Review

The role of agent-based models in wildlife ecology and management

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ABSTRACT

Conservation planning of critical habitats for wildlife species at risk is a priority topic that requires the knowledge of how animals select and use their habitat, and how they respond to future developmental changes in their environment. This paper explores the role of a habitat-modeling methodological approach, agent-based modeling, which we advocate as a promising approach for ecological research. Agent-based models (ABMs) are capable of simultaneously distinguishing animal densities from habitat quality, can explicitly represent the environment and its dynamism, can accommodate spatial patterns of inter- and intra-species mechanisms, and can explore feedbacks and adaptations inherent in these systems. ABMs comprise autonomous, individual entities; each with dynamic, adaptive behaviors and heterogeneous characteristics that interact with each other and with their environment. These interactions result in emergent outcomes that can be used to quantitatively examine critical habitats from the individual- to population-level. ABMs can also explore how wildlife will respond to potential changes in environmental conditions, since they can readily incorporate adaptive animal-movement ecology in a changing landscape. This paper describes the necessary elements of an ABM developed specifically for understanding wildlife habitat selection, reviews the current empirical literature on ABMs in wildlife ecology and management, and evaluates the current and future roles these ABMs can play, specifically with regards to scenario planning of designated critical habitats.

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Contents

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1. Introduction

Wildlife species are under tremendous pressure from both natural and anthropogenic influences, including climate change, pollution, and habitat loss and fragmentation. Identification and protection of critical habitats is central to the management of species at risk, and the need to designate habitats as critical for species persistence is universally recognized by scientists, resource managers, and the general public. However, critical habitat designations will be challenged if they affect stakeholders who bear the lost opportunity costs of economic activity (Rosenfeld and Hatfield, 2006). As a result, political decision-makers involved in conservation planning of critical habitats face difficult challenges when it comes to balancing economic development and the maintenance of a healthy environment.

Conservation planning is the process of locating, configuring, implementing and maintaining areas that are managed to promote the persistence of biodiversity (Margules and Pressey, 2000). Effective conservation planning also acknowledges the complexity imposed by dynamic updating of priorities for both biodiversity patterns and processes as decisions are made. For instance, anticipated changes to species distributions in response to environmental and/or landscape change will influence decisions about conservation design (Pressey et al., 2007). Scenario planning is one important component of conservation planning, and is necessary for assisting the development of knowledge and planning tools required by managers and decision makers. A technique for making decisions in the face of uncontrollable, irreducible uncertainty, scenario planning offers managers a method for creating more resilient conservation policies by considering multiple possible futures, both socio-economic and ecological (Peterson et al., 2003). Benefits of using scenario planning include increased understanding of key uncertainties, the incorporation of alternative perspectives into conservation planning, and greater resilience of decisions to surprise. This approach has direct implication for the process of delineating critical habitats for species at risk, since in addition to determining wildlife habitat space and usage, conservation planning of wildlife habitats also involves the analysis of future habitat-linked population demographics under various land-use development scenarios.

To better inform management in the determination of critical habitat, wildlife research has long focused on understanding wildlife use of habitats and, when combined with the availability of resources, what animals select and avoid on the landscape, and how, and why they select the features that they do (Morris et al., 2008). Specifically, information on the wildlife's adaptive behaviors of habitat selection, movement ecology, and its responses to a dynamic environment are integral to successful conservation and scenario planning. For instance, an examination of the underlying processes and mechanisms of habitat-selection by the individual will provide the ability to distinguish habitat use based on adaptive preferences, maladaptive preferences (ecological traps), or non-ideal habitat selection (i.e., the fitness consequences of habitat selection; for an example see Arlt and Pärt, 2007). This distinction is of considerable value in the ranking of habitat types for conservation planning. Next, the movement ecology of the organism, which includes the internal state, motion capacity, and navigation capacity of the individual, provides insight into how wildlife

are affected by matrix heterogeneity, and can generate emergent properties that improve our understanding of the demographics of stochastic, spatially structured populations (Revilla and Wiegand, 2008). Because the dynamic nature of the environment plays such an influential role in affecting organism state, behavioral decisions, and motion, a representation of the animal's actual environment in a spatially explicit manner in habitat modeling can improve the effectiveness of conservation planning, since it can highlight the causal links between organism movement and environmental change (Nathan et al., 2008). Finally, the capacity to accommodate the dynamism of the environment, the spatial patterns of inter- and intra-species mechanisms, and the feedbacks and adaptations inherent in these systems can allow one to explore how animals will respond to and be affected by future and novel changes in their landscape, which is an essential criterion for scenario planning.

Management of wildlife therefore requires the stewardship and/or conservation of cognizant and adaptive individuals that interact with one another and their environment, the combination of which comprises very diverse and dynamic populations. It is this diversity and dynamic nature that makes populations robust and capable of handling perturbations in environmental conditions, and therefore this information should not be overlooked. What is needed is a thorough understanding of the individual behaviors and motivations of wildlife involved in habitat selection and use, and the ability to utilize and project these fitness-maximizing decision and movement rules in a spatio-temporal context to assess how animals will respond to future changes in their environment. A range of habitat models are available and are capable of addressing one or more of these issues independently or in concert; for instance, resource-selection models (e.g., Johnson et al., 2004), dynamic optimization models (e.g., Chubaty et al., 2009), and population-level land-use change models (e.g., Copeland et al., 2009), to name but a few. Our intent is not to conduct a systematic comparison of each approach as they often complement, as opposed to supersede one another. Rather, we review here a further methodology that can accommodate spatio-ecological information, and which links detailed knowledge of animal behavior and movement with explicit and dynamic environment variables: agent-based modeling.

Agent-based models (ABMs) are computational simulation tools cable of incorporating intelligence, by combining elements of learning, adaptation, evolution, and fuzzy logic. Specifically, ABMs rely on a bottom-up approach that begins by explicitly considering the components of a system (i.e., individual agents) and tries to understand how the system's properties emerge from the interactions among these components (Grimm, 1999; Grimm et al., 2005). A community of agents acts independently of any controlling intelligence, they are goal-driven and try to fulfill specific objectives, they are aware of and can respond to changes in their environment, they can move within that environment, and they can be designed to learn and adapt their state and behavior in response to stimuli from other agents and their environment. This emphasis on interactions between agents and their environment is what distinguishes agent-based modeling (also referred to as individual-based models) from other systemic modeling approaches (Marceau, 2008).

Over the past fifteen years, ABMs have been applied to address a broad range of issues related to environmental resource management, such as water, forest, and agro-ecosystem management

(see review by Bousquet and Le Page, 2004). ABMs have also been extensively used in ecology to study species relationships, population dynamics, and to understand how animals perceive, learn and adapt to their environment (DeAngelis and Mooij, 2005). Recently, ABMs have begun being used cross-disciplinarily to address human-wildlife interactions and their management (An et al., 2005; Anwar et al., 2007). The recent proliferation of ABMs in ecological applications and specifically in the realm of animal movement and behavior (Wang and Grimm, 2007; Stillman, 2008) suggests they could play a key role in understanding habitat selection and use for conservation planning. Further, the ability for ABMs to incorporate dynamic representations of the environment through cellular automata (CA) also suggests a critical function for these models when it comes to future-scenario development and implementation of management strategies.

Due to the identifiable need in wildlife ecology and management for the inclusion of individuality of wildlife species as adaptive, responsive entities, the use of an ABM as a tool for management is advantageous: dynamic interplay between agents is readily accommodated, realistic environmental conditions can be approximated, and hypothetical scenarios can be simulated. An ABM specifically developed for use in the determination of critical habitat is one that explicitly incorporates individual fitness-seeking behaviors of animal movement in a spatially-realistic representation of the environment that is then subjected to alternate scenarios of land-use development.

This paper explores the role of ABMs in wildlife habitat selection for the purpose of unifying different fields of study (i.e., behavioral ecology, animal-movement ecology, geographical information science, and computational intelligence) into a cohesive realm for the benefit of wildlife conservation planning, emphasizing the need for a multi-disciplinary approach. It is aimed specifically at those in the disciplines of behavioral ecology, animal-movement ecology, geography, and geocomputation, as well as on-site managers and decision makers responsible for the management and conservation of wildlife and wildlife habitat. Increasingly, wildlife-management is becoming more multidisciplinary in nature and marked by an increase in stakeholder participation as it moves away from the near exclusive reliance on biological science and decision-making by so-called experts (Riley et al., 2002). ABMs are an excellent tool for wildlife-management, since they allow for the integration of expertise from multiple disciplines, as well as the interests of stakeholders that fall outside of the core sciences. The paper begins by first describing the fundamental elements required to develop the specific wildlife-management ABM set forth in this paper, from the representation of space to the animal *agent* attributes. Next, each key element is specifically addressed, with a thorough review of how ecologists have implemented it in their models. A summary of the trends is then provided, with an evaluation of the models' fit with the objectives of the wildlife-management ABM, and where future directions lie. The paper concludes with a description of the ecological data requirements needed to implement these ABMs, how the models can then be robustly evaluated, and the tools available to ecologists and managers to create ABMs.

2. Critical components of agent-based models in wildlife ecology and management

The diversity of ABMs and their flexibility to include any number of species, behaviors, and environments allows for an impressive suite of ecological relationships to be investigated, modeled, predicted, and monitored through time. This dynamic ability lends itself to management strategies, as long as special attention is given to the development of the critical components of the ABM. These critical components include environment representation, animal behavior, animal movement, and animal memory and learning.

A survey of the literature used to investigate recent progress in each of these four critical components with respect to the use of ABMs in animal habitat selection for the purposes of wildlife ecology and management is summarized in Table 1. This table provides a reference for each example from the literature, whereby the reader can identify specifics pertaining to model category, focal species, environment representation, animal behavior, animal movement, memory and learning, model purpose and location of the study, if applicable. In the following sections, we expand on these examples, highlight important concepts pertaining to each of the critical components, and discuss future areas of development.

3. Representation of the environment

Essential to wildlife ecology and management through the use of ABMs of habitat selection is the inclusion of some form of environmental characterization. Agents interact with their environment directly, and therefore the manner in which the environment is represented can have a profound effect on behavior and movement patterns of those agents. In its most basic form, the environment in a wildlife-oriented ABM includes *where* and *within what bounds* the agent exists spatially. The way the environment is represented is dependent on the research question being investigated; however, several important concepts from the literature can be highlighted: (i) the representation of environment as real-world or artificially-created, (ii) the representation of environment as a discrete (object-based) or continuous (cell-based) entity, and (iii) whether the environment is static or dynamic. Each of these concepts is considered below.

3.1. Real world or artificial

The environment in habitat-selection ABMs used for wildlife ecology and management has been represented both realistically and artificially during the past decade. Realistic environment representations in an ABM have a Cartesian coordinate system from an identifiable study area, with the parameters of the projection and datum maintained within the model. In addition, these models have cell values or object attributes either modeled from empirical relationships or recorded (either indirectly through remote sensing or directly from in situ measurements) from the location. Realistic environment representations are often imported from geographic information systems (GIS), and are used when researchers want to answer ecological questions specific to a certain geographic area, or compare their model results to empirical data collected at a specific location. For example, Alderman et al. (2005) represented the environment realistically in their ABM for modeling the effects of dispersal and landscape configuration on Eurasian nuthatch (*Sitta europaea*) populations. Their program, PatchMapper, combined a nuthatch population simulator with a 200 × 200 grid-based representation of habitat quality, which was imported from a GIS. Alderman and Hinsley (2007) further developed this model to include the realistic representation of topography using a digital elevation model (DEM), to study the effect of topography on dispersal patterns on nuthatches. Similarly, Metsaranta (2008) used a realistic environment for woodland caribou (*Rangifer tarandus*) by creating a grid-based land-cover classification, converted from a vector-based forest resource inventory. The land-cover classification was further processed into seasonal habitat-preference values, which were determined by a compositional analysis.

Artificial environment representations may have either a Cartesian coordinate system with projection and datum parameters or modeled/recorded values from a known location, but not both. Arti-

Table 1

Examples from literature showing the use of ABMs to aid in wildlife ecology investigations. Acronyms under Environment correspond to the type of environment representation, i.e., Artificial (A) or Realistic (R), Cell-Based (C), Object-Based (O), Dynamic (D) or Static (S), Biotic Factors (BF), and Abiotic Factors (AF). Acronyms under Animal Behavior correspond to Habitat Selection (HS), Foraging (F), Reproduction (R), and Dispersal (DI). Acronyms under Animal Movement correspond to Random Walk (RW), Biased Random Walk (BRW), Correlated Random Walk (CRW), Correlated Habitat Dependent Walk (CHDW), Levy Flights (LF), and Behavior Based (BB). Acronyms under Purpose correspond to Animal Population and Behavior Elucidation (APBE), Animal Behavior Elucidation (ABE), and Wildlife Management (WM).

Model category	Focal species	Environment	Animal behavior	Animal movement	Memory and learning	Purpose	Location	Author/year
Spatially-implicit, Mechanistic	*Callinectes sapidus* (Blue Crab)	A-C-D-BF	HS; F; DI	RW	None	ABE	Chesapeake Bay, USA	Hovel and Regan (2008)
	Generic Grazing Species	A-C-D-BF	HS; F	LF	None	ABE	Undefined	Mouissie et al. (2008)
	Generic Species	A-C-S-BF	HS; DI	LF	None	APBE	Undefined	Gauestad and Mysterud (2005)
	Generic Predator/Prey	A-C-D-BF	HS	CRW	Episodic	ABE	Undefined	Gras et al. (2009)
	Sorex araneus (Common Shrew)	A-C-D-BF	HS; R; DI	CHDW	None	APBE	Undefined	Wang and Grimm (2007)
	Canis latrans (Coyote)	A-C-S-BF	HS; R; DI	CHDW	None	WM	Undefined	Conner et al. (2008)
	Generic Foraging Species	A-C-D-BF	HS; F	BRW; RW	Reference	ABE	Undefined	Nonaka and Holme (2007)
Spatially-implicit, Behavior-based	*Salmo* spp. (Salmonids)	A-C-D-BF-AF	HS; F	BB	None	ABE	Undefined	Railsback and Harvey (2002)
	Generic Foraging Species	A-C-S-BF	HS; F; R	BB	None	ABE	Undefined	Hancock et al. (2006)
	Generic Foraging Species	A-C-S-BF	HS; F	BB	None	ABE	Undefined	Rands et al. (2004)
	Branta leucopsis; *Branta bernicla* (Barnacle Geese; Brent Geese)	A-O-D-BF	HS; F; R	BB	None	APBE	Various locations in Europe	Pettifor et al. (2000)
	Rattus norvegicus (Lab rat)	A-O-D-BF-AF	HS; F	BB	Episodic; Reinforcement	ABE	Undefined	Butz and Hoffmann (2002)
	Generic Homing Species	A-O-S-AF	HS	BB	Reference; Episodic; Hebbian	ABE	Undefined	Cruse and Hubner (2008)
	Generic Predator Species	A-O-S-BF	HS; F	BB	None	ABE	Undefined	Grand (2002)
	Canis latrans (Coyote)	A-O-S-BF	HS; DI; R	BB	None	ABE	Undefined	Pitt et al. (2003)
Spatially-explicit, Mechanistic	*Rangifer tarandus* (Woodland Caribou)	R-C-O-S-BF-AF	HS	RW; CHDW	None	ABE	Manitoba, Canada	Metsaranta (2008)
	Sitta europaea (Eurasian Nuthatch)	R-C-D-BF-AF	HS; R; DI	CRW	None	ABE	Eastern England, UK	Alderman et al. (2005)
	Sitta europaea (Eurasian Nuthatch)	R-C-S-BF-AF	HS; R; DI	CRW	None	ABE	Cambridgeshire, UK	Alderman and Hinsley (2007)
	Sciurus carolinensis (Squirrel)	R-C-S-BF-AF	HS; DI	CRW	None	ABE	Western Kentucky, USA	Robinson and Graniero (2005)
	Canis lupus (Wolf)	R-C-S-BF-AF	HS; F; DI	CRW	None	WM	Banff National Park, Canada	Musiani et al. (2010)
	Xanthocephalus xanthocephalus; *Barbastella barbastellus* (Yellow-Headed Blackbirds; Barbestelle Bats)	R-O-S-BF	HS; F; DI	CRW	None	WM	Calumet, Illinois; Southwest England	Bennett et al. (2009)
	Panthera tigris (Tiger)	R-O-S-BF	HS; F; R; DI	CRW	None	WM	Teari Forest, Nepal	Ahearn et al. (2001)
	Lynx lynx (Eurasian Lynx)	R-C-S-BF	HS; DI	CHDW	Episodic	WM	Jura Mountains, Switzerland	Kramer-Schadt et al. (2004)
	Ursus arctos (Brown Bears)	R-C-S-BF	HS; R; DI	CHDW	None	APBE	Central Austria	Wiegand et al. (2004)
	Puma concolor coryi (Panther)	R-C-S-BF-AF	HS; D	CHDW	Reference; Episodic	WM	Florida, USA	Cramer and Portier (2001)
	Alces alces (Moose)	R-O-D-BF-AF	HS; F; DI	CHDW	None	WM	Laurentides Wildlife Reserve, Canada	Grosman et al. (2009)
Spatially-explicit, Behavior-based	*Haematopous ostralegus* (Oystercatcher)	R-C-D-BF	HS; F	BB	Episodic	WM	Devon, England	Goss-Custard and Stillman (2008)
	Brant leucopsis (Barnacle Geese)	R-C-D-BF	HS; F; R; M	BB	Reference	ABE	Helgeland, Norway	Kanarek et al. (2008)
	Sardinops melanostictus (Japanese sardine)	R-C-D-BF-AF	HS; F; R; M	BB	Episodic; ANN	ABE	Central and Southern Japan	Okunishi et al. (2009)
	Cervus elaphus (Elk)	R-C-S-BF-AF	HS; F; DI	BB	Reference; Episodic	APBE	Yellowstone National Park, USA	Bennett and Tang (2006)
	Cervus elephus nelsoni (Elk)	R-C-S-BF-AF	HS; DI	BB	Reference	ABE	New Mexico, USA	Rupp and Rupp (2010)
	Gadus morhua (Larval Cod)	R-O-D-BF-AF	HS; F	BB	None	ABE	Georges Bank, USA	Kristiansen et al. (2009)
	Gadus morhua (Larval Cod)	R-O-D-BF-AF	HS; F; DI	BB	None	ABE	Moskenesgrunnen, Norway	Filksen et al. (2007)
	Anser brachyrhynchus (Pink-Footed Geese)	R-O-D-BF-AF	HS; F; M	BB	None	ABE	Northern Europe	Duriez et al. (2009)
	Marmota marmota (Alpine Marmot)	R-O-S-BF	HS; F; R; DI	BB	None	APBE	Berchtesgaden National Park, Germany	Stephens et al. (2002)

ficial representations are useful when a specific geographic location is not necessary for the investigation, such as when empirical data are not sufficient for direct comparison, or when more of a focus is being placed on behavioral rules as opposed to the dynamics of a particular ecosystem. For example, Pettifor et al. (2000) created an artificial environment representation whereby ten sites were created to represent the principle wintering regions of the brent goose (*Branta bernicla*) population. As a means of simplicity, the ten sites were placed in a straight line equidistant from one another, with the distance between the sites approximately equal to the average real-world distance between neighbouring areas. Behavioral rules were implemented to predict the response of migratory populations to environmental change in a year-round and spatially-explicit manner. Railsback and Harvey (2002) also utilized an artificial environment in their analysis of habitat selection rules for salmonids. Stream reaches were modeled in two dimensions using a rectangular grid of cells of varying size that maintained modeled depth, velocity, benthic food, and drift food, while tracking which cell each fish occupies. Habitat selection objectives were tested to see whether or not the modeled fish could reproduce patterns of habitat selection observed by real fish. Also using an artificial approach, Wang and Grimm (2007) created a 10,000 hexagonal cell artificial environment with grassland, hedgerow, and cereal crop cell values. In this study, food resources of each cell were allowed to vary (calculated from previous empirical studies), as well as the size of home ranges to determine the impact of home range dynamics on a model population of common shrew (*Sorex araneus*).

Choosing either a real-world or artificial-environment representation for use in an ABM is dependent on the type of investigation, since either choice has potential benefits and drawbacks. A real-world representation allows the researcher to closely mimic the actual conditions existent in the ecosystem under study. However, the availability of data is not always consistent and often comes from a variety of sources, each with its own standards, formats, and scale. Conversely, an artificial representation is often simpler to create; however, the lack of real-world representation will limit the applicability of the model to answering questions pertaining to specific areas of concern.

3.2. Cell or object

In addition to being real-world or artificially-created, the way that the environment is represented in ABMs applied to wildlife ecology and management can also be characterized as either cell-based or object-based, corresponding roughly to continuous-field and discrete-object conceptual models of geography, respectively (Goodchild, 1989). The debate between these alternative modeling views had been persistent in the GIS literature for the last 20 years, mostly because they represent different perspectives of reality. Choosing the appropriate data model for environment representation is critical, since it dictates how the spatial database is presented to the user and therefore how the user judges its empirical truth (Goodchild, 1992). Unfortunately, the representation of the environment is often driven by data availability and convenience, rather than through an understanding of the geographic phenomena being represented and the processes that created them.

The majority of the wildlife ecology and management ABM literature uses the cell-based spatial representation of environment, since it allows for simple computation of animal movement and behavior, introduces no area-related bias of selection, and conforms to many widely available environmental data formats (remote sensing, digital elevation models, etc.). For example, Rands et al. (2004) created a two-dimensional grid of square cells based on a torus for the investigation of simulated individual behavior and its affects on group behavior and foraging success. A set number of cells (SEED) were randomly chosen, from which the cells within a ran-

domly chosen distance were assigned a randomly chosen amount of energy. An individual's decision to move to a new cell or to rest was made based on its energy reserve level, the level of energy provided by the cell, and the proximity of neighbours. Hancock and Milner-Guilland (2006) also utilized a cell-based environment representation to investigate density-dependent habitat selection theory for foragers with limited knowledge of local resources, which they refer to as a map lattice model. In this lattice, each cell is assigned a certain resource level and age, while movement to a cell is determined on the basis of the perceived resource level in each direction. Also using a cell-based representation, Hovel and Regan (2008) created an environment whereby cells represented areas of the sea floor, classified as seagrass patch interior, seagrass patch edge, and matrix. Fragmentation through different spatial configurations of these classified cells was used to investigate how seagrass habitat fragmentation and loss, prey mobility, and prey and predator behavior influence predator–prey interactions. Further, Musiani et al. (2010) used a cell-based representation of the environment through several spatial datasets, including elevation, aspect, slope, land cover, and rasterized road and trail networks. The authors combined these spatial datasets with cell-based resource selection functions (RSFs) for elk (*Cervus elaphus*) and grizzly bears (*Ursus arctos*), human presence data, and cognitive wolf (*Canis lupus*) agents to study how humans shape wolf behavior in Banff and Kootenay National Parks, Canada. In a novel investigation using a grid-based representation of environment, Robinson and Graniero (2005) used a fuzzy membership function to model the likelihood that a grid cell is reached by an eastern gray squirrel (*Sciurus carolinensis*), given a particular starting point.

Although less abundant, there are examples from the literature where a vector-based approach is used for the environment representation in ABMs for wildlife ecology and management. For example, Ahearn et al. (2001) defined a basic vector coordinate space within which tiger (*Panthera tigris*) agents moved about and interacted with prey. Similarly, Grosman et al. (2009) used vector-based forest inventory maps, land-cover polygons, and salt pool locations in their model to assess the possibility of reducing moose (*Alces alces*)-vehicle collisions. Metsaranta (2008) also used a vector-based forest inventory that included 12 different forest types in their model assessing the factors associated with space use of woodland caribou (*R. tarandus*).

Both cell-based and object-based representations of environments have their advantages and disadvantages. Cell-based representations generally come from remote sensing image products and are often post-processed into information classes that are more beneficial to modeling than basic spectral information. The proliferation of remote sensing data products in recent years has lead to an abundance of data sources, and thus cell-based information is often easy to come by. However, cell-based environments typically require large amounts of data storage, and can cause computational problems related to computer memory capacity, particularly when dealing with large areas. Resultant from an investigation of the representation of environment in the context of individual-based modeling, Bian (2003) believes that the cell-based representation (which she refers to as a regular-grid data model) is advantageous for modeling an environment that is heterogeneous and dynamic. Conversely, the object-based representations of an environment typically take up less storage space, making some computations more efficient. This equates to faster model simulations and larger areas of coverage, given a fixed set of resources. However, an object-based environment representation will also ensure that available habitat is of unequal size and thus more critical thought needs to be put into the development of animal-movement rules. Bian (2003) believes that the strength of object-based (which she refers to as a patch model) environment lies in its explicit between-feature topology and is best suited

for modeling projects that require a clear identification of landscape features, spatial relationships between them, and a rich set of attributes associated with the features.

3.3. Static or dynamic

ABMs designed for wildlife habitat-selection generally have a static environment, indicating that the environment stays the same while interactions between agents within that environment are occurring through time. This is indicative of the focus of most models being set on how animals perceive their landscape, and how behavior leads to the emergence of overall patterns. For example, Pitt et al. (2003) defined a static environment in their model of territoriality and social structure of *Canid* populations. Railsback and Harvey (2002) also defined a static environment with a constant production rate of benthic food availability in their analysis of habitat selection rules. However, some of these models also incorporate a changing environment as a key element that influences animal behavior. For example, Duriez et al. (2009) modified the environmental variables of temperature and growing-degree days for each year between 1991 and 2004 to assess likely decision rules for pink-footed goose (*Anser brachyrhynchus*) migration departure in Europe. More simply, rules can be given to agents to not return to previously visited areas, under the assumption that resources there have recently been depleted. Grosman et al. (2009) incorporated a simple rule into the moose agent's repertoire that if the agent selected a previously visited polygon, the selection process was to be repeated until a new polygon was chosen.

Static-environment representations are best utilized when the desire is to use the ABM to investigate the emergent properties that originate from the local interactions among agents in a given environment. However, when a researcher wants to isolate the effect that a changing environment might have on the behavior and interactions of animal agents, then a dynamic representation is more suitable.

3.4. Integration of biotic and abiotic factors

In addition to the simple spatial location and extent that an agent inhabits, the representation of the environment in habitat-selection ABMs can also be more elaborate. The environment in these cases can be identified as a set of resources available to the agent, occurring as either biotic or abiotic factors. Biotic factors are those resources that can be considered living organisms, examples of which may be food resources, potential mates, humans, etc. These biotic factors are generally represented as a field of cells, calculated by previously defined functions. For example, Cramer and Portier (2001) used density maps of white-tailed deer (*Odocoileus virginianus*) (food resource) and human population (disturbance) as biotic factors in their model of panther (*Puma concolor coryi*) movement in response to human attributes on the landscape. Similarly, Kanarek et al. (2008) created a grid-work of cells, each of which was ascribed the amount of available biomass for a population of barnacle geese (*Brant leucopsis*) to assess foraging behavior in a changing environment. However, biotic factors of environment can also be discrete objects. For example, Ahearn et al. (2001) defined spatial databases of points representing densities of wild and domestic prey for input into their ABM for simulating tiger (*P. tigris*)/human interaction in multiple-use forests. These biotic factors can also be either static or dynamic, depending on how important the changing of resources is to the model. However, once an object-based environmental biotic factor becomes dynamic, i.e., situated in space and time, it begins to take on the characteristics of an agent itself, albeit a primitive one.

Abiotic factors are those resources that can be considered non-living organisms, such as land cover, elevation, temperature, water,

etc. These factors are less common than environmental biotic factors; however some models do incorporate them and they can take the form of either fields of cells or vector-based objects. For example, Kristiansen et al. (2009) used vector-based vertical profiles of temperature and turbulence as input into a bioenergetics model for assessing habitat selection and growth-survival tradeoff of larval cod (*Gadus morhua*). Conversely, environmental abiotic factors of elevation and topography were represented in a grid of cells by Alderman and Hinsley (2007) to study the effect of topography on dispersal patterns of Eurasian nuthatches (*S. europaea*). The use of both biotic and abiotic factors is essential if emergent properties are sought from the local interactions of wildlife agents in a realistic and complex ecosystem.

4. Animal behavior

One of the key concepts in ecology is the continual adaptation and change in state of animals in response to internal and external conditions (Zhivotovsky et al., 1996; Roff, 2002). The decision rules that the individual animal uses are best described as being based on the optimization of *adaptive behaviors*. This optimality paradigm explores the relative efficacy of different strategies in optimizing some particular fitness currency (e.g., energy gain, survival, or reproduction) over ecological or evolutionary time frames (Nathan et al., 2008). An important differentiation in the literature occurs between direct fitness-seeking and indirect fitness-seeking adaptive traits in ABMs. Direct fitness-seeking adaptive traits are those that explicitly incorporate the fitness consequences of alternative adaptive behaviors for an individual, whereas indirect fitness-seeking adaptive traits are those that exist in real-world organism but that are harder to link to fitness directly (Grimm and Railsback, 2005).

4.1. Direct fitness-seeking traits

The adaptive behaviors produced by direct fitness-seeking traits are the most common found in the ABM literature and include, but are not limited to, habitat selection, foraging, and reproduction. Habitat selection is considered a direct fitness-seeking trait, widespread in wildlife ecology and management ABMs, because animals not only travel between habitat patches, but also live, feed, and breed in them. Therefore, the criteria an animal uses to assess its habitat and the requirements needed to make an adaptive choice will have direct consequences on its fitness. Kanarek et al. (2008) incorporated habitat selection in their investigation of environmental fluctuations on a barnacle geese (*B. leucopsis*) population in Helgeland, Norway. In their model, geese choose unoccupied habitat according to their rank in the population-structured dominance hierarchy, their memory of previously visited sites in past years, past reproductive success, inherited genetic influence towards site preference, and knowledge of the available biomass density. Grand (2002) also incorporated habitat selection in her study on the simulated effect of alternative forms of competition and predation on the process of habitat selection. Two habitat types were used, along with exploitative and interference competition types and frequency dependent predation types to describe that the assumed forms of predation and competition result in very different predicted patterns of habitat selection. Grossman et al. (2009) further incorporate habitat selection in their investigation of salt-pool removal and displacement and its effect on reducing moose-vehicle collisions in Quebec, Canada. In their model, moose have to choose between habitats based on five parameters: food quality, cover quality, minimal slope, proximity to water bodies, and streams, and proximity to roadside salt pools.

Foraging behavior (searching for food resources) is a type of habitat selection and is considered a direct fitness-seeking trait since an optimization of foraging will lead to higher energy levels at the lowest cost to itself and thus better reproductive fitness. Foraging has been the focus of several studies, in particular the development of optimal foraging strategies for wildlife species. For example, Nonaka and Holme (2007) investigated the joint effects of patch clumpiness and habitat productivity on the maximum net energy intake of a simulated forager through the use of the marginal value theorem outlined by Charnov (1976). Rands et al. (2004) also looked at foraging strategy, in particular the emphasis that the individual puts on protective herding versus individual foraging behavior, with the decision being based on the energy reserves of the individual and the proximity and actions of its neighbours. Goss-Custard and Stillman (2008) also incorporated the optimization of foraging in their model that assessed the impact of environmental change on a population of European oystercatchers (*Haematopous ostralegus*) in southwest England. The study sought to understand the underlying processes behind starvation functions of oystercatchers through adaptive behaviors that balanced meeting energy demands with individual competitive abilities that depended on the interference-free intake rate and the susceptibility of interference.

Reproduction is the most obvious direct-fitness seeking trait, since the results of reproduction are the main goal of fitness-seeking individuals. It is not explicitly included in a model unless the emergent properties of successive generations of reproductive success are integral to the research question being addressed. For example, Stephens et al. (2002) incorporated the explicit representation of reproduction in their study on the complexity and population prediction capability of a model of alpine marmots (*Marmota marmota*). The model was used to predict the effect of density dependence on population growth and dispersal patterns over a 1000-year period in order to properly address the emergent phenomena. Wang and Grimm (2007) also explicitly included reproduction in their investigation of home-range dynamics and population regulation of the common shrew (*S. araneus*). In this study, the authors incorporated several reproductive attributes, including: start/end of breeding season for both males and females, time lag before females become fertile, gestation length, lactation length, sex ratio at birth, litter size, and the time it takes for off-spring to reach sexual maturity, which lead to emergent properties of home range size of 50-year model periods.

4.2. Indirect fitness-seeking traits

The adaptive behaviors produced from indirect fitness-seeking traits are also common in literature, with the most prominent being dispersal and migration. Dispersal, or moving away from a population or parent organism, is an example of an indirect fitness-seeking adaptive trait, since the result of dispersal is difficult to link to fitness directly. Leaving a population or parent organism can be spurned by many causes including an increased competition for resources or increased pressure from predation; however the decision to depart under these circumstances is not necessarily directly linked to the reproductive fitness of the individual. The inclusion of dispersal in wildlife behavior- and movement-based ABMs, like most indirect fitness-seeking traits, is often provided by empirical data observation. For example, Kramer-Schadt et al. (2004) developed a model to investigate the probability of dispersing Eurasian lynx (*Lynx lynx*) reaching other patches in heterogeneous landscapes. The dispersal rules utilized in this study were extracted from general knowledge and dispersal movement analysis of Iberian Lynx (*Lynx pardinus*; Revilla et al., 2004). Dispersal can also be indirectly addressed, such as in the study by Conner et al. (2008), whereby individual coyotes (*Canis latrans*) were allowed to transition to transients and move among a neighbourhood of territories without leaving the simulated area. This can be thought of as quasi-dispersal and was meant to emulate the observed dynamics of coyote structure whereby alpha individuals do not leave their territory, and open territories are taken by individuals in neighbouring populations.

Migration can be considered an indirect fitness-seeking trait since the individual is following rules that cause them to migrate with the idea that the probability of reproducing successfully is highest if they migrate to previously beneficial and relatively distant locations. Of course, not all wildlife exhibit migratory behavior, however examples of those that do can be found in the literature. For example, Bennett and Tang (2006) investigated the migratory behavior of elk populations in Yellowstone National Park. The authors modeled the decision to migrate as a stochastic response to the change in snow water equivalent (SWE), the possibility of better forage at a distant location, and the energy differential between moving and staying. The migratory behavior of birds has also been studied. For example, Duriez et al. (2009) studied the behavioral rules behind the migratory behavior of pink-footed geese (*Anser brachyrhynchus*) between wintering grounds in Denmark and breeding grounds in Svalbard, Norway. By comparing predicted and observed departure dates, the most accurate predictions were made by a combination of cues including: the amount of body stores, date, and plant phenology. Decision rules changed over the course of the migration, with external cues becoming decreasingly important and time-related cues becoming increasingly important as the geese approached their breeding grounds.

4.3. Multi-species interactions

While the main focus of this review is centered on the actions of focal species in the context of scenario planning for critical habitat, wildlife-management can also require the consideration of species-species interactions at the community and/or ecosystem levels (Root et al., 2003). Indeed, agent-based models of trophic ecology have been developed, for example, to theoretically assess evolutionary aspects of social behaviors (Charnell, 2008), to understand the dynamics of community assembly (Giacomini et al., 2009), to identify dynamically relevant organizational scales for predicting community patterns (Schmitz, 2000), and to gain insight into fluctuating population dynamics of individual species (Reuter, 2005). In more applied studies, ABMs of trophic interactions have been used to assess ecosystem effects of fishing (Shin and Cury, 2004), and to examine the role of habitat fragmentation of predator–prey relationships (Hovel and Regan, 2008). In these ABMs, the species may be represented as cognitive or non-cognitive agents, depending on the intent of the researcher. For instance, in Musiani et al. (2010), wolves (*C. lupus*), the cognitive agents, would respond to the presence of non-cognitive competitor and prey agents, who in turn, would appear and disappear in the environment at realistic temporal and spatial patterns. ABMs, via their process overview and scheduling procedures, can readily accommodate multiple species whose life-history traits differ on temporal scales (e.g., masting of trees vs. small mammal life spans) and spatial scales (e.g., dispersing larvae vs. sedentary adults). Of note, however, is that careful attention must be given to the updating/scheduling methodology in multispecies interaction (i.e., asynchronous vs. synchronous; Caron-Lormier et al., 2008). Nevertheless, ABMs are very versatile in integrating various types of agents and their actions, and can be well-suited to exploring complex wildlife-management issues involving multispecies interactions.

Regardless of which fitness-seeking trait to model (as it depends on the scope and intent of the research), and the number of agent types to incorporate, adaptive behaviors remain an important aspect in the study of ABMs of wildlife habitat selection and

management. They can produce emergent system-level processes that allow one to ask ecological questions that extend beyond the individual itself. Imposing system behavior by giving individuals mechanistic, empirically-derived traits provides an alternative. However this might lead to the simple reproduction of reactive abilities and behaviors observed in real systems without providing the desired ultimate causations necessary to understand animal movements and habitat selection. This distinction is particularly important for scenario planning, as the use of optimizing behavioral strategies allows researchers the ability to predict how animals will most likely respond to novel changes in their environment, since the underlying processes are consistent with evolutionary concepts (i.e., how animals will tradeoff fitness-maximizing behaviors and find an optimum).

5. Animal-movement rules

Animal movement is often a response to short-term goals such as reproduction, maintenance (including feeding), and survival (including escaping threats). It may also be shaped by longer-term fitness implications, such as avoidance of inbreeding and population extinction (Holyoak et al., 2008). Movement is therefore an adaptive behavior that has a very important role. Most wildlife species are mobile and try to improve their fitness by moving to areas that have higher survival and reproductive success. Therefore, the rules by which this movement is characterized in ABMs have a profound affect on the outcome of the model and influence the types of research questions that can be investigated. Two types of animal-movement rule characterizations are apparent in the ABM literature: mechanistic and behavior-based. The following sections will focus on these animal-movement rules and provide specific examples; however, for a more thorough evaluation of animal-movement and agent-based modeling, we recommend Tang and Bennett (2010).

5.1. Mechanistic

A mechanistic approach to animal-movement rules can be considered a *proximate* explanation of how an animal moves, as opposed to a robust, ultimate one. Mechanistic movement rule sets are simple procedures that dictate movement behavior of an animal according to a pre-determined mathematical model that mimics a reactive response to local stimuli, if a reaction is included at all. The most basic mechanistic movement rule is random walk theory, which can be traced back to the irregular motion of particles studied by Brown (1828) and popularized by Pearson (1905) and Malkiel (1973). In random walk theory, the opportunities to the animal in terms of habitable space are all equal, i.e., an animal has an equal probability of moving in any direction. Today, there are several variations of random walk theory for animal movement present in the literature. For example, Bennett et al. (2009) applied a correlated random walk movement strategy to all foraging animals and recreationists in their investigation of wildlife response to human disturbance. The *correlated* random walk strategy differs from random walk in that it involves a correlation between successive steps, which can also be called persistence (Patalak, 1953). Alderman and Hinsley (2007) also used a correlated random walk to model dispersing nuthatches searching for habitat as they traversed across a matrix. Musiani et al. (2010) used correlated random walk as well to model wolf movement in an ABM designed to investigate human–wolf interaction. A variation of the correlated random walk, the *correlated habitat-dependent walk*, was used by Kramer-Schadt et al. (2004), whereby dispersal direction was dependent on previous direction and local habitat quality as perceived by an individual lynx.

Another variant of the random walk is the *biased random walk* movement strategy, which occurs when an animal movement path contains a consistent bias in a preferred direction or towards a given target. For example, Wiegand et al. (2004) used a biased random walk to model dispersal of independent grizzly bears (*U. arctos*), whereby movement to a new cell was directly proportional to the attractiveness of the cell (based on habitat suitability and the number and sex of the occupants), relative to that of the other neighbouring cells. Movement in this model stopped when a bear found an appropriate home range, which was determined if the sum of the attractiveness of the current cell and eight neighbouring cells exceeded a defined threshold. Conner et al. (2008) also used a biased random walk to model transient coyote (*Canis latrans*) movement among a neighbourhood of territories to emulate observed dynamics in coyote social structure. In this model, a random focal territory was chosen and a focal neighbourhood was observed for open alpha positions, which were filled with available betas or transients (with a priority placed on age).

A Lévy flight (named after the French mathematician Paul Pierre Lévy) is a scale-free type of random walk, where steps lengths are not constant, but rather are derived from heavy-tailed probability distributions (Viswanathan et al., 1996). A variety of different organisms have been found to follow a Lévy distribution of flight lengths or times, from microzooplankton (Levandowsky et al., 1988) to sharks (Humphries and Sims, 2009). The use of Lévy flights is not as prevalent in the literature as are other variations of random walk. However Gauestad and Mysterud (2005, 2006) implemented a truncated Lévy flight algorithm (Mantegna and Stanley, 1994) to express population kinetics in a multi-scaled framework, whereby a model animal is able to relate to its habitat over a range of spatiotemporal scales through parallel information processing. In addition, Mouissie et al. (2008) witnessed an approximate Lévy flight as the emergent grazing movement from the outcome of optimal foraging in a heterogeneous environment, further indicating its usefulness for habitat-selection ABMs in wildlife ecology and management.

The decision of which mechanistic movement algorithm to use largely depends on the scale of movement. Typically, correlated random walks are used for short- and middle-scaled animal movement; animal paths involving large spatial or temporal scales are reproduced using Lévy flights (Bartumeus et al., 2005). However, continually emerging theoretical and empirical studies of animal movement reflect an ongoing field of study, with new models being developed to accommodate hierarchical, multi-scale and multi-state movement data and processes (for a more thorough review, see Schick et al., 2008). Their application in ABMs is eagerly anticipated.

5.2. Behavior-based

In contrast to a mechanistic approach, the behavior-based approach leads to a more complex web of decisions, and the responses of the animal to stimuli are often more multifaceted. Important to this approach is the inclusion of the internal state of the animal. For example, Stephens et al. (2002) incorporated an ideal free, behavior-based rule of fitness optimization to allow state transitions of alpine marmots (*M. marmota*) to be decided by an evolutionary stable approach of maximizing an individual's fitness. Also important is a focus on the cognitive abilities of the individual. For example, Gras et al. (2009) modeled predator and prey agents in an evolving ecosystem using a fuzzy cognitive map (FCM) as the behavior model, which allowed for the inclusion of a distinction between sensation and perception, the detection of paranoia and stress levels, and the ability for memory of past experience. In addition, the decision rules that feed this approach often come from ecologically sensible rules consistent with evolutionary prin-

ciples (Berec, 2002), direct observation of animal species, or past empirical studies cited in the literature. For example, Filksen et al. (2007) developed an algorithm of behavioral rules for larval cod (*Gadus morhua*) when changing depth preference using ontogeny and size, internal condition (hunger), and daily light cycle, based on the empirical studies done by Lough and Potter (1993) and Leis et al. (2006).

The two basic animal-movement rules have both their advantages and weaknesses. Mechanistic rules are characterized by being unable to infer movement itself nor how the organism–environment interaction influences movement processes while behavior-based rules suffer from a lack of empirical data against which to validate the model. An amalgamation of the two types of rules is best-suited for agent-based modeling of habitat selection. Mechanistic-based rules are particularly useful in the face of search uncertainties; when the heterogeneity of the environment causes animals to have no information about where targets are located (i.e., resource patches, mates, etc.), random search strategies may provide different opportunities to find them (Bartumeus et al., 2005). Incorporating behavior-based rules into movement decisions made by agents can further obtain better fits to movement data, correlate behaviors with landscape features, and reveal how the environment can influence within-state movements as well as switches between behavioral states (Schick et al., 2008).

6. Memory and learning

Memory and learning are adaptive behaviors that are very important for wildlife. Having an effective memory and being able to learn quickly are attributes that will directly benefit the fitness of an animal; therefore the way each is represented in an ABM is crucial for a realistic and appropriate representation of the ecosystem under study. Bennett and Tang (2006) outlined two forms of spatial memory that are thought to lead to spatial knowledge and that are important for the fitness of wildlife: reference and episodic. Reference memory can be thought of as the map-like representation of the environment, which can be used for navigation (Bailey et al., 1996). Kanarek et al. (2008) utilized reference memory in their model of barnacle goose (*B. leucopsis*) foraging through an increased efficiency due to traditional foraging. An individual goose achieves a higher level of fitness if it returns to a traditional foraging area and remembers which foraging sites on which island it spend previous years in. As the goose ages and establishes dominance in the flock, returning to past productive sites provides even more fitness, thus utilizing its spatial (reference) memory. In contrast to reference memory, episodic memory is sensory perceptual knowledge of recent experience that is retained for short periods of time (Conway, 2002). Goss-Custard and Stillman (2008) used episodic memory in their shorebird model, allowing foragers to remember their foraging success during a given number of previous steps. Gras et al. (2009) also used episodic memory in their FCM model by not allowing activation levels of agents to be reset, which translates into all previous states of an agent during its life participating in the computation of its current state, therefore giving the agent a memory of its own past states. It is beneficial to utilize both reference and episodic memory if realistic representation of animal memory is desired, since many animal species display the usage of both.

The repetition of events and experiences, combined with an animal's ability to store and recall that information, are required in order for an animal to learn. Thorpe (1963) identifies four types of animal learning that are still acknowledged today (although the separation between each type is not universally recognized): habituation, associative learning, latent learning, and insight learning.

Habituation learning takes place when repeated exposure to an event or experience leads to a reduction in the response to an event. Associative learning occurs when something is learned through association with a separate, pre-occurring element. Latent learning is the type of learning whereby a response is not immediately apparent. Insight learning can be described as the rapid apprehension of solutions to problems.

Although considerable research has gone into animal learning theory, reproducing and representing different learning types are a challenge in any modeling exercise, including ABMs. Nevertheless, some studies have attempted to mimic animal learning, with the most promising representation likely being artificial neural networks (ANNs), which attempt to simulate the structure and functional aspects of the neural networks that exist in biological organisms (Bishop, 1995). For example, Okunishi et al. (2009) used an ANN to model the decision to migrate from input environmental variables in their ABM to investigate spawning migration and growth of Japanese sardine (*Sardinops melanostictus*) in the western north Pacific. Another animal learning representation approach, reinforcement learning (RL), is concerned with how an agent ought to take action in an environment so as to maximize its long-term reward, or fitness. The basic principle of RL is learning how to map situations to actions so as to maximize a numerical reward signal, and includes both trial and error search and delayed reward characteristics (Sutton and Barto, 1998). Butz and Hoffmann (2002) used RL in their ABM to investigate the role of anticipations in controlling rat (*Rattus norvegicus*) behavior in an anticipatory learning classifier system. In terms of spatially explicit learning, Hebbian learning has shown promise. It originates from Hebb's (1949) postulate: when two neurons are activated at the same time, the association between them is enhanced. Similar to ANNs, the associations are representative of synaptic connections and are modeled as weighted links. When combined with inhibition mechanisms that can decrease link weights given the absence of stimuli, a differentiation of weights is possible and thus reinforcement and penalization can be mimicked. Cruse and Hubner (2008) use Hebbian learning in their model investigating self-organizing memory and the process of active learning of landmarks used for navigation in homing species.

ANNs have the benefit of mimicking the neural systems existent in biological organisms and can be trained directly on data with hundreds or thousands of inputs, showing their great potential when it comes to the inclusion of memory in to wildlife habitat selection ABMs. However, they often require considerable parameter tweaking and retraining (which is computationally expensive). RL has the benefit of dealing with feedback systems that maximize fitness, which provides a more flexible framework than others. However, some algorithms for RL can suffer from the amount of time required to learn an effective strategy. The advantage of Hebbian learning is apparent when it comes to an agent learning about its environment, however it is less applicable when it comes to learning a particular task. The use of one or several of these learning algorithms is dependent on how well known the behavior, memory and learning of a particular organism that will be represented in the ABM is.

7. Discussion

Agent-based models are a versatile tool, and as shown in this review, have an important role to play in modeling animal behavior and movements for wildlife-management objectives. They represent the synthesis of dynamic optimization models, movement models, and land-use models. They can accommodate individual behaviors, spatial systems, and dynamic changes in habitat, all of which can then emerge into wildlife population-level processes

of resilience, persistence and patterns of abundance over space and time. The studies showcased in this review concern studies of animal habitat selection and use, as these traits are essential for the delineation and management of critical habitats. The models can be categorized according to four broad criteria based on whether the environmental representation is artificial or real (i.e., an actual coordinate system), and whether animal movements are mechanistic or behavior-based (Table 1). While the objectives of these studies ranged from elucidating animal population demographics, fitness consequences of individual behaviors, to the express purpose of wildlife-management, we found a single example with a wildlife-management mandate that was also a spatially explicit, behavior-based ABM (Goss-Custard and Stillman, 2008). We believe this type of ABM to be the most beneficial for modeling wildlife habitat selection for two reasons: to establish a more accurate representation of the animal's movement ecology, and for a more insightful approach to conservation-based scenario planning.

The ABM specific for wildlife-management of critical habitats should include a dynamic, cell-based and real-world environment representation that includes both abiotic and biotic factors, both direct and indirect fitness-seeking traits, a combination of mechanistic and behavior-based movement rules, as well as proper representation of memory and learning. A dynamic environment representation is important because wildlife continually adapt to changing environmental conditions, whether those changes come from seasons, anthropogenic influences or by the wildlife themselves as they interact in their environs. An important parsimonious caveat however, is that if the reasoning for the investigation does not specifically require the environment to change, then it should remain static (e.g., the researcher can vary the biotic elements, instead). A dynamic environment for the sake of being dynamic will not add anything to the management scenario and may lead to unnecessary model complexity.

The use of cell-based environment representation is advantageous because it is computationally simple when compared to the object-based alternative. Representing the environment as a grid allows for the agents to move to new cells in accordance with the time step of the ABM. Conversely, the use of vector objects would require the creation of a distance variable for the agent, and directional bias would have to be accounted for when moving in areas with different sizes of patches. Objects certainly permit the inclusion of geometry and variable geographic representation of environmental phenomena; however, if these attributes are not necessary for the investigatory purpose of the ABM and the precise location of the agent is not needed, then it is advantageous to use a cell-based environment representation over an object-based one.

The inclusion of both biotic and abiotic factors is essential in habitat-selection ABMs because wildlife use both of these factors to make decisions regarding fitness. The relevance of biotic factors for wildlife agents are straightforward: factors such as food resources directly impact decisions and movement. An animal agent will seek out the most abundant food resources and move to them, as long as it can perceive those resources and there are not any other negative impacts outweighing the benefits of moving. Abiotic factors are just as important, however. For example, an abiotic factor such as topography would have an impact on the amount of energy used and therefore, as long as the wildlife agent can perceive the change in elevation it will use this abiotic factor in its decision-making process to achieve the highest level of fitness.

Much like biotic factors, direct fitness-seeking traits are obviously beneficial when it comes to the use of ABM in wildlife ecology and management. The use of habitat selection and foraging adaptive behaviors directly affect the fitness of the individual and therefore they are integral to the model. Indirect fitness-seeking traits such as dispersal and migration are also important traits, as

they can play a major role in determining the fate of individuals. Not all wildlife migrate or disperse, however, and some behaviors may be more integral than others to the survival of the individual, so it is important to evaluate the purpose, the temporal and spatial scales of the model, and the appropriate fitness measure of the real-world animal when selecting which adaptive behaviors to model in an ABM.

A combination of mechanistic and behavior-based movement rules is best suited for habitat-selection ABMs. Accounting for the internal state (i.e., the organism's physiological state and its short-term motivation in relation to its long-term goals) of the wildlife agent that is characteristic of the behavior-based movement algorithms is essential, since it maintains a currency that can be constantly evaluated and referred to as a level of fitness. This closely mimics true animal internal evaluation that dictates behavior, which is desired. However, there may be instances where the exact behavior information for an animal is not known, or a lack of empirical data does not allow for the full use of a behavior-rule based approach to movement. In these instances, the use of mechanistic movement models such as correlated random walk or correlated habitat-dependent walk are useful, as long as they closely mimic true movement of the wildlife under study.

Proper inclusion of memory and learning is essential for reproducing the behavior of cognizant and adaptive wildlife. A species' memory of its habitat, especially when pertaining to food resources, will have a profound effect on its energy intake and thus its fitness. Memory of potential sources of danger or locations of potential mates will also have an effect on fitness and thus if a wildlife species encounters resources predictable in time and/or space, memory may be an important trait to include in the ABM. Learning will only come about if the wildlife agent is capable of memory; however, many wildlife species exhibit learning capabilities and the outcome of management scenarios can be significantly altered if those species use their learning capabilities to adapt to changing conditions.

The characteristics of habitat-selection ABMs deemed essential in this review for the management of wildlife critical habitat is a shared viewpoint held in the broader study of movement ecology. A recent call for a more conclusive understanding of the causes, patterns, mechanisms, and consequences of wildlife movement has emphasized these traits as being central to managing and restoring degraded landscaped and their occupants (Nathan et al., 2008). The general consensus is that movement paths of wildlife result from the dynamic interplay of four basic components: the internal state of the organism, its motion capacity (i.e., the ability and choice to move under its own locomotion), and its navigation capacity (the ability to orient and navigate, including the implied use of memory or inherited capacity). The fourth factor is the external environment, since it can modify animal movement either through landscape attributes, the distribution of resources and differing environmental conditions, and other organisms (Holyoak et al., 2008; Revilla and Wiegand, 2008). The ABM we advocate can include all of these variables, and, more importantly, is capable of accommodating how all four components interact to produce the emergent movement patterns critical to determining how wildlife populations may respond to landscape change.

Insight into how animals may respond to future changes in their landscape is a relatively unexplored advantage of ABMs under the tenets of scenario planning. While the future of an ecosystem cannot be perfectly predicted, it is partially decidable, and desirable pathways of development can be encouraged through appropriate regulations and policies. Therefore, the objective of the modeling exercise in scenario planning is not prediction but rather interactive learning to identify desirable options based on various management scenarios (Marceau, 2008). In the successful design of an ABM one can formulate questions about potential future conditions

and run simulations to observe what outcomes might be possible. The focus here is not on predicting the future, but rather on exploring possible futures, leading to an enhanced understanding of the system under investigation. As highlighted in the wildlife-management studies presented in this review, ABMs can be used to assess: the differential effects of proposed predator sterilization versus removal (Conner et al., 2008); the long-term success of reintroduction efforts potentially impeded by road mortality and habitat connectivity (Kramer-Schadt et al., 2004); the sustainability of an endangered species given the density of prey and the attitudes and behaviors of people (Ahearn et al., 2001); habitat selection and associated population demographics of animals under predicted future human development and habitat loss (Cramer and Portier, 2001; Goss-Custard and Stillman, 2008; Stephens et al., 2002); impacts of different management policies on the reduction of road-side vehicular mortalities of wide-ranging animals (Grosman, 2009); and potential park designs on the nesting success of bird populations (Bennett et al., 2009). Incorporating both adaptive behaviors and animal-movement ecology in a changing landscape with possible alternative futures is a mostly untapped potential of ABMs that should be a focus for further model developments.

7.1. Beyond the design of ABMs

Agent-based modeling has become a well-established and accepted methodology, and we have explored the components of an ABM we believe suitable for wildlife ecology, and specifically, conservation planning for critical habitat management. Beyond the fundamental design of the ABM, further attributes concerning data needs, model calibration and evaluation, and communication are worth mentioning briefly. Data types commonly used in calibrating and in evaluating ABMs of habitat use are movement-path data, demographic data (birth rates, survival, etc.), and expert knowledge. The chosen parameters typically have direct biological and/or evolutionary significance and are often closely related to empirical investigations, thus limiting the range of plausible values considerably (Breckling et al., 2006). These data are also often incorporated into a pattern-oriented modeling (POM) approach to increase the rigor and comprehensiveness of the modeling procedure, thereby subjecting the model to the stringencies of traditional natural science. This protocol, first introduced by Grimm (1994) and subsequently expanded on by Railsback and Harvey (2002), Wiegand et al. (2003) and Grimm et al. (2005), is based on the assumption that patterns are the defining characteristics of a system and are indicators of essential underlying structures and processes. POM requires the researcher to begin with a pattern found in the real system, posit hypotheses to explain the pattern, and then develop predictions which can be tested. By observing multiple patterns at different hierarchical levels and scales, one can systematically optimize model complexity, parameterize the model, and simultaneously make it more general and testable (Grimm and Railsback, 2005). POM has been used extensively in recent studies (e.g., Railsback et al., 2002, 2005; Kramer-Schadt et al., 2004; Revilla et al., 2004; Petersen et al., 2008; Topping et al., 2010a; Chion et al., in press), demonstrating its utility in addressing model complexity, unknown data requirements, variable parameterization, generality, and standard theories for model development.

An effective means of communicating the model is another important criteria for ABMs. A standard communication mechanism to present ABMs is the overview design concepts and details (ODD) protocol (Grimm et al., 2006). The purpose of the ODD protocol is to provide a structure for presenting the information about an ABM in the same sequence, no matter the scope, structure, complexity, and implementation details of the ABM. The structure of the ODD protocol has context and general information first (overview), followed by strategic considerations (design concepts)

and finishing with technical details (details). With examples of the ODD protocol becoming more apparent in the literature (e.g., Polhill et al., 2008 and Topping et al., 2010b), it has now become easier for others to follow the protocol in the absence of advice of its developers, and easier to see where changes are needed to clarify requirements, facilitate the model description process, and fit the description needs of different models (Polhill et al., 2008).

Lastly, from a technical viewpoint, ABM software has greatly improved in recent years, from initial models that required extensive programming skills, to software packages that are accessible to researchers in multiple fields (Railsback et al., 2006). More recently, ABM software programs have also improved their ability to represent space through integration with GIS. In sum, agent-based modeling is a continually developing field of research, characterized by improving methodology, refinement of tools, targeted applications, increasingly concise and comparable communication of models, and evidence of increased experience of the research community (Heckbert et al., 2010).

8. Conclusion

The purpose of this review was to showcase the strong potential of ABMs as habitat models in wildlife-management with respect to conservation planning of critical habitats. ABMs can be useful to scientists, managers, decision-makers, and even the general public in providing a conceptual and computational framework to simulate the behavior of environmental systems under various scenarios and at multiple scales, to reproduce aspects of the human decision process and the feedback mechanism between natural and human systems, and to help identify appropriate management strategies (Marceau, 2008). While we perceive ABMs that encompass a multidisciplinary approach as the most complete and promising habitat models for ecological research, the full potential of agent-based modeling still remains to be fulfilled; and more advanced concepts required to capture the complexity of movement ecology in dynamic environments still need to be incorporated within ABM architectures.

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