AN AGENT-BASED SIMULATION OF YELLOWSTONE'S NORTHERN RANGE ELK HERD: A COGNITIVE APPROACH

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INTRODUCTION

Over the past 150 years Yellowstone's northern range has experienced significant change. A patch-work of ownership patterns and management strategies has been overlaid onto what was a highly integrated ecosystem, wolves were extirpated and then reintroduced, and land cover patterns evolved to serve human interests. Throughout this time elk (*Cervus elaphus*) had to adapt to survive. These adaptations have fundamentally changed the migratory behavior of elk in this region (Houston, 1982, Boyce, 1989). In this research we explore how and why elk adapt their migratory behavior in response to landscape change. Changes in behavior are modeled using realistic assumptions about elk learning and decision-making strategies. We then use this model to evaluate whether hypothesized changes in elk behavior represent a rational response to environmental change given bounded knowledge and limited problem solving capabilities.

Animal migration is a complex spatial behavior adapted to cyclical changes in habitat or environment (Baker, 1978). Past attempts to model elk migration assumed that elk responded mechanistically to local stimuli (Turner et al. 1994) or behaved optimally with complete knowledge of important state variables (Noonburg et al. in review). Field studies suggest that the truth falls somewhere between these two extremes (Pearson et al, 1995). Migration is an adaptive behavior that emerges from long term interaction with the environment (Baker,1978, Houston and McNamara, 1999) and, as such can be viewed as a self-organized response to ecosystem dynamics (Levin,1998, Malanson, 1999). Evidence suggests that the kinds of spatial memory needed to support migration are deeply rooted in the hippocampus (O'Keefe,1978, Muller et al, 1996) and that this portion of the brain plays an important role in how animals adapt to and learn from spatially contextualized experiences (Laca,1998, Dumont and Hill, 2001). More specifically, neurons in the hippocampus (referred to as place cells) fire when an animal enters into a previously visited geographic space (referred to as place fields). Repeated interaction, both positive and negative, reinforces links between these cells and increases the magnitude of the response produced by subsequent visits to a location. While the exact mechanism is not yet understood, research has shown that place cells are used by animals (including humans) to navigate through heterogeneous landscapes (O'Keefe, 1978, Muller et al, 1996, Jacobs, 2003). Muller et al. (1996) illustrated how a network of hippocampal place cells can be encoded as a weighted graph to model spatial memory and spatial learning. We develop a similar approach to the simulation of elk migratory behavior in an attempt to fill the conceptual space between mechanistic response and optimal decision-making.

METHODS

Elk are simulated as agents in a multi-agent system (Ferber, 1999, Janssen, 2002, Bousquet and Page, 2004). Each elk is characterized by a collection of state variables and biophysical functions (e.g. bioenergetics) (Turner et al., 1994). Elk are aggregated into cow/calf herds comprised of a group of individuals, Yellowstone's northern range elk herd is comprised of many spatially dispersed cow/calf herds. Movement decisions are driven by the collective influences of an elk's current state, environmental variables (e.g., available forage and snow depth), short-term working memory, and long-term reference memory (Kitchin and Blades, 2002). Field observations suggest that elk migratory behavior responds to large-scale landscape patterns (Pearson et al., 1995). To represent these patterns we used isodata classification to produce generalized patches from high-resolution vegetation data. While patch-scale patterns may drive migratory behavior, finer scale spatial patterns of food and snow directs local movement and foraging behavior. Elk decision-making, therefore, depends on local and landscape level characteristics stored in short (working) and long (reference) term memory.

In this research, reference memory is restricted to spatial memory. Following Muller et al. (1996), the patch structure extracted from the vegetation pattern is captured as a bidirected graph representing the spatial memory of the elk. Nodes in the graph are located at patch centroids as landmarks and correspond to place cells in the elk's spatial memory. Patches represent place fields. An edge in this graph corresponds to a directed movement from one place field to another. Each node produces an attractive or repulsive force. Elk, for example, are pulled across edges to areas that are expected to have high levels of food and pushed across edges from areas that typically have deep snow. The magnitude of these intercellular forces are stored with the edge and used to guide large-scale movement decisions during migration. This spatial memory is held in common at the cow/calf herd level and guides landscape-scale movement during mirgration. The working memory of an elk is modeled by recording its most recently visited locations and by "sensing" the state of environmental variables within its perceptual range. Working memory determines the specific path taken through an environment and, thus, the amount of forage available to the elk. A 1ha grid is used to capture these local-scale movements. This high spatial resolution together with the rate at which an elk can travel, necessitated a 10 minute time step (Martin,1993,). The decision to migrate or not is based on snow depth (Rudd et al., 1983, Sweeney and Sweeney, 1984).

A spatial memory reflecting the pattern of successful migratory routes is produced using an evolutionary algorithm (Goldberg, 1989). The chromosomes manipulated by this algorithm are representative of the strength of attraction or repulsion associated with the directed edges that link place cells in spatial memory, which is distributed among herd groups. The fitness value is a function of biological indicators associated with the elk (e.g., elk body mass) and the characteristic of migration routes (e.g., total movement distance). Elk agents are routed through the landscape guided by spatial memory (edge strength). Edges on paths that lead to high end of winter fitness are reinforced, those that lead to low end of winter fitness are penalized.

Alternative scenarios were run to examine the learning performance of the simulation model. Scenarios employed different patch patterns (e.g., patches produced from cluster analysis or raster surfaces), connectivity rules (e.g., neighborhood or small-world rules (Watts and Strogatz, 1998)), and herd distributions.

RESULTS AND CONCLUSIONS

The migration routes learned using a graph-based representation of spatial memory and an evolutionary algorithm produced realistic migration patterns that adapted to changing environmental conditions. Simulated elk gained a solid (but decidedly bounded) understanding of their environment and made rational decisions given available data and simulated experiences. The utility of frequently explored routes near an elk's summer range was better known than more distant routes. Adaptation to spatial heterogeneity and bounded knowledge help to explain the diversity of migratory behavior exhibited by elk herds.

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