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Research Article

Modelling adaptive, spatially aware, and mobile agents: Elk migration in Yellowstone

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The potential utility of agent-based models of adaptive, spatially aware, and mobile entities in geographic and ecological research is considerable. Developing this potential, however, presents significant challenges to geographic information science. Modelling the spatio-temporal behaviour of individuals requires new representational forms that capture how organisms store and use spatial information. New procedures must be developed that simulate how individuals produce bounded knowledge of geographical space through experiential learning, adapt this knowledge to continually changing environments, and apply it to spatial decision-making processes. In this paper, we present a framework for the representation of adaptive, spatially aware, and mobile agents. To provide context to this research, a multiagent model is constructed to simulate the migratory behaviour of elk (*Cervus elaphus*) on Yellowstone's northern range. In this simulated environment, intelligent agents learn in ways that enable them to mimic real-world behaviours and adapt to changing landscapes.

Keywords: Agent-based modelling; Mobile agents; Spatial cognition; Machine learning; Elk migration

1. Introduction

Geographic information science was originally focused on the digital representation of two-dimensional spatial phenomena (Goodchild 1992). Over the past two decades, progress has been made on the representation of spatio-temporal dynamics (Langran 1992, Yuan 2001) and the design of data structures that capture the space–time paths of mobile, geographically situated objects (Koubarakis *et al.* 2003). With the emergence of agent-based technologies, there is growing interest in modelling the spatial decision-making processes of the individuals who interact in these dynamic spaces and produce these paths. Agent-based models that represent the spatio-temporal behaviour of individuals can provide unique insight into, for example, the spread of disease (Barrett *et al.* 2005), the flow of people through built environments (Batty *et al.* 2003), and the movement of people or animals over large spaces (Ahearn *et al.* 2001, Bennett and Tang 2005). The representation of spatio-temporal behaviour, however, presents unique challenges to geographic information science. Motivation, decision-making processes, navigation, spatial awareness, adaptation, agent–agent interaction, and agent–environment interaction all must be considered in a representational framework that is designed to model cogent, purpose-driven, spatially aware mobile agents. In this paper, we present a framework for such

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agents, describe unique schemes for the representation of spatial memory and learning, and report proof-of-concept results that illustrate the utility of our approach.

1.1 *Context*

To provide context to our work, we consider the spatio-temporal behaviour of elk (*Cervus elaphus*) on Yellowstone National Park's (USA) northern range. Over the past 150 years, this area has experienced significant change as shifting ownership patterns, and management strategies were overlain onto what was once a highly integrated ecosystem. Changes in the past 10 years have been particularly evident; wolves were reintroduced, the northern range elk herd population rapidly declined from its mid-1990s high, riparian vegetation began to sprout to heights not seen for 100 years, and the number of northern range elk using private and public land to the north of the park (Paradise Valley) increased significantly (Lemke unpublished data).

Throughout this time, elk had to adapt to survive, and these adaptations have led to fundamental changes in the way these animals use their environment (Houston 1982, Boyce 1989, Ripple *et al.* 2001, Fortin *et al.* 2005). If we can understand how landscape-level changes affect the spatial and temporal behaviour of elk, we can better manage this regionally important resource (Forman 1995, Houston and McNamara 1999, Owen-Smith 2002, Kondoh 2003). Gaining this understanding, however, through the direct manipulation of the landscape is not feasible (Bailey *et al.* 1996). Experimentation through simulation provides a plausible alternative, but models of the spatial behaviour of elk require sophisticated techniques for the representation of: (1) bioenergetics; (2) resource selection; (3) threat avoidance; (4) navigation and spatial memory; and (5) spatial learning. Most existing ecological models of ungulate behaviour focus on the simulation of bioenergetics and resource selection (Turner *et al.* 1994, Bian 2003, Noonburg *et al.* submitted). Less attention has been given to those behaviours that drive adaptation, such as threat avoidance, spatial memory, and spatial learning (Kamil and Roitblat 1985, Giske *et al.* 1998).

The work presented here is part of an interdisciplinary effort designed to better understand how changes in land use/land cover (e.g. conversion of working ranches to amenity homes) and wildlife management (e.g. changes in hunting patterns and the reintroduction of wolves) have affected the spatial behaviour of elk. Our focus is on migratory behaviour because this behaviour places elk in direct conflict with humans. Elk migration is a complex behaviour adapted to changing environments (Baker 1978, O'Kelly 1980) and, thus, can be viewed as an adaptive, self-organized, spatial response to ecosystem dynamics (Levin 1998, Malanson 1999). Furthermore, given evidence that migratory patterns change in response to short-term management decisions (Lemke 1995) and that some herds choose not to migrate at all (Boyce 1989), we can assume that spatial learning is integral to migratory behaviour. These properties of spatial adaptation and spatial cognition provide an appropriate test for our framework.

Our approach draws upon several different research domains, including elk ecology, multi-agent system (MAS) simulation, machine learning, and spatial cognition. Relevant literature is reviewed in section 2. In section 3, we present our model framework, and in section 4, we discuss how spatial learning can be simulated. Model results are presented in section 5. We conclude with a discussion of

the general utility of spatially aware agent-based modelling techniques and the need for future work on this topic.

2.   Relevant literature

Agents, at a minimum, sense, respond to, and interact with their environment and with each other. The design of spatially aware mobile agents must also include a representation of motivation (why an individual moves) and decision-making (processes that determine where an individual moves to). Movement requires energy and exposes the traveller to potential threats (e.g. predation), and thus a failure to move efficaciously across the landscape can have serious consequences; firms can go out of business, humans can get lost, and animals can starve. The drive to move may be completely reactive (e.g. the phototactic response of a moth toward light) or purposeful (e.g. a planned route across dangerous territory). Purposeful movement is facilitated by spatial memory and navigational skills (Trullier *et al.* 1997). Spatial memory implies spatial learning, and the ability to learn suggests that an organism can adapt to changing environmental conditions. Learning and adaptation are self-modifying behaviours that take experience as input and, if successful, transform it into improved decision-making (McFarland and Houston 1981). Motivation, spatial memory, spatial learning, navigation, and adaptation present unique challenges for the representation of spatially aware agents that have not been fully explored in the geographic or ecologic literature.

   Agent-based technologies have been used extensively in geographic research on land-use/land-cover change (e.g. Bennett *et al.* 1999, Janssen *et al.* 2000, Etienne *et al.* 2003, Parker *et al.* 2003, Sengupta and Bennett 2003, Brown *et al.* 2005). Mobility and spatial cognition, however, have not been developed in the context of these models, although an argument could be made that spatial perception is important to land-use/land-change dynamics. Westervelt and Hopkins (1999) and Bian (2003) describe spatially explicit frameworks for modelling mobile animals, and Batty *et al.* (2003) model the movement of people through an urban landscape. These examples provide valuable insight into the representation of mobile interacting agents but do not address spatial learning. Agent-based technologies (often referred to as individual-based models (IBM)) have an even longer history in the ecological sciences (Huston *et al.* 1988, DeAngelis and Gross 1992, Huse *et al.* 1999, Janssen *et al.* 2000, Ahearn *et al.* 2001, Dumont and Hill 2004). Grimm (1999) provides a useful review of the earlier work in this area, and Railsback (2001) provides insight into the future of IBMs. IBMs, as a product of computational ecology, are often focused on trophic relationships and reproduction. Railsback (2001) and Recknagel (2003) note that agent interaction, learning, and adaptation are often key to the representation of complex ecological processes characterized by nonlinear feedback and emergent behaviour. However, learning in general, and spatial learning in particular, has not been fully explored in the context of ecological simulation.

2.1   *Elk models*

Existing models of elk migration can be placed into context by considering what agents know about the spatial and temporal pattern of resource availability and the manner in which they transform this knowledge into decisions about movement and resource selection (figure 1). In mechanistic models, it is assumed that an agent's
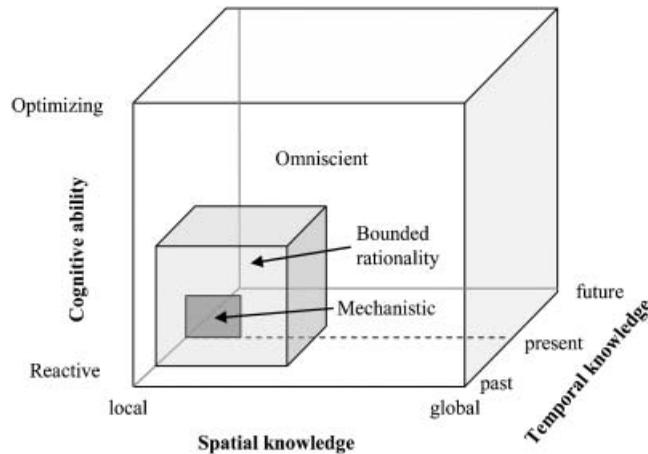
Figure 1.   Existing models of adaptive mobile agents can be placed into context by considering what agents know about the spatial and temporal pattern of other agents and available resources and their ability to transform this knowledge into useful decision.

spatial knowledge is limited to its perceptual range and that it has limited ability to remember past experiences or predict future states. Decision-making becomes a reactive response to local stimuli and agent state (Russell and Norvig 1995). Since experiences are not stored, learning does not occur. Mechanistic models provide a useful illustration of what agents are capable of given minimal assumptions about their cognitive abilities. While the principle of parsimony is often appropriate, assumptions about what elk know about their environment in this approach are overly conservative. There is evidence, for example, that elk often exhibit considerable fidelity to winter and summer ranges, and this suggests large-scale, long-term memory (Boyce 1989). The elk model presented by Turner *et al.* (1994) is most representative of this approach.

As an alternative, it can be assumed that agents are omniscient; they know the state of a system at all locations and at all times. Furthermore, they possess the cognitive ability to transform this knowledge into rational decisions. Learning is not relevant in this approach, as it is assumed that agents have all the information needed to make optimal migratory decisions. The elk model produced by Noonburg *et al.* (submitted) based on stochastic dynamical programming is illustrative of this approach. Optimizing models provide useful benchmarks by documenting what elk would do under ideal conditions, but the underlying assumptions about the cognitive ability of elk are unrealistically high. While an argument can be made that evolution has led to near-optimal behaviour, the assumption that elk can perceive the spatial pattern of forage and risk at distant locations and at all times is not supportable. Furthermore, these models tell us little about how the spatial behaviour of elk adapts to changing environmental conditions.

Common sense, field studies, and work in the cognitive sciences all suggest that reality falls somewhere between these two modelling extremes. Models based on bounded rational behaviour are characterized by limited knowledge about resources and threats, and limited ability to process this knowledge into effective decisions (Conlisk 1996). Learning and adaptation are crucial to the success of boundedly rational agents.

2.2   *Motivation and decision-making in agent-based elk models*

As elk migrate, they must balance the cost of travel and exposure to threats against the possibility of finding needed resources. Quality forage acts as an attractive force that pulls elk across the landscape (Arkin 1998), while areas with deep snow or high predation rates are associated with reduced survival rates and, thus, act to repel elk. The spatial distribution of resources and threats can be conceptualized as a field of attractive and repulsive forces (Arkin 1998) that can dynamically affect the movement pattern of mobile agents. Through repeated interaction with the environment, elk can learn these patterns and adapt to associated changes.

Needed resources can be tangible objects to be consumed, or they can fulfil behavioural or social needs (e.g. security or reproduction). Most researchers agree that elk migration is motivated by bioenergetic needs, which are relatively well studied and documented (Boyce 1989). Turner *et al.* (1994) review this literature and incorporate salient elements into their model. Elk fitness can be defined in terms of body mass, which affects survival and reproductive success (Turner *et al.* 1994), and a daily energy budget can be calculated to estimate the change in mass over time. Energy is gained by foraging and expended to maintain existing body mass and to travel. The spatial distribution of snow affects elk bioenergetics by reducing access to forage and increasing energy expenditures.

2.3   *Spatial memory and navigation*

Evidence suggests that spatial memory guides the foraging and migratory behaviour of many animals (Bailey *et al.* 1996, Giske *et al.* 1998, Dumont and Hill 2001), and research in neurobiology has shown that this memory is deeply rooted in the hippocampus of the brain (O'Keefe and Nadel 1978, Poucet 1993, Schmajuk 1997). Neurons in the hippocampus (i.e. place cells) fire when animals enter familiar geographic spaces (i.e. place fields) (Muller 1996, Shapiro *et al.* 1997, Eichenbaum *et al.* 1999). Repeated interactions at particular places, both positive and negative, reinforce these cells and increase the magnitude of the response produced by subsequent visits. A cognitive map, therefore, can be conceptualized as a set of place cells linked by synapses to form a physiological analogue of a physical environment (O'Keefe and Nadel 1978, Eichenbaum *et al.* 1999). While the exact mechanism is not yet fully understood, research has shown that place cells are used by animals (from rats to humans) to navigate through heterogeneous landscapes (O'Keefe and Nadel 1978, Muller *et al.* 1996, Eichenbaum *et al.* 1999, Jacobs 2003). Two forms of spatial memory, episodic and reference, are thought to lead to spatial knowledge (Bailey *et al.* 1996, Conway 2002). Episodic memory stores previously visited places for relatively short time periods and provides the conceptual foundation on which many studies in optimal foraging theory are built (Giske *et al.* 1998, Houston and McNamara 1999). Reference memory is thought to provide long-term navigational information (Bailey *et al.* 1996).

2.4   *Learning and adaptation*

The process of spatial learning ties spatial memory, location, and context to successful decision-making strategies. Muller *et al.* (1996) and Trullier and Meyer (2000) illustrate how a network of hippocampal place cells can be encoded as a weighted bidirectional cognitive graph (a digital cognitive map) to model spatial memory and behaviour. Machine-learning algorithms provide a way to make these

cognitive maps meaningful in specific environments. Four forms of machine learning are commonly used in agent-based simulation: evolutionary algorithms (Holland 1975), artificial neural networks (Bishop 1995), reinforcement learning (Sutton and Barto 1998), and Hebbian learning (Hebb 1949, Wasserman 1993). Each of these forms is biologically plausible, domain-independent, flexible, and robust, and thus can be used to represent adaptive spatially aware organisms. We experimented with each of these learning strategies as we produced this model. The model version presented in this paper relies on evolutionary algorithms, neural networks, and Hebbian learning processes.

2.4.1 Evolutionary algorithms. Evolutionary algorithms (EA) are based, at least metaphorically, on the concept of natural selection (Holland 1975). A population of solutions is created through selective pressures and the manipulation of 'genetic material', and individuals in this population evolve over successive generations toward optimal solutions. The genetic material of individuals (their genotype) is defined by a set of distinguishing characteristics and is often implemented as a one-dimensional array of values. These characteristics can be physical (e.g. height) or behavioural (e.g. the probability that an animal will migrate when snow depth exceeds a certain threshold). The state of this array directly or indirectly affects an individual's fitness (e.g. body mass at time t), which is a measure of how well an individual responds to selective pressures (Bäck 1996, Bäck *et al.* 1997). The overall objective of an EA is to evolve a population of individuals that possess those characteristics that maximize fitness. EAs have been used in a number of animal studies. Dagorn *et al.* (1995) develop a model to capture the adaptive behaviour of tuna using an EA. Giske *et al.* (1998) present a review of behavioural models that were designed to help study the spatial dynamics of fish and emphasized the utility of EAs for the representation of evolutionary adaptation. Huse (2001) uses an EA to represent the habitat preferences of fish.

There are many excellent sources for detailed descriptions of EAs (Holland 1975, Goldberg 1989, Bäck 1996, Bäck *et al.* 1997, Deb 2001) and their geographical applications (Chambers and Taylor 1996, Krzanowski and Raper 1999, Xiao *et al.* 2002, Brookes 2001, Bennett *et al.* 2004). The reader is referred to these sources for in-depth discussions on this approach.

2.4.2 Artificial neural networks and Hebbian learning. Artificial neural networks (ANN) were originally designed to simulate brain activity (Hertz *et al.* 1991, Bishop 1995). Virtual neurons are organized into layers connected through weighted links that are representative of synapses. These links map stimuli to responses, and successful responses are reinforced by adjusting link weights. Hertz *et al.* (1991) discuss the alternative methods by which link weights can be learned. Some of these methods are unique to ANN; others rely on related methods, such as EA and Hebbian learning processes, to perform this important role.

Hebbian learning is a simple yet effective algorithm that is well suited to the representation of spatial knowledge (Trullier *et al.* 1997). According to Hebb's (1949) postulate, when two neurons are activated simultaneously, the association between these neurons is enhanced. These associations are, again, representative of the synaptic connections among neurons and modelled as weighted links. The Hebbian learning rule by itself is not sufficient to solve problems since it only allows positive feedback on the change in link weights, which may cause an unbounded increase in these values (O'Reilly 2001). This problem can be remedied by

introducing inhibition mechanisms (O'Reilly 2001, Gerstner and Kistler 2002, Milner 2003). Inhibition mechanisms decrease link weights given an absence of stimuli, modelling the loss of memory, or negative stimuli. Hebbian learning has been shown to be biologically plausible (Muller *et al.* 1996, Trullier *et al.* 1997) and computationally efficient (Grzywacz 1998). Furthermore, it is structurally compatible with graph-based representations of cognitive maps (O'Reilly 2001, Milner 2003). Place cells linked together via synapses can represent paths across the landscape. Successful paths (e.g. those that lead to high survival rates or minimize winter body mass loss) are reinforced, and unsuccessful paths (e.g. those that lead to death) are penalized.

The integration of complementary learning approaches proves particularly useful in ecological studies because complex natural environments generate large sets of stimuli that often possess significant levels of noise and uncertainty. This produces a large solution space that renders the problem intractable when traditional ANN methods are used. In such situations, EAs can be used as heuristic problem solvers that efficiently estimate link weights. Dagorn *et al.* (1997) apply a similar approach to simulate the adaptation of tuna to environmental gradients. Huse *et al.* (1999) developed an individual-based simulation framework, based on feed-forward neural networks and genetic algorithms, to support models of animal behaviour. Strand *et al.* (2002) use this approach to simulate the behavioural decisions of Muller's pearlside (a marine planktivorous fish). Morales *et al.* (2005) apply evolutionary neural networks to simulate the foraging behaviour of elk.

3.   Model framework

Yellowstone's northern range elk population is represented as a multi-agent system (Ferber 1999, Janssen 2002, Bousquet and Le Page 2004) comprised of autonomous intentional agents interacting on and with a digital representation of the associated landscape (figure 2). This model was created using the Visual C++ programming environment. In this section, we discuss the structure of elk agents and the environment within which they operate.

3.1   *A multi-scale representation of the environment*

Field observations suggest that elk respond to large-scale landscape patterns when migrating (Pearson *et al.* 1995). The fine-scale spatial patterns of snow, available vegetation biomass, and topography, however, affect an elk's ability to meet bioenergetic requirements and, thus, movement at the local scale (Rudd *et al.* 1983, Sweeney and Sweeney 1984, Turner *et al.* 1994). This suggests a multiscale representation of the environment (figure 3). In our model, landscape-scale patches are linked together to form a graph over which coarse-grain (direction and destination) elk movement decisions are made. Attributes associated with each patch act to attract (e.g. forage) and repel (e.g. risk of predation by wolves or humans) elk. We use a $1\,km^2$ grid to represent patch structure. Mean biomass and snow characteristics are computed for each patch. The fine-grain pattern of snow and forage is captured using 1 ha grid cells. Snow data are routinely collected at only a small number of sparsely distributed points, and statistical models are often used to produce snow maps with sufficient detail to study elk behaviour. Fortin *et al.* (2005), for example, used the Yellowstone Snow Model produced by Farnes *et al.* (1999) to study wolf/elk/vegetation dynamics in Yellowstone National Park. This is
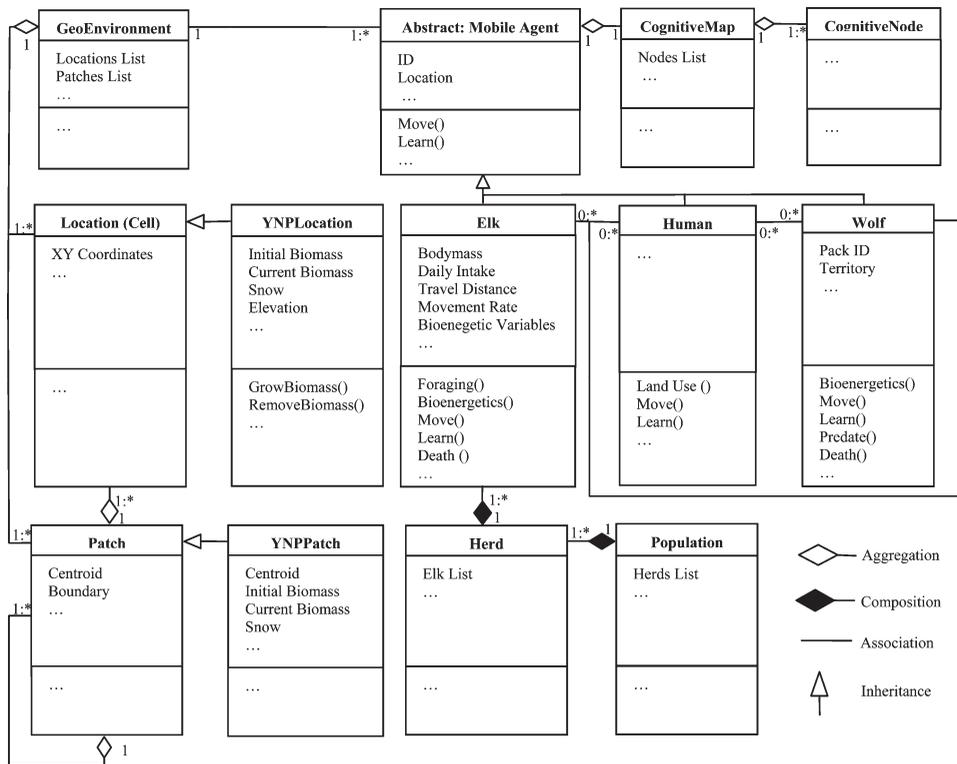
Figure 2.   Class diagram of our multi-agent simulation model.

a regression model that estimates snow water equivalency (SWE) from elevation and then adjusts this estimate for differences in solar radiation (a function of gradient, aspect, and vegetation cover). Following Fortin *et al.* (2005), the Yellowstone Snow Model is used to produce snow cover datasets for this research.

3.2 *Elk agents*

Each elk is represented as an aggregation of state variables (e.g. lean body mass), bioenergetic functions (e.g. foraging, metabolism), spatial memory, and learned decision-making processes (e.g. path selection). Elk are aggregated into cow/calf herds, and Yellowstone's northern range elk population is represented as the set of all such herds. Movement decisions are driven by the collective influences of an elk's current state, environmental variables (e.g. available forage and snow depth), episodic memory, and long-term reference memory (Kitchin and Blades 2002).

   The rate of movement is assumed to be $5 \, \mathrm{m \, min^{-1}}$ while foraging and $10 \, \mathrm{m \, min^{-1}}$ while travelling (Wickstrom *et al.* 1984, Turner *et al.* 1994). While reported movement rates vary significantly in the literature, the rates used in this study are representative of commonly reported values. Following Turner *et al.* (1994), elk stop moving when one of two conditions is met: (1) the maximal daily intake threshold is reached; or (2) the maximal daily travelling distance is reached. Maximal daily intake is a function of initial body mass and gender (Turner *et al.* 1994), and maximal daily travel distance is adjusted by snow depth according to the procedures documented in Turner *et al.* (1994).
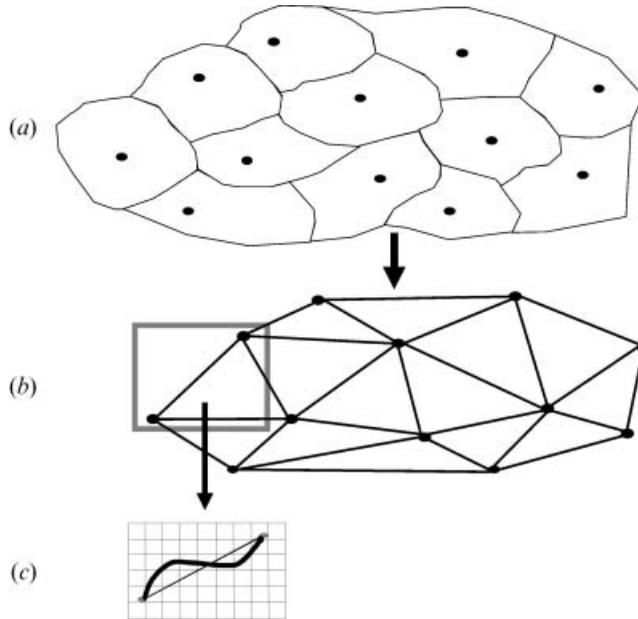
Figure 3. Multiscale representation used to represent the environment. Large-scale movement decisions are based on patch-level information (*a*) stored as a graph (*b*). Small-scale movements driven by resources available within a local window (*c*) embedded in a raster representation of space.

The bioenergetic functions used to calculate changes in elk state are taken from Turner *et al.* (1994) essentially without modification. What differs is the temporal resolution at which these processes are simulated. The model of Turner *et al.* was based on a raster representation with a spatial resolution of 1 ha and a time step of 1 day. They assumed that elk can travel up to 4 km day^{-1} (40 grid cells). We, however, are interested in how cow/calf herds compete with one another for forage as they merge together along common migration routes. To model the impact of this conspecific competition, however, an accounting of where and when forage is removed from the landscape must be maintained. Given a temporal resolution of one day, a spatial resolution of 1 ha, and a travel speed of 4 km day^{-1}, it is not possible to determine the amount of forage an elk removes from each cell, and thus we cannot accurately calculate the change in biomass across space—the spatial and temporal resolution of the simulation are not well balanced, given the movement capabilities of elk. An appropriate balance between the temporal and spatial resolution of the model can be determined by using the Courant–Friedrichs–Lewy (CFL) criterion (Martin 1993):

$$\Delta t \leq \frac{\Delta x_c}{c} \qquad (1)$$

where Δt is the smallest time step; Δx_c is the spatial resolution; and c is the fastest speed of the phenomenon of interest.

This relationship ensures that information does not travel faster through space than it does through time (e.g. we do not lose information about resource-utilization patterns because of an imbalance between the temporal and spatial resolution of the simulation). Given a typical migratory movement rate of 10 m min^{-1} (*c*) and a 1 ha

spatial resolution (Δx_c), a 10 min (100 m/10 m min^{-1}) temporal resolution (Δt) is required.

3.2.1 Representing spatial memory. The primary differences between our model and previous models concern the assumptions made about what elk know, how they gain this knowledge, and how they use it to guide movement decisions. Here, we assume that elk store spatial information gathered from direct experience and can use this information to make informed decisions. Their knowledge about the environment in which they live is incomplete, and uncertainty exists concerning the current state of those regions beyond their perceptual range. While elk may be able to generalize this knowledge to similar environments, we do not assume that they are omniscient or capable of deductive thought. We model spatial knowledge at the cow/calf herd level. Modelling at this level of aggregation is considered appropriate because of the close relationships that exist among members of these herds and their tendency to follow a lead elk.

Following Muller *et al.* (1996), the patch structure is represented as a bidirected graph that captures the spatial memory of the elk. This graph is of the form:

$$G = (V, E, W) \tag{2}$$

where G is a directed graph; V is the vertices of graph G; E is the edges of graph G; and W is the weights on edges E in G.

Patch centroids representing place cells are linked to first-order patch neighbours. Since each vertex in V corresponds to a real-world landscape patch, the resulting cognitive maps of elk are isomorphic to graphs of landscape structure (Diestel 2000). Each edge e_{ij} in the resulting graph represents a directed movement from vertex v_i to vertex v_j and thus corresponds to a movement from one place field to another. The weight w_{ij} of edge e_{ij} represents the relative attractive force from vertex i to vertex j and is used to guide large-scale movement decisions of elk. We use $V_i' = \{v'_1, v'_2, \ldots, v'_p | v'_i \in V, 1 \leqslant i \leqslant p\}$ to denote the set of vertices associated with the outwardly directed edges of vertex v_i.

3.2.2 Decisions regarding when to migrate. Conceptually, migration decisions balance the possibility of better forage at a distant location against the energy required to travel to that location. This decision is modelled as a stochastic response to SWE at times t and $t-1$ and an elk's current patch location; migration is conditioned on SWE and the rate at which SWE is changing through time. The relationship between snow characteristics and the desire to migrate is a learned behaviour that balances local foraging opportunities (w_{for}) against the benefits of migration (w_{mig}) (section 4.1):

$$P_{mig|t} = \begin{cases} nw_{mig} & \text{if } w_{mig} > w_{for} \\ \text{otherwise, } 0 \end{cases} \tag{3}$$

where $P_{mig|t}$ is the probability that an elk will initiate a migratory movement at time t, and nw_{mig} is the normalized value of w_{mig}.

At each time step, elk determine whether or not to make a migratory movement. If the decision is to migrate, then a destination patch is selected and acts as an attractive force on elk movement. Otherwise, local resources and threats guide elk movement decisions.

3.2.3 Selecting a destination patch. A migratory movement begins with the selection of a destination vertex (v_d) from the set of all vertices adjacent to an elk's current location (v_c). The probability that vertex i ($v_i \in V_c'$) will become the destination vertex is calculated as:

$$P(v_i|t) = \frac{a_{ci}}{\sum\limits_{j=1}^{np} a_{cj}} \tag{4}$$

where: $P(v_i|t)$ is the probability that vertex i is chosen as the destination given time t; a_{cj} is the attraction of vertex j relative to vertex c; and np is the the number of adjacent patches.

The attraction of vertex j to an elk at vertex c can be calculated as:

$$a_{cj} = \left(1 - w_{\text{mig}|vc,t}\right) * h_j' + w_{\text{mig}|vc,t} * w_{cj}' \tag{5}$$

where: h_j' is the accessible vegetation of v_j, normalized to the range of accessible biomass associated with vertices in V_c'; w_{cj}' is the edge weight w_{cj}, normalized to the range of weights associated with vertices in V_c'; and $w_{mig|vc,t}$ is the relative importance of migration compared with accessible forage at vertex c and time t.

The value associated with each w_{ij} is learned through repeated interaction with the environment (section 4.2). Currently, $w_{mig|vc,t}$ is set to 1 when learning spatial memory. In future work, agents will attempt to learn the appropriate value of $w_{mig|vc,t}$ given the state of the elk and the environment.

3.2.4 Selecting the next cell. The path an elk takes as it moves through the landscape from one patch to the next depends on the utility of cells found within a moving 3×3 cell window. This utility is calculated by considering the pull of vertex v_d as a destination along a migratory path and the pull of cell i as a foraging site (i.e. short-term vs. long-term reward). More specifically, the probability that a cell i will become the destination cell c_d for a movement at time t ($P_i(c_i|t)$), is calculated as:

$$P_i(c_i|t) = \frac{u_{i|t}}{\sum\limits_{k=1}^{m} u_{k|t}} \tag{6}$$

where $u_{i|t}$ is the utility value for cell i at time t; and m is the number of cells in the local window ($m=9$ for a 3×3 window). $1 <= i <= m$.

The utility of cell i at time t is, therefore, calculated as:

$$u_{i|t} = w_{mig} * u_{i|t}' + w_{for} * u_{i|t}'' \tag{7}$$

where: w_{mig} is the weight on migration to the next patch $\sim f(w_{hab}|_t, w_{hab}|_t - 1)$ (a learned value, see section 4.1); w_{for} is the weight on foraging at the local level; $u_{i|t}'$ is the normalized utility of cell i as a link in the path to vertex v_d at time t; and $u_{i|t}''$ is the normalized utility of cell i as a foraging site at time t, based on accessible biomass in cell i.

The value of $u_{i|t}'$ is assumed to be inversely proportional to the distance between cell i and vertex v_d:

$$u_{i|t}' = \frac{1}{d_{id}^{\beta}} \tag{8}$$

where d_{id} is the distance from the destination vertex d to cell i; and β is constant ($\beta=2$).

We do not allow an elk to go directly back to those cells stored in its episodic memory (currently set to the previously visited cell).

4. Learning movement decisions

As a proof-of-concept, we produce digital elk that learn to migrate in a way that mimics real elk behaviour. The learning process is divided into two tasks, decisions on when to migrate and decisions on where to migrate. These decisions will be based on stimulus–response relationships learned through repeated interactions with the simulated environment. All decisions require bounded knowledge about a changing environment, the elk's condition, and the expected consequences of alternative actions. While the intent is to replicate real-world behaviour, the specific objective of the implemented learning algorithms is to produce cognitive maps and movement rules that maximize elk fitness given incomplete knowledge about the environment.

4.1 *Learning when to migrate (the value of w_{mig})*

The literature suggests that elk migration begins when snow depth exceeds a threshold value. The magnitude of reported values varies from 20 to 46 cm; most, however, are toward the upper end of this range (Rudd *et al.* 1983, Parker *et al.* 1984, Sweeney and Sweeney 1984). The learning objective is, therefore, to infer the value of migratory behaviour compared with local foraging (i.e. the value of w_{mig} and w_{for}) given snow depth at times t and $t-1$. Since we are concerned only with the relative values of w_{mig} and w_{for}, we can set $w_{for}=1$ and learn those values of $w_{mig|sdepth,\ t,t-1}$ that optimize elk fitness at the end of the migratory season. If the weight on inter-patch movements (w_{mig}) is greater than one (i.e. w_{for}), given the snow depth in an elk's current patch at times t and $t-1$, it will tend to migrate; otherwise, local movement is preferred.

Snow depth is normalized to the maximum depth through which elk typically move (i.e. snow depth up to the bottom of an animal's chest, also referred to as brisket height). These normalized values are used to calculate an index of habitat quality:

$$hq_i = \frac{\max SWE - SWE_i}{\max SWE} \tag{9}$$

where hq_i is the habitat quality index for vertex i; max SWE is the brisket height of adult elk; and SWE_i is the SWE at vertex i.

The habitat quality index is classed into 10 bins to simplify the decision space. This produces a 100-element decision matrix, the snow depth at time $t-1$ represented by row-wise headers, and the snow depth at time t represented by column-wise headers (figure 4). Each element in this matrix stores a state specific value of $w_{mig|sdepth,\ t,t-1}$). The two-dimensional decision matrix is transformed into a one-dimensional vector based on row-wise ordering to represent the chromosome operated on by the EA. The initial values of w_{mig} are randomly selected from U[0,10]. Two-point crossover is implemented with a probability of 0.9, and mutations occur at a rate of 0.05. Elitism with a gap size of 0.9 and rank-based roulette style selection are used. The genetic algorithm ran for 300 generations.

Habitat index at time *t*

	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1
0.1	4.2	9.7	3.5	2.8	6.9	5.0	2.3	3.6	8.1	5.0
0.2	4.0	0.0	0.7	0.9	4.4	4.9	3.0	5.6	0.4	7.1
0.3	7.5	8.1	6.8	0.2	5.4	5.2	5.6	6.4	1.4	6.7
0.4	3.1	5.8	0.3	9.7	3.4	4.9	6.5	6.4	5.5	9.8
0.5	8.4	3.5	1.3	0.2	8.6	9.8	2.0	2.2	3.0	9.3
0.6	3.9	8.4	0.7	9.3	5.4	3.3	4.8	1.6	4.5	8.9
0.7	5.7	7.2	6.0	0.3	0.7	5.4	9.2	2.6	0.2	7.5
0.8	8.8	7.7	8.7	9.4	0.5	1.4	6.7	4.9	9.2	8.7
0.9	5.2	7.8	9.8	7.4	1.4	3.9	7.1	6.8	7.0	9.7
1	0.9	9.7	9.7	1.0	7.2	4.5	8.4	6.9	7.4	7.6

(Row-wise header, rotated on the left: Habitat index at time *t*–1)

Figure 4. Decision matrix for when to migrate. Row-wise and column-wise headers represent normalized habitat quality (from snow depth) at time *t*–1 and *t*. The value of each cell is randomly drawn from a uniform distribution U[0,10].

The objective function to be optimized is:

$$\text{Max}\left(\sum_{i=1}^{nh} \text{Fitness}(\text{Herd}(i)) \right) \tag{10}$$

where:

$$\text{Fitness}(\text{Herd}(i)) = \sum_{i=1}^{ni} \text{Fitness}(\text{Elk}(j));$$

$$\text{Fitness}(\text{Elk}(j)) = \text{Body Mass}(\text{Elk}(j));$$

nh = number of herds; and

ni = number of individuals in a herd (herd size).

Changes in body mass are calculated from the bioenergetic requirements of elk and available forage (Turner *et al.* 1994). Bioenergetic requirements are based on the need to support existing body mass (a function of age, gender and size) and the energy needed for travel (a function of distance traveled, topography, and snow conditions). Available forage is a function of biomass at the beginning of the simulation (estimated from satellite imagery), consumption by elk agents, and snow cover. Elk agents were subjected to the snow conditions associated with the 1996/1997 winter, a particularly harsh winter. As these agents interact with the landscape, they make decisions about whether to forage or migrate based on the change in habitat quality, their current location, and their decision matrices. Movement decisions were based on the rules documented in sections 3.2.3 and 3.2.4.

4.2 *Learning migratory paths (the value of w_{ij})*

Spatial knowledge, stored in cognitive maps represented as directed weighted graphs (section 3.2.1), is learned by mimicking the behaviour of successful elk (e.g. the lead elk in a cow/calf herd), the reinforcement of successful paths, and exploration. At the beginning of the simulation, it is assumed that elk have no spatial knowledge (e.g. they are relocated to a new region); the weights on all edges in a cognitive map are initialized to 0. The goal is to maximize elk fitness by learning an optimal set of edge weights (w_{ij}).

4.2.1 Learning paths through observation and mimicry. Without observation and mimicry, the knowledge-base of each elk would be limited to its own experiences. Successful cognitive maps are communicated to and mimicked by simulated elk in two ways. First, all elk in the same herd share a common cognitive map. This replicates a process by which spatial knowledge is passed down through successive generations as calves follow cows across the landscape. Second, an EA is used to identify and evolve migratory paths that lead to high end-of-winter fitness. Selection and recombination within this EA act as a form of communication and mimicry by distributing knowledge of successful paths throughout the population. The chromosome to be operated on comprises the set of edge weights that represents the cognitive maps of cow/calf herds (i.e. each allele represents an edge that connects landscape patches). During each generation in the EA, simulated elk attempt to migrate from summer to winter range over the time frame of November to April. The objective was to maximize end-of-winter body mass at the population level. At each time step, elk use spatial memory, environmental information, and the decision rules described in section 4.1 to make movement and foraging decisions.

We use intermediate recombination to produce the next generation of solutions. Intermediate recombination, also referred to as weighted crossover, is implemented as follows:

Let $W(G_1)$ and $W(G_2)$ be two selected chromosomes and $W(G_3)$ the new chromosome to be generated. According to intermediate recombination:

$$W(G_3) = r * W(G_1) + (1-r) * W(G_2) \tag{11}$$

where r ($r \in [0, 1]$) is a constant used to adjust the contribution of parent chromosomes $W(G_1)$ and $W(G_2)$ to the offspring chromosome $W(G_3)$.

The value of r is set at 0.5 in our model, and so the value of each allele in the child solution is the mean of the two parent solutions. Rank-based selection and elitism (gap size equals 0.9) are used to determine the set of solutions that is used to produce offspring. The algorithm was allowed to run for 100 generations.

Unlike most implementations of EAs, each allele in our model can have value both as an independent connection between two patches and as an element in a set of alleles that represents a successful path. The weights associated with a set of connected edges that forms a path should, therefore, be strongly correlated. Traditional EA implementations will have difficulty evolving this kind of structure in chromosomes. Mutation, in particular, is problematic because it introduces noise that would disconnect useful edges and inhibit convergence toward a solution. To address this issue we introduce Hebbian learning into the EA algorithm and implement mutation as a phenotypic (rather than genotypic) response to system state.

4.2.2 Reinforcing successful paths through Hebbian learning. We apply Hebbian learning to reinforce (or penalize) all edges in a given path proportionately to the fitness of the associated elk at the end of the winter migration (i.e. after each generation in the EA). Recall that each vertex v_i in an elk's cognitive map can be viewed as a place cell, and each edge e_{ij} the synapse that links place cell i to place cell j. Now, let path P_k be defined as the set of all vertices V_p and edges E_p traversed by elk k during one generation. Given place cells v_i and v_j, and synapse e_{ij}, we can formulate the learning process as follows:

$$\delta w_{ij|t} = \begin{cases} \eta_1 * a_{i|t} * a_{j|t} & \text{if } v_i \in V_p \text{ and } v_j \in V_p \\ -\eta_2 * a_{i|t} * a_{j|t} & \text{if } v_i \in V_p \text{ and } v_j \notin V_p \\ 0 & \text{if } v_i \notin V_p \text{ and } v_j \notin V_p \end{cases} \quad (12)$$

where $\delta w_{ij|t}$ is the change in the weight of edge e_{ij} at time t; η_1 is a learning rate that determines how quickly δw_{ij} increases in response to positive (Hebbian) reinforcement ($0 <= \eta_1 <= 1$); η_2 is a discount rate that determines how quickly δw_{ij} decreases in response to negative (inhibition) reinforcement ($-1 <= \eta_2 <= 0$); and $a_{i|t}$ and $a_{j|t}$ are the activity states of neurons v_i and v_j at time t.

The activity state of a neuron is a function of elk fitness:

$$a_{i|t} = a_{j|t} = f\left(\text{Fitness}\left(\text{Elk}_{k|t}\right)\right)^\alpha \quad (13)$$

This process rewards edges that comprise paths that are associated with high end-of-winter fitness values and penalizes those associated with low fitness values. We assume that the relation between synaptic weight and elk fitness should be approximately linear and, thus, set α to 0.5 (equation (12)).

4.2.3 Exploration through stochastic phenotypic response. Adaptation cannot occur without exploration. The traditional EA method to promote exploration in the solution space is to randomly mutate the values of alleles in chromosomes. As suggested above, this introduces noise that disconnects useful edges that form migratory paths. Without mutation, however, EAs are likely to converge prematurely to local optima. To encourage exploration without the deleterious effects of random mutation, we perturb the phenotypic expression of the genotype, rather than the genotype itself. This is accomplished by allowing elk to respond stochastically to environmental stimuli (equations (4) and (5)). If these perturbations from more established paths prove to be successful, they will be reinforced through selection and Hebbian learning. By adding a stochastic component to movement behaviour, we also account for the imperfect perceptual abilities of elk, environmental factors that are not explicitly modelled, and decision-making error.

5. Results and discussion

We simulated elk migratory behaviour using snow and vegetation data for 1996/1997. Vegetation biomass was estimated using an empirical model that regressed field data against data derived from Landsat imagery (Crabtree unpublished data), and snow cover was estimated using the Yellowstone Snow Model (Farnes *et al.* 1999). The results of the when-to-migrate model are presented in figures 5 and 6. From these graphs, we see that simulated elk behaviour changes abruptly as habitat quality drops from 0.7 to 0.6; the weight on migration (w_{mig}) quickly rises above one, indicating a sudden and strong migratory response. A habitat quality of zero is
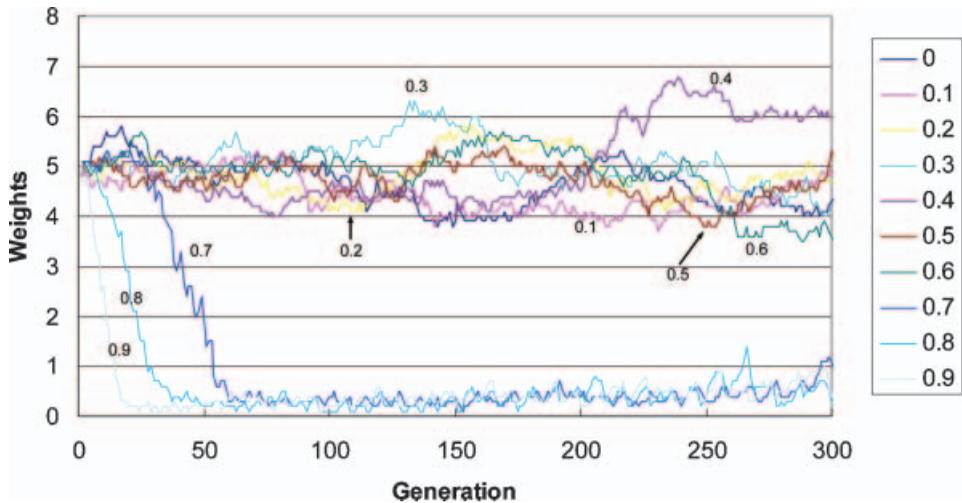
Figure 5. Learned weights for migration (w_{mig}) given habitat quality over generations. The EA converges in approximately 75 generations. As weights rise above 1, migration becomes increasingly probable. This graph suggests that agents learn to respond very differently to environmental change as habitat quality drops below 0.7.

associated with the most SWE elk tolerate—about 40 cm (Turner *et al.* 1994). Therefore, a habitat quality index of 0.6 is equal to 16 cm SWE $(1-0.6) * 40$. Assuming a snow density of 0.4, the simulated elk learned to migrate when snow depth exceeded 40 cm (results suggest that the model is relatively insensitive to assumptions about snow density). Sweeney and Sweeney (1984) noted that 40 cm produced migration movement in Colorado. Turner *et al.* (1994: 482) working in YNP, and citing Parker *et al.* (1984) and Sweeney and Sweeney (1984), stated that: '… free ranging herds are generally restricted in distribution by snow depths >46 cm'. While these results look promising, it should be noted that there is variability in the reported snow depths associated with migration. Rudd *et al.* (1983), for example, stated that some elk in YNP began to migrate at 20 cm. Furthermore, there is uncertainty in our estimates of many model parameters. Even
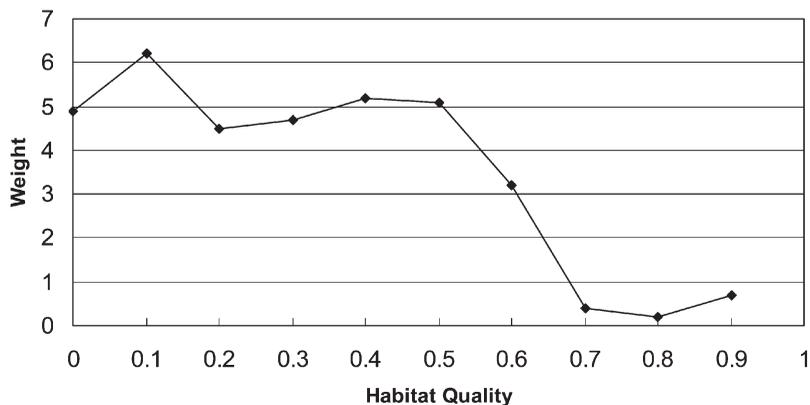
Figure 6. Profile of learned weights for migration (w_{mig}) over habitat quality. Elk learn to migrate when habitat quality drops to 0.6.

so, these results suggest that intentional agents can learn a realistic response to changing environmental conditions.

5.1 *Where to migrate*

We investigated the relationship between spatial behaviour and bounded spatial knowledge by altering the way the initial elk population is distributed across the landscape. We began by distributing 500 elk randomly across the landscape parameterized to reflect the 1996/1997 winter conditions. The results of this experiment are presented in figure 7. Edges in this cognitive map represent the maximally weighted outwardly directed edge (i.e. the outwardly directed edge associated the maximum mean weight) from each vertex. We see clearly defined routes in logical locations. Biomass consumed, represented in blue, provides a useful visualization of the cumulative effect of migratory decisions. In figure 8, we see that the final positions of elk match the available 1995 elk count data reasonably well. Note that this comparison between observed and simulated patterns is preliminary because we are not simulating the entire migratory range, and we do not know the initial locations of elk. As a proof-of-concept, however, we find these results promising. The winter kill rate for cows for the harsh winter of 1996/1997 was 20%, and 30% of the calves died. Winter kill rates reported in the literature for nearby herds compare favourably with these simulated values (Turner *et al.* 1994, Garrott *et al.* 2003). While these published data are not directly comparable with our simulated results, the fact that they do compare well provides us with some level of confidence that our model is performing well.

5.2 *Evaluation*

The stated objective of this paper is to present an approach for the representation of spatially aware mobile agents. To provide context to this work, we applied our ideas to the simulation of elk migratory behaviour. It is beyond the scope of this paper to fully investigate the ability of the resulting model to replicate real-world processes. It is important, however, to evaluate the degree to which the simulation model produces consistent and logical results. To conduct this evaluation, we ran three experiments.

5.2.1 Experiment 1: Model stability. The first experiment was designed to assess the effect of stochastic behaviour on simulation results. The 'where to migrate' simulation was run 100 times without changing model parameters or input data. Two outcomes were expected. First, model results would be stable at the aggregate level (i.e. there would be little difference in general migratory patterns). Second, variability in model results would be greatest in those portions of the landscape that were explored least by elk agents (e.g. higher elevations and areas with low biomass). A composite cognitive map was produced by calculating the mean weight for all edges in 100 runs. Figure 9 illustrates maximal outwardly directed edges of the composite map. The overall structure of the resulting migratory paths is very similar to the paths illustrated in figure 7. For each vertex in the graph, we calculated the number of times that the maximal edge of an individual run was the same as the maximal edge of the composite map. The results of this calculation were mapped to visualize variability in path selection across space (figure 10(a)); high values suggest that elk tend to travel in exactly the same direction from one vertex to the next, low values suggest significant variability in edge selection. In figure 10(b), we present the results of a similar analysis,
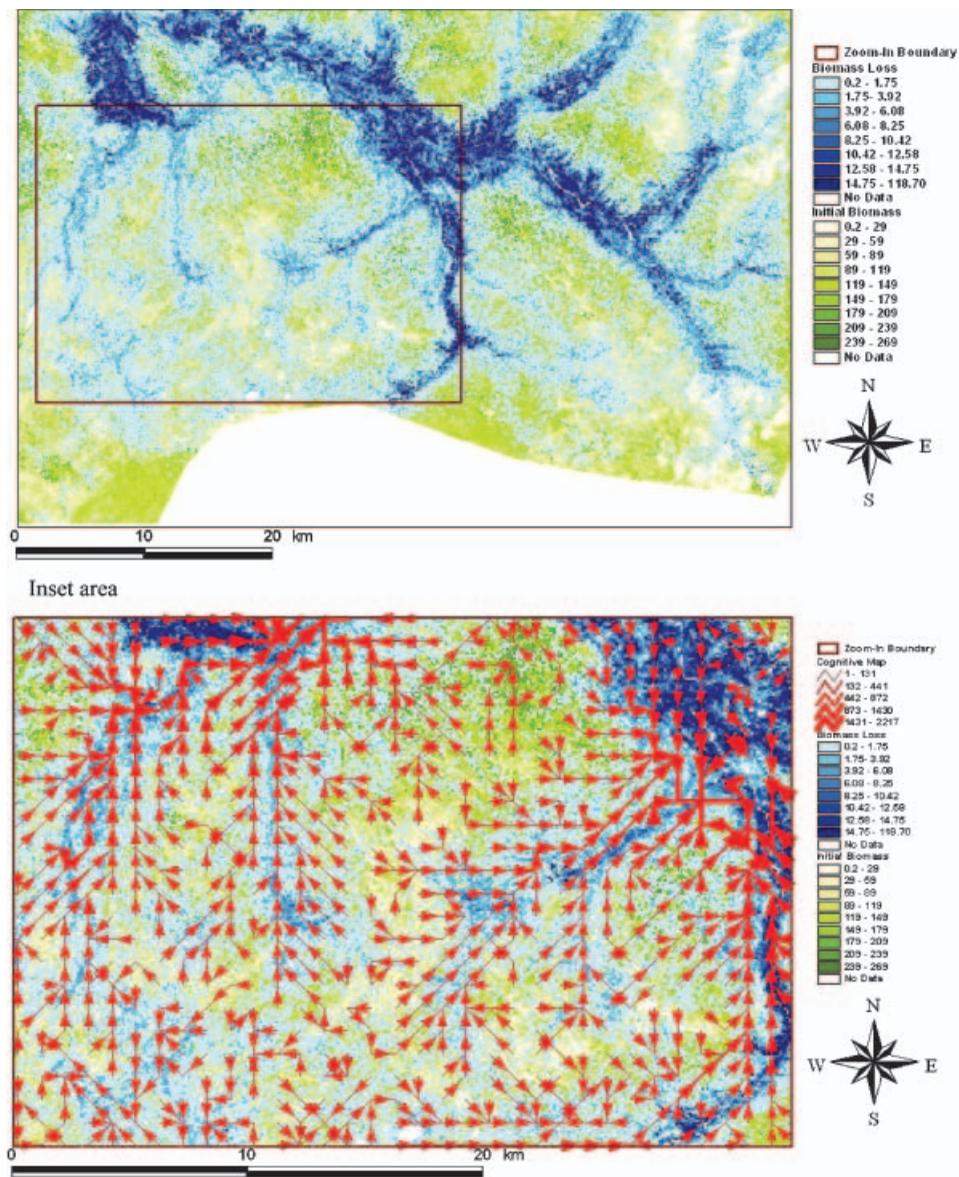
Figure 7.   Results of a single simulated migration. The spatial distribution of elk at time t_o was random. The top map represents total biomass foraged (in blue) from November to April and is representative of cumulative migration patterns. The bottom map represents the cognitive map that produced these results. Edges represent the maximally weighted outwardly directed edge from each vertex. The background layer (green) is initial biomass.

but in this case we look for a tendency for elk to travel the same general direction by including in the calculation edges that are adjacent to the maximal edge of the composite map (e.g. if the edge from the composite map runs north, the edges from individual maps that run north, northeast, or northwest will also be included). As expected, figures 7, 9, and 10 suggest that the overall structure of migratory paths remains relatively stable, and stability increases in those areas most travelled.
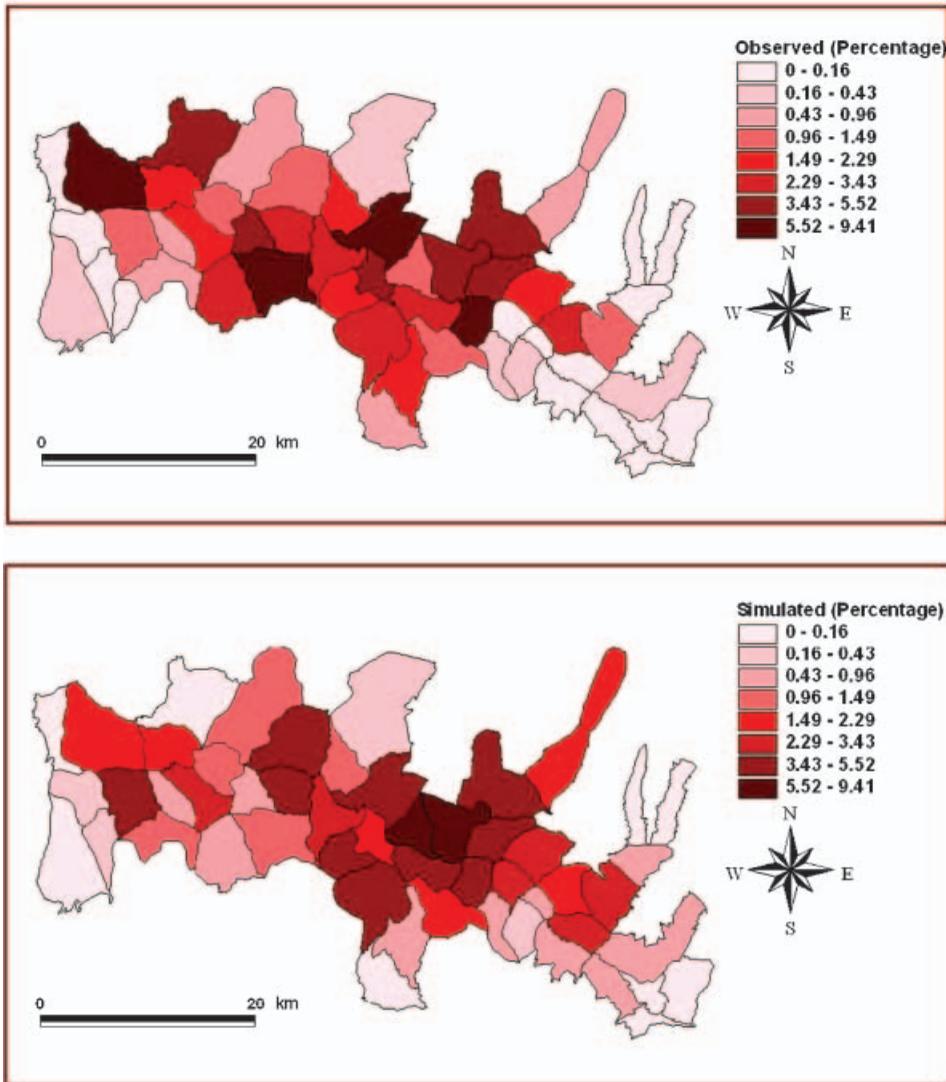
Figure 8.   Simulated pattern of elk compared with 1995/1996 elk count data (1996/1997 data were unavailable).

5.2.2   Experiment 2. Bounded knowledge. The simulation results presented in section 5.1 were based on an assumption of complete communication among elk cow/calves herds (i.e. knowledge is shared among all herds). In reality, this level of communication, and the resulting knowledgebase of elk, is likely to be more limited. We would assume, for example, that an elk's spatial memory would become less accurate and more uncertain the farther it gets from its summer range and from well-travelled migratory paths. Bounded spatial knowledge leads to uncertainty as organisms move away from core areas. To investigate this assumption, we reran the simulation presented in section 5.1 with the initial distribution of elk constrained to a single patch (location A). Elk spread out in search of forage until heavy snowfalls begin, then they start their migration. Figure 11 illustrates the results of this
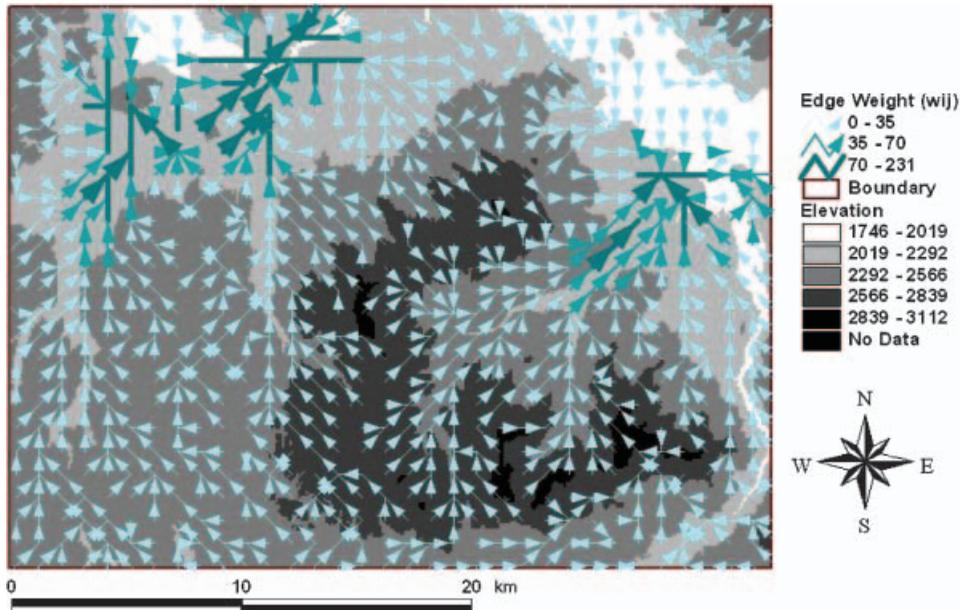
Figure 9. Composite cognitive map produced by calculating the mean edge weight of 100 simulations. A comparison between this map and that depicted in Figure 7 suggests that at the macro-scale, stochastic behavior has little impact on results (the learning algorithms are stable).

simulation. We see from this map that the paths taken by elk who start their migration near to their home patch (i.e. in well-explored territory near location A in figure 11) are more direct and, thus, efficient than those taken by elk who begin their migration farther away (i.e. in less well-explored territory, location B in figure 11). The utility of frequently explored routes near an elk's summer range was better known than equally good (compare with figure 7) but more distant routes. Bounded knowledge and adaptation to spatial heterogeneity helps explain the diversity of migratory behaviour exhibited by real elk herds. Furthermore, the reuse of known winter and summer ranges, behaviour that may be deemed sub-optimal given rational choice theory, may be appropriate given uncertainty and bounded knowledge.

5.2.3 Experiment 3. Stimulus. We hypothesized that cognitive maps would become more highly structured as the strength of stimuli increased. To test this hypothesis, we executed a series of five simulations where snow depth was systematically reduced to 50% of the 1996/1997 winter depth in 10% steps. According to our hypothesis, lower snow depths (lower stimuli) should produce cognitive maps with less structure than higher snow depths. The results of the original 1996/97 run and the 50% run are presented side by side in figure 12. A comparison of these two cognitive maps illustrates that there is, in fact, less spatial structure at the 50% level; this is particularly apparent in the two circular zones indicated on the map. The low snow cognitive map is also associated with significantly lower edge weights suggesting greater variance in the movement decisions of individual elk agents. A comparison of all maps suggests that the cognitive maps of elk begin to show significant organizational structure at around the 80% level. While these results are

(*a*)

(*b*)
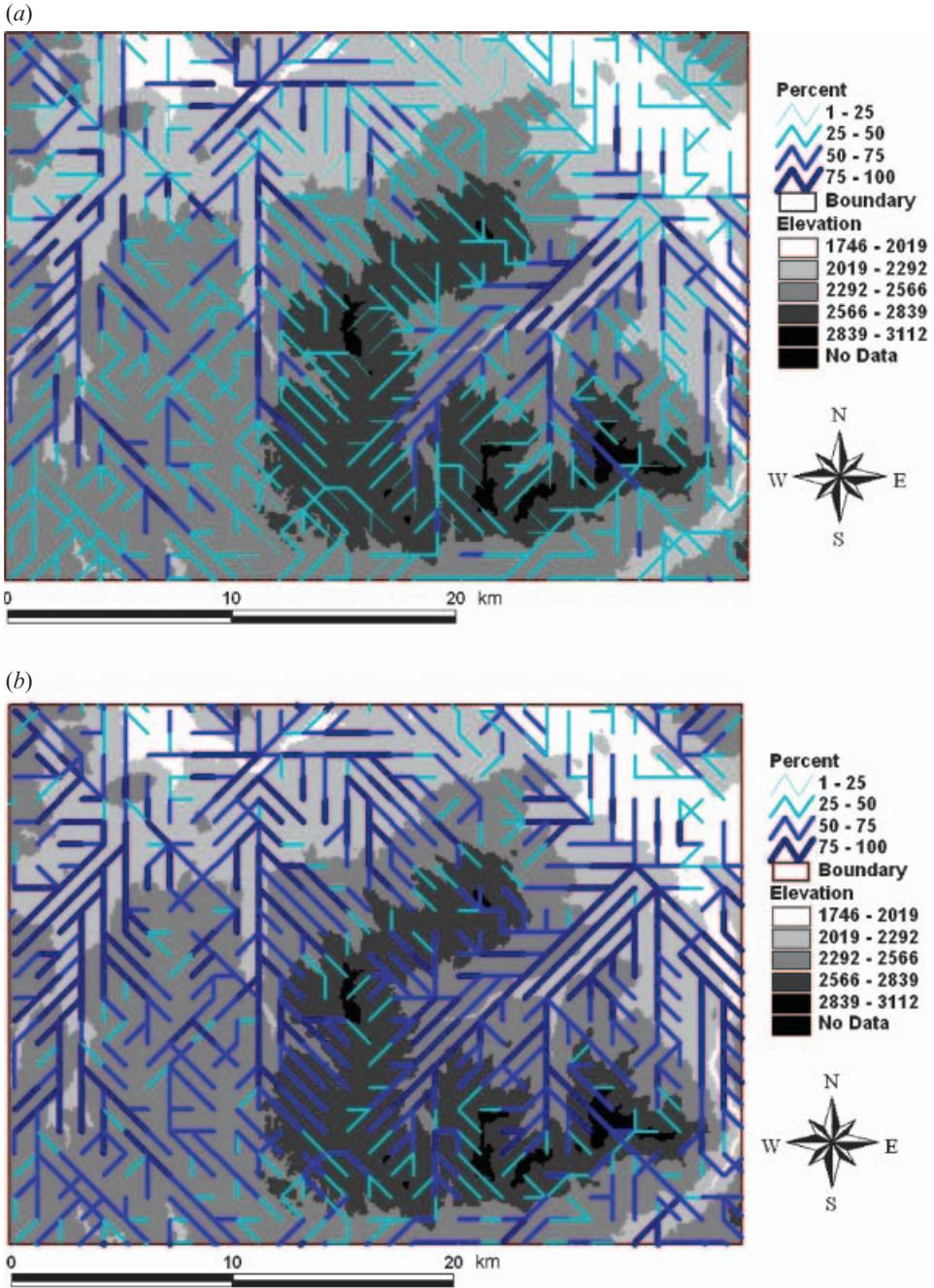
Figure 10. These maps depicts the stability of edge-specific results. In (*a*), edges are symbolized by the number of times that the maximal edge of an individual run, in the 100 run series, is exactly the same as the maximal edge of the composite map (animals will tend to move in exactly the same direction). In (*b*), adjacent edges are included (animals will tend to move in the same general direction).
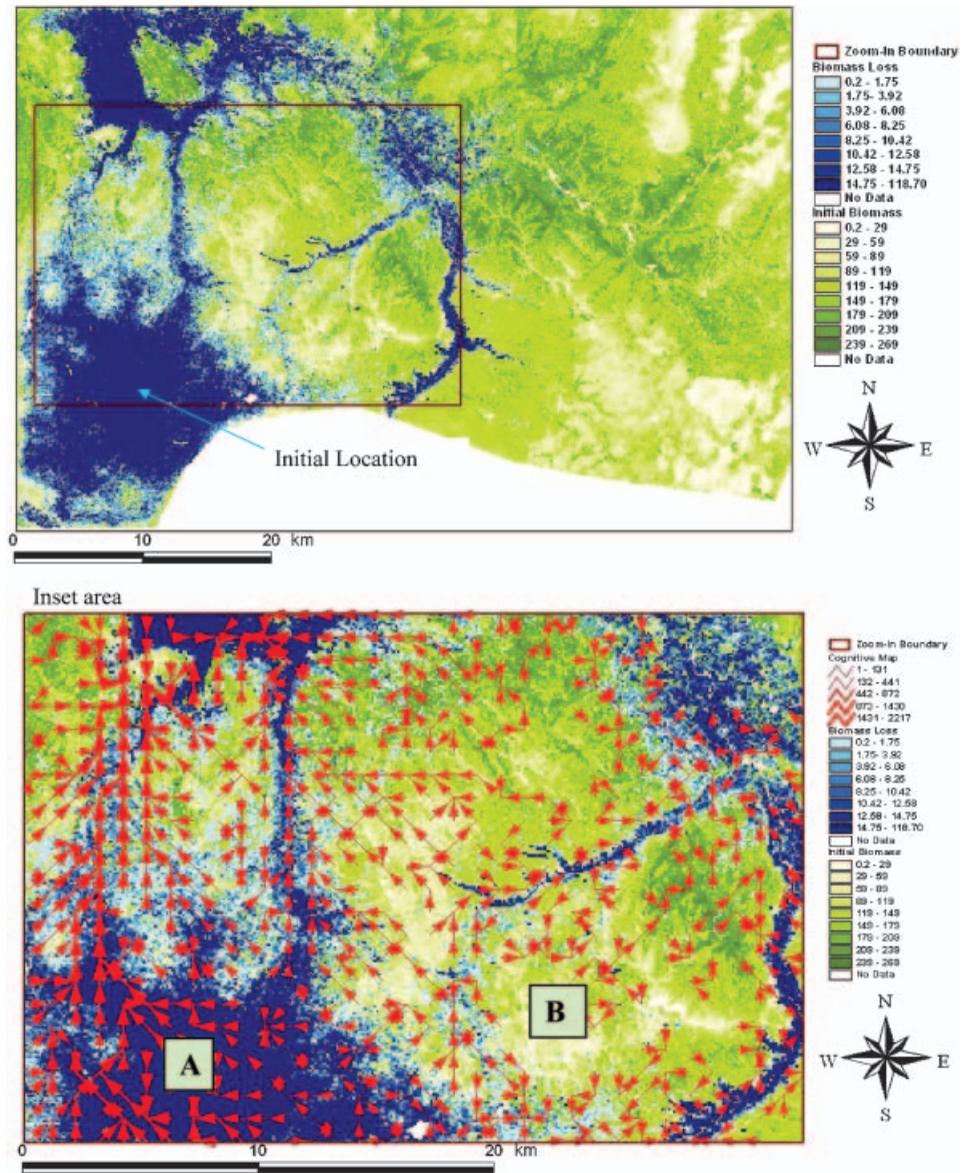
Figure 11. Results of simulated migration—elk initially located in a single patch. The top map represents total biomass foraged (in blue) from November to April and is representative of cumulative migration patterns. The bottom map represents the cognitive map that produced these results. The background layer (green) is initial biomass. Elk migrate more efficiently from well-explored areas near their 'home' patch.

qualitative, they do suggest a nonlinear behavioural response to environmental stimuli.

6. Future research

Our work to date has explored alternative ways of representing spatial memory, learning, and behaviour in mobile virtual agents. Although additional validation

(*a*)
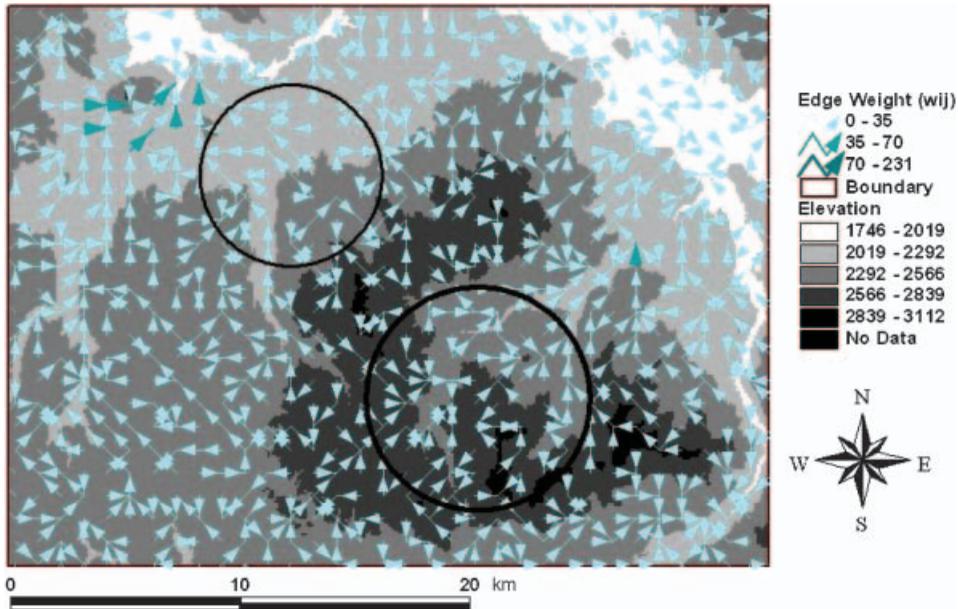
(*b*)
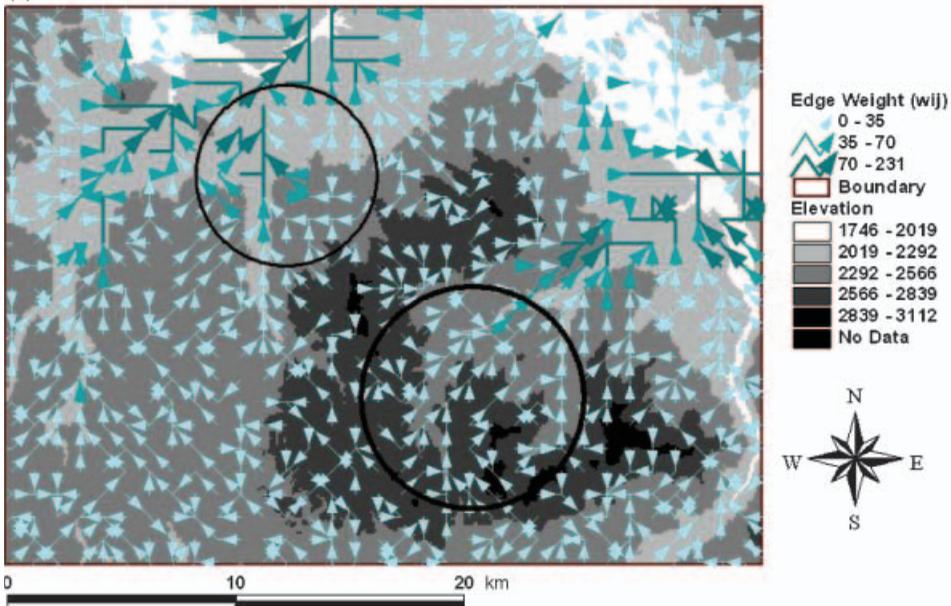
Figure 12. Learned patterns become more highly structured as the stimulus becomes stronger. The migratory paths produced by elk agents exposed to low snowfall levels (*a*) are less well developed than those produced by elk exposed to high snowfall levels (*b*).

work is needed, the initial results suggest that such agents can, in fact, learn realistic spatial behaviour. Current and future work will focus on refining this model and using it to help study ecosystem dynamics in Yellowstone's northern elk winter range. Two issues are of particular interest.

First, we began by suggesting that existing agent-based models of mobile entities can be placed into context by considering what agents know about the spatial and temporal patterns of resources and threats. A continuum exists with mechanistic (stimulus/response) models on one end and omniscient models at the other. Our work is placed somewhere in the middle of this continuum, which we believe represents reality. Exactly where reality exists in this middle range is difficult, perhaps even impossible, to know. We can, however, begin to simulate the response of elk to different assumptions about the 'boundedness' of their knowledge and cognitive abilities, and compare these results with real-world data. These kinds of sensitivity tests are currently under way.

Second, the model results presented in this paper represent a pre-wolf, park-interior state (i.e. no predation by wolves and humans). Current work is focused on building a realistic representation of predation. Once this component is added, we hope to use the model to help extend ongoing discussions about trophic cascades by including considerations of human impacts on land use and management.

7. Conclusions

Over the past decade, spatially explicit agent-based models have been the focus of considerable research, and significant progress has been made in a few key areas (e.g. resource utilization and land-use/land-cover change). These models are often built to help scientists understand how systems adapt to changing environmental systems. However, relatively little attention has been paid to how agents learn, store, and use spatial knowledge to make decisions. We argue that the simulation of such processes is crucial to the representation of adaptive agents that respond to changing environment conditions, or to other agents, in realistic ways. In this paper, we address this issue by constructing a model of adaptive, spatially aware, and mobile agents. To motivate this work, we consider how the migratory behaviour of elk in Yellowstone's northern elk range adapts to changes in land cover and resource-management strategies. Elk agents are designed to learn about and adapt to changing environments through repeated interaction with a digital representation of the northern range. They gain knowledge about the spatial location of resources and threats and develop migratory behaviours that help them survive the winter season. The learning procedures used here are based on evolutionary algorithms and Hebbian learning.

Learned behaviour is used to simulate elk migratory behaviour. To evaluate the ability of the MAS to mimic real-world patterns we compared the conditions under which migration began, location of elk at the end of the simulation, and winter mortality rates with published data. The simulated results compared favourably with these data. While much work remains to be done in the representation of spatially cognizant agents, these promising results suggest that MAS, built from adaptive, spatially aware, and mobile agents, can be used to help explore complex responses to changing environmental conditions.

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