterns and elk's long-term spatial memory are modeled as graphs that guide the migratory movement of elk).

animal movement that may, in turn, modify the spatiotemporal patterns of resources and risks (e.g. predator and prey continually adapt to one another).

The representation of spatially explicit environments is of particular importance for investigations into the impact of external factors on animal movements using ABM. Empirical data obtained from remote sensing, global positioning systems (GPS), and sensor networks can be incorporated into ABM to support such representations. These data are often spatially referenced and maintained in a variety of formats and resolutions. Spatial and spatiotemporal data models in GIS allow for the representation of spatially explicit environments in ABM (Bian 2003; Brown et al. 2005b; Tang 2008; Yuan 2001).

Modeling motion capacities of animals

Animals use different movement modes (e.g. walk, run, fly, and swim) to change their locations in space-time (Nathan et al. 2008; Pyke 1983) and sometimes change their mode of movement in response to their internal states (e.g. energy or forage levels) and external conditions (e.g. risks from predation or climate change; see Nathan et al. 2008). In ABM, animal movement can be modeled as random walks (or random movement) on the landscape. Corresponding to different movement modes, different types of random walk (including complete, directed, correlated, or biased) can be used (see Turchin 1998). These random walks are driven by stochastic processes that can be constrained by internal and external variables (e.g. high probabilities of moving towards high resources). Wolff (1994) used two movement modes that guide the food searching activities of wood storks: random search and flocking. Huse and Giske (1998) examined the role of two types of movement modes: reactive and predictive, in explaining the spatial distribution of fish in response to growth pressure and predation risk. In Ahearn (2001)'s TIGMOD model, the movement types of tigers, modeled as random walks (with directional and persistence bias; see Turchin 1998), are intricately tied to their goals (e.g. hunting, feeding, and mating) and environments (e.g. home territory). In Hölker and Breckling (2005)'s fish model, the movement of fish can be changed between two swimming modes: low- and high-cost in response to such environmental conditions as temperature and food distribution. Bennett and Tang (2006) investigated elk migration by designing two movement modes for elk: local movement constrained by resource patterns and inter-patch movement directed by snow distributions. The switching between these two movement modes is controlled by a threshold defined by snow levels. Linard et al. (2009) designed two movement modes for mosquitoes: simulating the search for blood meals and for breeding sites.

The choice of movement modes can be defined by a set of stimulus–response rules. In most current ABM, the probability that an animal switches its modes is fixed. However, effective switching rules can also be learned by agents through interactions with their environments or other agents during their movement. For example, Morales et al. (2005) used neural networks to establish adaptive stimulus–response relationships that guide the movement of large herbivores during foraging and exploration. An evolutionary algorithm was used in the elk migration model developed by Bennett and Tang (2006) to simulate how elk agents learn when to initiate their migratory behavior in response to changing weather conditions (i.e. switch from local random movement to long-distance movement biased by targeted patches). Furthermore, the study of behavior-based robotics (see Arkin 1998) provides support for modeling adaptive switching among behavioral modes.

Modeling navigation capacities of animals

Animals can use both external environmental cues (e.g. magnetic field, sun, wind, and landmarks, see Able 1980; Baker 1978) and their cognitive capabilities (e.g. spatial memory; see Bailey et al. 1996; Golledge 1999) to navigate across landscapes and reach their destinations (i.e. spatial goals or sub-goals). Animal navigation is situationally dependent and goal-driven (see Baker 1978; Nathan et al. 2008). Based on acquired stimulus information from their sensors and their previous experience stored in memory, animals evaluate the utility of alternative movement decisions and then initiate the appropriate movement behavior, which can be modeled as random movement in ABM. The literature of neurobiology (McNaughton et al. 2006; Trullier et al. 1997) has suggested animals navigate across landscape via landmarks or other cues, path integration, and cognitive maps. For destinations within the perceptual range of animals, direct targeting can be used to guide animal movement that does not require spatial memory and learning capabilities (Trullier et al. 1997). For destinations outside of the perceptual range of animals, four types of navigation strategies have been identified by Trullier et al. (1997): guidance that uses the spatial pattern of landmarks, place recognition-triggered response by local environments – places associated with goals and landmarks, topological navigation guided by spatial relationships among landmarks, and metric navigation that requires a more precise estimate of distances and directions associated with the planned route. In the elk migration model developed by Bennett and Tang (2006, 2008), for example, elk use cognitive graphs that establish topological and metric relationships among patches to guide their navigation towards winter habitats. While these strategies provide guidelines for modeling animal navigation and have been well investigated in neurobiology (Trullier et al. 1997), their use in modeling animal movement within real-world ecological and social systems is rare.

The internal representation of the environment and the spatial learning algorithms needed to populate this representation are essential to the application of these four navigation strategies (Prescott 1996; Trullier et al. 1997). Spatial learning, based on stimulus–response–reward mechanisms, allows animals to explore and exploit their environments and, thus, establish relationships among visited patches or cells (see Arkin 1998; Prescott 1996; Trullier et al. 1997). Machine learning algorithms can be used to represent spatial learning mechanisms in animals during navigation. In a series of fish models (see Dagorn et al. 2000; Giske et al. 1998; Huse and Giske 1998; Huse et al. 1999), neural networks have been used to provide navigation support (e.g. swimming rates or directions) for fish movement. Likewise, Morales et al. (2005) applied neural networks to guide movement directions of large herbivore. In the elk migration model developed by Bennett and Tang (2006, 2008), machine learning algorithms (including evolutionary algorithms, Hebbian learning, and reinforcement learning) were used by elk to learn to update their cognitive maps for winter migration.

MODELING ANIMAL MOVEMENT PATTERNS

The modeling of animal movement patterns, including representation and analysis, in ABM allows us to understand the underlying movement processes that lead to these patterns. In ABM, the movement trajectory or pathway of an animal can be represented as a sequence of discrete time-stamped location variables, which can be geographic coordinates or vectors including step lengths and turn angles (Turchin 1998). Because environment representation in ABM can be raster- or vector-based, the location variables can be further indexed by raster cells or vector-based patches. Animal movement trajectories can be aggregated into different spatial and temporal scales through, for example, resampling techniques (Turchin 1998) and captured using spatiotemporal data models (Bian 2000; Brown et al. 2005b; Pelekis et al. 2004; Yuan 2001). Spatiotemporal database techniques (Pfoser et al. 2000; Wolfson et al. 1998) provide support for storing and retrieving animal movement patterns.

The analysis of animal movement patterns in ABM raises a challenging but intriguing issue. The empirical study of animal movement has led to a set of quantitative metrics, potentially at different levels (e.g. individual, population, and location; see Figure 6), to enable the analysis of animal movement patterns using statistical approaches (see Tischendorf 1997). Turchin (1998) discussed quantitative metrics for analyzing movement patterns of species. These metrics include angular correlation and net squared displacement based on step lengths and turn angles (individual-level), residence index for capturing the impact of landscape heterogeneity (location-based), and fractal dimension for evaluating the scale-independent characteristics of individual-level movement paths. Besides these, landscape metrics (see Gustafson 1998; Turner et al. 2001) and spatial point pattern analysis (Dale 1999; Diggle 2003) can be used to analyze and compare the spatial patterns of animals during their movement.

These quantitative metrics not only support the evaluation of simulated animal patterns, but also allow for model calibration and validation using empirical movement data. The choice of metrics depends on how the animal movement paths are represented (e.g. raster- or vector-based), and level of analysis (e.g. individual, population, or location; see Figure 6). Morales et al. (2005) used net squared displacement and histograms of turning angles to analyze the movement paths of simulated herbivore. Tang (2008) applied spatial point pattern analysis (including quadrat analysis and nearest neighborhood distance analysis) to compare the spatial distribution patterns of elk to examine the impact of spatial learning on the migratory performance of elk.

Challenges and Issues in Agent-based Models of Animal Movement

As ABM have been developed for the simulation of animal movement, it is important that the issues and challenges associated with the current modeling paradigm be identified and key research areas pinpointed. These challenges include spatial adaptation, multi-scale environment representation, validation, and computation. We highlight here two specific

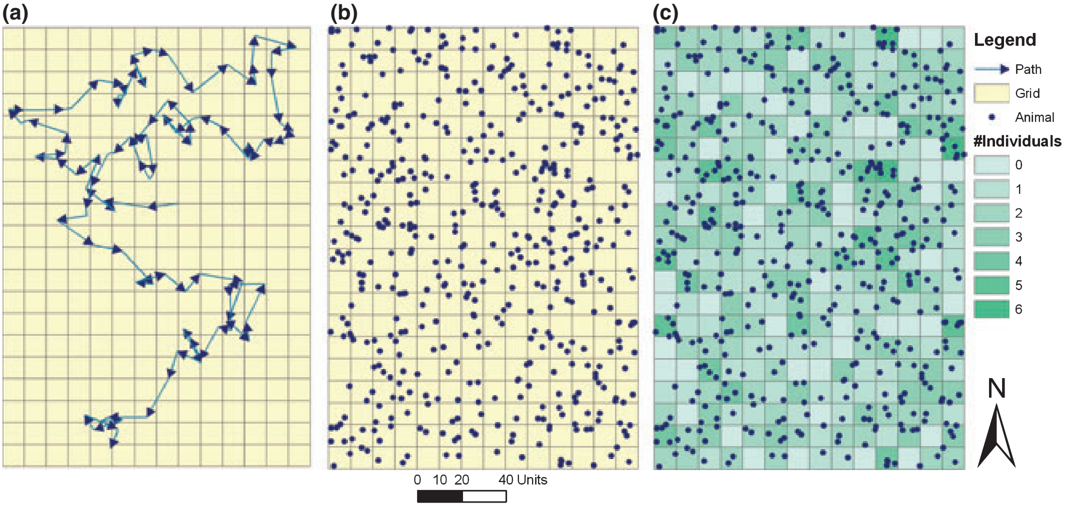

Fig. 6. Simulated animal movement patterns at different levels. (a) Movement path of an individual; (b) population-level spatial distribution patterns of animals at a specific time step; (c) location-based distribution patterns of animals at a time step; spatial distribution patterns were produced using Hawths Tools (http://www.spatialecology.com/htools/) in ESRI ArcGIS).

challenges that we believe are particularly important to the advancement of ABM for animal movement: spatial adaptation and multi-scale environmental representation. For discussion on validation, the readers are directed to Brown et al. (2005a), Moss and Edmonds (2005), and Windrum et al. (2007); for computation, please refer to Abbott et al. (1997), Armstrong (2000), Wang et al. (2006), and Tang and Wang (2009).

SPATIAL ADAPTATION

Interactions among animal movement patterns and their driving processes lead to complex dynamics in ecological and social systems. The movement patterns of many animals (e.g. migration) can be regarded as emergent and self-organized spatial phenomena developed from local-level processes (DeAngelis and Mooij 2005; Railsback 2001). Understanding, representing, and modeling associated feedback loops between movement patterns and processes in ABM and, thus, capturing the complex system characteristics present an important research challenge. These feedback loops are closely related to the adaptive behaviors of animals that allow them to adjust their response (at individual or collective levels) to internal and external stimuli (Belew and Mitchell 1996; DeAngelis and Mooij 2005; Railsback 2001). Machine learning techniques (including evolutionary algorithms, neural networks, and reinforcement learning) have been used to simulate the adaptive animal movement behavior (Bennett and Tang 2006, 2008; Huse and Giske 1998; Morales et al. 2005). However, the application of these techniques to modeling spatial adaptation in real-world ecological and social systems is still in its initial stage.

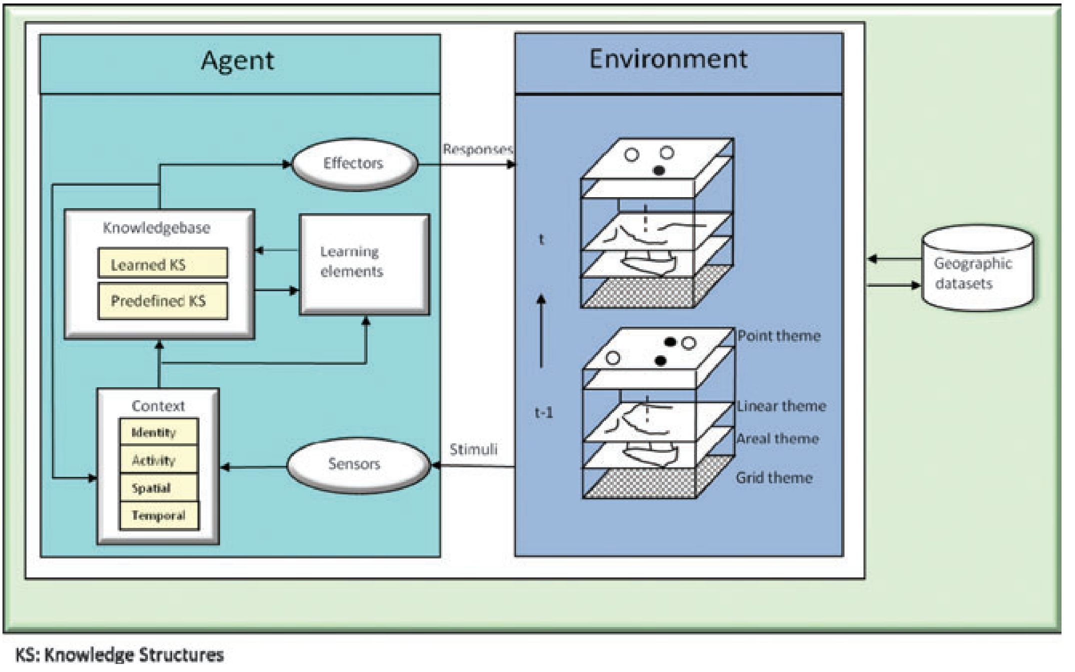

Fig. 7. A geographically aware intelligent agent framework (reprinted with permission. Cartography and Geographic Information Science, vol. 35, no. 4, pp. 239–263. Simulating complex adaptive geographic systems: a geographically-aware intelligent agent approach. Tang 2008).

Tang (2008) proposed a geographically aware intelligent agents (GAIA) framework (see Figure 7) that employs context, knowledge structures, and learning for the modeling of spatially aware, knowledge-driven, and intelligent agents. This framework provides partial insight into the spatial adaption issue related to animal movement.

MULTI-SCALE ENVIRONMENTAL REPRESENTATION

Movement patterns and processes often operate across different spatial and temporal scales (Johnson et al. 1992; Turner et al. 2001). The representation and capture of multi-scale interactions among movement patterns and processes using ABM raise a challenging issue. Researchers have attempted to use a multi-scale representation of spatially explicit environments, based on hierarchy theory (Simon 1962), to gain insight into cross-scale landscape dynamics (O'Neill et al. 1986; Wu and David 2002). Beecham and Farnsworth (1998), for example, organized patches into a hierarchical structure to guide the searching behavior of large herbivore. Bennett and Tang (2006) combined cell- and patch-based approaches to represent heterogeneous landscape dynamics in their elk migration model. While elk perform local movement at the cell level, they rely on patch-level information to guide their long-distance winter migration. Multi-scale environmental representation can support the investigation of scale issues using ABM and facilitate our understanding of, for example, individual movement behavior in response to spatiotemporal heterogeneity on landscapes.

Conclusion

Agent-based models provide an integrative modeling framework that allows for the simulation of complex animal movement dynamics in a bottom-up manner. As research focus shifts from population-level diffusion to individual-level movement models (Turchin 1998) and new paradigms like movement ecology emerge (Nathan 2008; Nathan et al. 2008), ABM will increasingly be used for the simulation of animal movement. ABM support the explicit modeling of cross-scale interactions between animal movement processes and patterns, and offer a viable alternative to conventional pattern-centric empirical models when exploring the complexity of animal movement. Furthermore, existing movement-related theories (e.g. biomechanical, cognitive, random, and optimization; see Nathan et al. 2008) can be synergistically applied into the integrative framework of ABM and, thus, enhance our understanding of animal movement dynamics.

Agent-based modeling of animal movement is challenging in part because of the mobile and interactive nature of animal movement and the associated computational requirements. Our discussion on animal movement behavior is based on the four movement components (i.e. internal states, external factors, motion and navigation capacities) proposed in the conceptual movement ecology framework (Nathan et al. 2008). These components are inherently related to the movement processes and patterns of animals and, therefore, provide solid support for leveraging ABM-based studies to explore the driving mechanisms of animal movement in heterogeneous landscapes. It is, however, important to keep in mind that the study of animal movement draws upon multiple domains (e.g. climatology, ecology, hydrology, and psychology) and the integration of data, models, and knowledge from multiple domains into ABM of animal movement is necessary if this promising approach is to reach its full potential.

Acknowledgement

The authors thank support from the National Science Foundation BE-CNH Award #0216588: "Complexity across Boundaries: Coupled Human and Natural Systems in the Yellowstone Northern Elk Winter Range", National Geospatial-Intelligence Agency University Research Initiatives, "Simulating Spatiotemporal Interactions of Mobile Entities", and NSF TeraGrid Supercomputing Resource Award TG-SES090019 and TG-SES070007: "Extending and Sustaining GISolve as a GIScience Gateway Toolkit for Geographic Information Analysis".

Short Biographies

Wenwu Tang is a research scientist in Department of Geography and National Center for Supercomputing Applications at the University of Illinois at Urbana-Champaign. He holds geography degrees from East China Normal University (B.S., 1998), Nanjing University, China (M.S., 2001), and the University of Iowa (Ph.D., 2008). His research interests include spatiotemporal simulation, biogeography and landscape ecology, geographic information systems (GIS), land use and land cover change, geocomputation, and cyberinfrastructure. He has published a series of work on the use of GIS-integrated agent-based models for the simulation of complex geographic systems.

David A. Bennett is an Associate Professor in Department of Geography at the University of Iowa. He is specialized in geographic information science and environmental modeling. He received his degrees from University of Northern Iowa (B.A., 1980), University of Michigan (Master of Regional Planning, 1982), and the University of Iowa (Ph.D., 1994). His research is focused on evolutionary computation, multi-agent systems, mobile computing, geographic information systems, and spatial decision support systems. Profession Bennett is particularly interested in applying these approaches to resolving complex geographic and environmental problems, represented by animal migration, human-environment interactions, and ecosystem management.

Note

* Corresponding address: Wenwu Tang, 324 Davenport Hall, 607 S. Matthews Avenue, Urbana, IL 61801, USA. E-mail: wentang@uiuc.edu

References

Abbott, C., et al. (1997). Parallel individual-based modeling of everglades deer ecology. *IEEE Computational Science & Engineering*, 4, pp. 60–72.

Able, K. P. (1980). Mechanisms of orientation, navigation and homing. In: Gauthreaux, G. S. A. Jr, (ed.) *Animal migration, orientation, and navigation*. New York: Academic Press, pp. 283–373.

Ahearn, S. (2001). TIGMOD: An individual-based spatially explicit model for simulating tiger/human interaction in multiple use forests. *Ecological Modelling*, 140, pp. 81–97.

Arkin, R. C. (1998). *Behavior-based robotics*. Massachusetts: The MIT Press.

Armstrong, M. P. (2000). Geography and computational science. *Annals of the Association of American Geographers* 90, pp. 146–156.

Arrignon, F., et al. (2007). Modelling the overwintering strategy of a beneficial insect in a heterogeneous landscape using a multi-agent system. *Ecological Modelling* 205, pp. 423–436.

Atkins, D. E., et al. (2003). *Revolutionizing science and engineering through cyberinfrastructure: report of the national science foundation blue-ribbon advisory panel on cyberinfrastructure*. [Online]. Retrieved on 11 March, 2010 from http://www.nsf.gov/od/oci/reports/atkins.pdf.

Bailey, D. W., et al. (1996). Mechanisms that result in large herbivore grazing distribution patterns. *Journal of Range Management* 49, pp. 386–400.

Baker, R. R. (1978). *The evolutionary ecology of animal migration*. New York: Holmes & Meier Publishing.

Batty, M. (2000). Geocomputation using cellular automata. In: Openshaw, S. and Abrahart, R. J., (Eds.) *Geocomputation*. New York: Taylor & Francis, pp. 95–126.

Batty, M., Desyllas, J. and Duxbury, E. (2003). The discrete dynamics of small-scale spatial events: agent-based models of mobility in carnivals and street parades. *International Journal of Geographical Information Science* 17, pp. 673–697.

Beecham, J. A. and Farnsworth, K. D. (1998). Animal foraging from an individual perspective: an object orientated model. *Ecological Modelling* 113, pp. 141–156.

Belew, R. K. and Mitchell, M. (eds) (1996). *Adaptive individuals in evolving populations: models and algorithms*. New York: Addison-Wesley Publishing Company, Inc.

Benenson, I. and Torrens, P. M. (2004). *Geosimulation: automata-based modeling of urban phenomena*. New York: John Wiley & Sons.

Bennett, D. A. and Tang, W. (2006). Modelling adaptive, spatially aware, and mobile agents: elk migration in yellowstone. *International Journal of Geographical Information Science* 20, pp. 1039–1066.

Bennett, D. A. and Tang, W. (2008). Mobile aware intelligent agents. In: Yuan, M. and Stewart, K., (eds.) *Understanding dynamics of geographic domains*. Boca Raton, FL: CRC Press/Taylor & Francis, pp. 171–186.

Bian, L. (2000). Object-oriented representation for modelling mobile objects in an aquatic environment. *International Journal of Geographical Information Science* 14, pp. 603–623.

Bian, L. (2003). The representation of the environment in the context of individual-based modeling. *Ecological Modelling* 159, pp. 279–296.

Bonabeau, E., Dorigo, M. and Theraulaz, G. (1999). *Swarm intelligence: from natural to artificial systems*. Oxford: Oxford University Press.

Bousquet, F. and Page, C. L. (2004). Multi-agent simulation and ecosystem management: a review. *Ecological Modelling* 176, pp. 313–332.

Brown, D. G., et al. (2005a). Path dependence and the validation of agent-based spatial models of land use. *International Journal of Geographical Information Science* 19, pp. 153–174.

Brown, D. G., et al. (2005b). Spatial process and data models: toward integration of agent-based models and GIS. *Journal of Geographic Systems* 7, pp. 1–23.

Clarke, K. C., Hoppen, S. and Gaydos, L. (1997). A self-modifying cellular automaton model of historical urbanization in the San Francisco Bay area. *Environment and Planning B: Planning and Design* 24, pp. 247–261.

Comiskey, E., et al. (1997). A spatially-explicit individual-based simulation model for Florida panther and white-tailed deer in the Everglades and Big Cypress landscapes. In: Jordan, D. (ed.) *Proceedings of the Florida Panther Conference*. Ft. Myers, FL, November 1–3, 1994, U.S. Fish and Wildlife Service.

Courant, R., Friedrichs, K. and Lewy, H. (1967). On the partial difference equations of mathematical physics (translated from the 1928 German original). *IBM Journal* 11, pp. 215–235.

Crist, T. O., Guertin, D. S., Wiens, J. A. and Milne, B. T. (1992). Animal movement in heterogeneous landscapes: An experiment with *Eleodes* beetles in shortgrass prairie. *Functional Ecology* 6, pp. 536–544.

Dagorn, L., Menczer, F., Bach, P. and Olson, R. J. (2000). Co-evolution of movement behaviours by tropical pelagic predatory fishes in response to prey environment: a simulation model. *Ecological Modelling* 134, pp. 325–341.

Dale, M. R. T. (1999). *Spatial pattern analysis in plant ecology*. Cambridge: Cambridge University Press.

DeAngelis, D. L. and Gross, L. J. (eds) (1992). *Individual-based models and approaches in ecology*. New York: Chapman & Hall.

DeAngelis, D. and Mooij, W. (2005). Individual-based modeling of ecological and evolutionary processes. *Annual Review of Ecology, Evolution, and Systematics* 36, pp. 147–168.

Diggle, P. J. (2003). *Statistical analysis of spatial point patterns*. Oxford, New York: Oxford University Press.

Dumont, B. and Hill, D. R. C. (2001). Multi-agent simulation of group foraging in sheep: Effects of spatial memory, conspecific attraction and plot size. *Ecological Modelling* 141, pp. 201–215.

Dumont, B. and Hill, D. (2004). Spatially explicit models of group foraging by herbivores: what can agent-based models offer? *Animal Research* 53, pp. 419–428.

Emlen, J. M. (1966). The role of time and energy in food preference. *American Naturalist* 100, pp. 611–617.

Epstein, J. M. (1999). Agent-based computational models and generative social science. *Complexity* 4, pp. 41–60.

Epstein, J. M. and Axtell, I. (1996). *Growing artificial societies: social science from the bottom up*. Cambridge: The MIT Press.

Ferber, J. (1999). *Multi-agent systems: an introduction to distributed artificial intelligence*. New York: Addison-Wesley.

Folse, J., Packard, J. and Grant, W. (1989). AI modelling of animal movements in a heterogeneous habitat. *Ecological Modelling* 46, pp. 57–72.

Forman, R. T. T. (1995). *Land mosaics: the ecology of landscapes and regions*. New York, USA: Cambridge University Press.

Foster, I. and Kesselman, C. (1999). *The grid: blue print for a new computing infrastructure*. San Francisco, CA USA: Morgan Kaufmann Publishers.

Gallistel, C. R. (1989). Animal cognition: the representation of space, time and number. *Annual Review of Psychology* 40, pp. 155–189.

Gardner, R. H., O'Neill, R. V., Turner, M. G. and Dale, V. H. (1989). Quantifying scale-dependent effects of animal movement with simple percolation models. *Landscape Ecology* 3, pp. 217–227.

Gilbert, N. and Troizsch, K. G. (2005). *Simulation for the social scientist*. 2nd ed. New York: Open University Press.

Gimblett, R. H. (2002). Integrating geographic information systems and agent-based technologies for modeling and simulating social and ecological phenomena. In: Gimblett, R. H., (Ed.) *Integrating geographic information systems and agent-based modeling techniques for simulating social and ecological processes*. Oxford: Oxford University Press, pp. 1–20.

Giske, J., Huse, G. and Fiksen, O. (1998). Modelling spatial dynamics of fish. *Reviews in Fish Biology and Fisheries*, 8, pp. 57–91.

Golledge, R. G. (ed.) (1999). *Wayfinding behavior: cognitive mapping and other spatial processes*. Baltimore, MD: Johns Hopkins University Press.

Goodchild, M. F. (1992). Geographical data modeling. *Computers & Geosciences* 18, pp. 401–408.

Goodchild, M. F., Yuan, M. and Cova, T. J. (2007). Towards a general theory of geographic representation in GIS. *International Journal of Geographical Information Science* 21, pp. 239–260.

Grimm, V. and Railsback, S. F. (2005). *Individual-based modeling and ecology*. Princeton, NJ: Princeton University Press.

Grimm, V., et al. (2005). Pattern-oriented modeling of agent-based complex systems: lessons from ecology. *Science* 310, pp. 987–991.

Grimm, V., et al. (2006). A standard protocol for describing individual-based and agent-based models. *Ecological Modelling* 198, pp. 115–126.

Gross, J., Zank, C., Hobbs, T. and Spalinger, D. (1995). Movement rules for herbivores in spatially heterogeneous environments: responses to small scale pattern. *Landscape Ecology* 10, pp. 209–217.

Gustafson, E. J. (1998). Quantifying landscape spatial pattern: what is the state of the art? *Ecosystems* 1, pp. 143–156.

Hemelrijk, C. (1999). An individual-orientated model of the emergence of despotic and egalitarian societies. *Proceedings of the Royal Society of London, Series B: Biological Sciences* 266, pp. 361–369.

Hölker, F. and Breckling, B. (2005). A spatiotemporal individual-based fish model to investigate emergent properties at the organismal and the population level. *Ecological Modelling* 186, pp. 406–426.

Huse, G. and Giske, J. (1998). Ecology in mare pentium: an individual-based spatio-temporal model for fish with adapted behaviour. *Fisheries Research* 37, pp. 163–178.

Huse, G., Strand, E. and Giske, J. (1999). Implementing behaviour in individual-based models using neural networks and genetic algorithms. *Evolutionary Ecology* 13, pp. 469–483.

Huston, M., Deangelis, D. and Post, W. (1988). New computer models unify ecological theory. *BioScience* 38, pp. 682–691.

Johnson, A., Wiens, J., Milne, B. and Crist, T. (1992). Animal movements and population dynamics in heterogeneous landscapes. *Landscape Ecology* 7, pp. 63–75.

Kennedy, J., Eberhart, R. and Shi, Y. (2001). *Swarm intelligence*. San Francisco, CA: Morgan Kaufmann Publisher.

Linard, C., Poncon, N., Fontenille, D. and Lambin, E. (2009). A multi-agent simulation to assess the risk of malaria re-emergence in southern France. *Ecological Modelling* 220, pp. 160–174.

Lomolino, M. V., Riddle, B. R. and Brown, J. H. (2006). *Biogeography*. 3rd ed. Sunderland, MA: Sinauer Associates.

MacArthur, R. and Pianka, E. (1966). On optimal use of a patchy environment. *The American Naturalist* 100, 603.

MacDonald, G. M. (2003). *Biogeography: space, time, and life*. New York: John Wiley & Sons.

Mace, G. M., Harvey, P. H. and Clutton-Brock, T. H. (1983). Vertebrate home-range size and energetic requirements. In: Swingland, I. R. and Greenwood, P. J., (eds.) *The ecology of animal movement*. New York: Oxford University Press, pp. 32–53.

Maes, P. (1994). Modeling adaptive autonomous agents. *Artificial Life Journal* 1, pp. 135–162.

Malanson, G. P. (1999). Considering complexity. *Annals of the Association of American Geographers* 89, pp. 746–753.

Malanson, G. P. and Armstrong, M. P. (1996). Dispersal probability and forest diversity in a fragmented landscape. *Ecological Modelling* 87, pp. 91–102.

Martin, P. (1993). Vegetation responses and feedbacks to climate – a review of models and processes. *Climate Dynamics* 8, pp. 201–210.

Matthews, R. B., et al. (2007). Agent-based land-use models: a review of applications. *Landscape Ecology* 22, pp. 1447–1459.

McNaughton, B., et al. (2006). Path integration and the neural basis of the 'cognitive map'. *Nature Reviews Neuroscience* 7, pp. 663–678.

Morales, J., Fortin, D., Frair, J. and Merrill, E. (2005). Adaptive models for large herbivore movements in heterogeneous landscapes. *Landscape Ecology* 20, pp. 301–316.

Moss, S. and Edmonds, B. (2005). Sociology and simulation: statistical and qualitative cross-validation. *American Journal of Sociology* 110, pp. 1095–1131.

Nathan, R. (2008). An emerging movement ecology paradigm. *Proceedings of the National Academy of Sciences* 105, pp. 19050–19051.

Nathan, R., et al. (2008). A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences* 105, pp. 19052–19059.

Newell, A. and Simon, H. A. (1972). *Human problem solving*. Englewood Cliffs: Prentice Hall.

O'Keefe, J. M. and Nadel, L. (1978). *The hippocampus as a cognitive map*. New York: Oxford University Press.

O'Neill, R. V., DeAngelis, D. L., Waide, J. B. and Allen, T. F. H. (1986). *A hierarchical concept of ecosystems*. Princeton: Princeton University Press.

O'Sullivan, D. (2008). Geographical information science: agent-based models. *Progress in Human Geography* 32, pp. 541–550.

Parker, K. L., Robbins, C. T. and Hanley, T. A. (1984). Energy expenditures for locomotion by mule deer and elk. *Journal of Wildlife Management* 48, pp. 474–488.

Parker, D. C., et al. (2003). Multi-agent systems for the simulation of land-use and land-cover change: a review. *Annals of the Association of American Geographers* 93, pp. 314–337.

Parrott, L. and Kok, R. (2002). A generic, individual-based approach to modelling higher trophic levels in simulation of terrestrial ecosystems. *Ecological Modelling* 154, pp. 151–178.

Pelekis, N., Theodoulidis, B., Kopanakis, I. and Theodoridis, Y. (2004). Literature review of spatio-temporal database models. *Knowledge Engineering Review* 19, pp. 235–274.

Peuquet, D. J. (2002). *Representation of space and time*. New York: The Guildford Press.

Pfoser, D., Jensen, C. S. and Theodoridis, Y. (2000). Novel approaches in query processing for moving object trajectories. *Proceedings of the 26th international conference on very large data bases*, pp. 395–406.

Prescott, T. (1996). Spatial representation for navigation in animats. *Adaptive Behavior* 4, pp. 85–123.

Pyke, G. H. (1978). Optimal foraging: movement patterns of bumblebees between inflorescences. *Theoretical Population Biology* 13, pp. 72–98.

Pyke, G. H. (1983). Animal movements: an optimal foraging approach. In: Swingland, I. R. and Greenwood, P. J., (eds.) *The ecology of animal movement*. New York: Oxford University Press, pp. 7–31.

Pyke, G. H. (1984). Optimal foraging theory: a critical review. *Annual Review of Ecology and Systematics* 15, pp. 523–575.

Quammen, D. (1996). *Song of the dodo: island biogeography in an age of extinction*. New York: Simon and Schuster.

Railsback, S. F. (1999). Movement rules for individual-based models of stream fish. *Ecological Modelling* 123, pp. 73–89.

Railsback, S. F. (2001). Concepts from complex adaptive systems as a framework for individual-based modeling. *Ecological Modelling* 139, pp. 47–62.

Railsback, S. F., Lytinen, S. L. and Jackson, S. K. (2006). Agent-based simulation platforms: review and development recommendations. *Simulation* 82, pp. 609–623.

Reuter, H. and Breckling, B. (1999). Emerging properties on the individual level: modelling the reproduction phase of the European robin *Erithacus rubecula*. *Ecological Modelling* 121, pp. 199–219.

Russell, S. J. and Norvig, P. (1995). *Artificial intelligence: a modern approach*. New Jersey: Prentice Hall.

Schelling, T. C. (1969). Models of segregation. *The American Economic Review* 59, pp. 488–493.

Sellers, W. I., Hill, R. A. and Logan, B. S. (2007). An agent-based model of group decision making in baboons. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences* 362, pp. 1699–1710.

Shaman, J. (2007). Amplification due to spatial clustering in an individual-based model of mosquito-avian arbovirus transmission. *Transactions of the Royal Society of Tropical Medicine and Hygiene* 101, pp. 469–483.

Shannon, R. E. (1975). *Systems simulation: the art and science*. Englewood Cliffs, N.J.: Prentice-Hall.

Shettleworth, S. J. (2001). Animal cognition and animal behaviour. *Animal Behaviour* 61, pp. 277–286.

Shugart, H. H., Smith, T. M. and Post, W. M. (1992). The potential for application of individual-based simulation models for assessing the effects of global change. *Annual Review of Ecology and Systematics* 23, pp. 15–38.

Simon, H. A. (1962). The architecture of complexity. *Proceedings of the American Philosophical Society* 106, pp. 467–482.

Siniff, D. B. and Jessen, C. B. (1969). A simulation model of animal movement patterns. *Advances in Ecological Research* 6, pp. 185–219.

Smith, T. R., Pellegrino, J. and Golledge, R. G. (1982). Computational process modeling of spatial cognition and behavior. *Geographical Analysis* 14, pp. 305–325.

Stephens, D. W. and Krebs, J. R. (1986). *Foraging theory*. Princeton, NJ: Princeton University Press.

Sutton, R. S. and Barto, A. G. (1998). *Reinforcement learning: an introduction*. Cambridge, MA: The MIT Press.

Swingland, I. R. and Greenwood, P. J. (1983). *The ecology of animal movement*. New York: Oxford University Press.

Tang, W. (2008). Simulating complex adaptive geographic systems: a geographically-aware intelligent agent approach. *Cartography and Geographic Information Science* 35, pp. 239–263.

Tang, W. and Wang, S. (2009). HPABM: a hierarchical parallel simulation framework for spatially-explicit agent-based models. *Transactions in GIS* 13, pp. 315–333.

Tang, W., Malanson, G. P. and Entwisle, B. (2009). Simulated village locations in Thailand: a multi-scale model including a neural network approach. *Landscape Ecology* 24, pp. 557–575.

Tischendorf, L. (1997). Modelling individual movements in heterogeneous landscapes: potentials of a new approach. *Ecological Modelling* 103, pp. 33–42.

Trullier, O., Wiener, S. I., Berthoz, A. and Meyer, J. A. (1997). Biologically based artificial navigation systems. *Review and Prospects* 51, pp. 483–544.

Turchin, P. (1998). *Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants*. Sunderland, MA: Sinauer Associates.

Turner, M. G. (1989). Landscape ecology: the effect of pattern on process. *Annual Review of Ecology and Systematics* 20, pp. 171–197.

Turner, M., et al. (1994). Simulating winter interactions among ungulates, vegetation, and fire in Northern Yellowstone Park. *Ecological Applications* 4, pp. 472–496.

Turner, M. G., Gardner, R. H. and O'Neill, R. V. (2001). *Landscape ecology in theory and practice: pattern and process*. New York, NY: Springer-Verlag.

Wang, D., Berry, M. W., Carr, E. A. and Gross, L. J. (2006). A parallel fish landscape model for ecosystem modeling. *Simulation* 82, pp. 451–465.

White, R. and Engelen, G. (1997). Cellular automata as the basis of integrated dynamic regional modelling. *Environment and Planning B: Planning and Design* 24, pp. 235–246.

Windrum, P., Fagiolo, G. and Moneta, A. (2007). Empirical validation of agent-based models: alternatives and prospects. *Journal of Artificial Societies and Social Simulation* 10. [Online]. Retrieved on 11 March, 2010 from http://jasss.soc.surrey.ac.uk/10/2/8.html.

Wolff, W. F. (1994). An individual-oriented model of a wading bird nesting colony. *Ecological Modelling* 72, pp. 75–114.

Wolfson, O., Xu, B., Chamberlain, S. and Jiang, L. (1998). Moving objects databases: issues and solutions. *Proceedings on the Tenth International Conference on Scientific and Statistical Database Management*, pp. 111–122.

Worboys, M. and Duckham, M. (2004). *GIS: a computing perspective*. 2nd ed. Boca Raton: CRC Press.

Wu, J. and David, J. L. (2002). A spatially explicit hierarchical approach to modeling complex ecological systems: theory and applications. *Ecological Modelling* 153, pp. 7–26.

Yuan, M. (2001). Representing complex geographic phenomena in GIS. *Cartography and Geographic Information Science* 28, pp. 83–96.

Yuan, M. and Stewart, K. (eds) (2008). *Understanding dynamics of geographic domains*. Boca Raton, FL: CRC Press/Taylor & Francis.

Zeigler, B. P., Kim, T. G. and Praehofer, H. (2000). *Theory of modeling and simulation: integrating discrete event and continuous complex dynamic systems*. 2nd ed. San Diego, CA USA: Academic Press.