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Integrating Spatial Behavioral Ecology in Agent-Based Models for Species Conservation

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1. Introduction

Anthropogenic activities are causing highly influential impacts on species persistence. The sustained environmental change wildlife are experiencing may surpass the capacity of developmental, genetic, and demographic mechanisms that populations have evolved to deal with these alterations. Undeniably, habitat fragmentation, habitat loss, and human disturbance are causing a decline in species numbers on a global scale, with shifts or reductions occurring in species-distribution ranges. The knowledge of species distribution is a vital component in wildlife conservation and management. Such information aids in quantifying animal–habitat relationships, describing and predicting differential space use by animals, and ultimately identifying habitat that is important to an animal (Beyer et al. 2010). The field of species distribution modeling (SDM) as a means of quantifying species–environment relationships has been extensively developed since the first formal definition of differential habitat selection theory by Fretwell and Lucas in 1969. It has since produced a variety of numerical tools that combine observations of species occurrence or abundance with environmental estimates based on statistically or theoretically derived response surfaces (Guisan and Zimmermann 2000). These models include presence/absence models, dispersal/migration models, disturbance models, and abundance models; they are now widely used across terrestrial, freshwater, and marine realms.

SDMs are used to determine the suitability of the organisms' habitat, relying on density/abundance measures or the ratio between used and available habitats to infer habitat quality. These models use spatial environmental data to make inferences on species' range limits (Kearney and Porter 2009). Most approaches are correlative in that they statistically link spatial data (typically geographic information systems data) to species distribution records. Despite the prevalence of SDMs in applied ecology, a review of recent papers cautions using a statistical description that implicitly captures these "habitat use" processes as they are statistically associated with the predictor variables, but may not be so biologically. Firstly, habitat use does not necessarily equate with high quality habitat, range requirements, nor resultant increased wildlife fitness because biotic and abiotic cues can cause animals to choose habitats that do not provide the necessary resources to ensure high fitness returns (Jonzén 2008; Pérot and Villard 2009). Secondly, SDMs are frequently applied for predicting potential future distributions of range-shifting species, despite these models' assumptions that (1) species are at equilibrium with the environments, and (2) the data used to train (fit) the models are representative of conditions to which the models are already

statistically associated, and not to which they are anticipated (Elith et al. 2010). Animal responses to novel environments, therefore, especially ones that may be a mismatch to the habitats in which the animal evolved, can render the predictions of SDMs ineffectual. A lack of insight into the processes that govern animal movement and habitat selection can have consequences on the predictive success of SDMs in determining range limits and habitat suitability. This can then have carryover effects on the resolving of spatial issues (such as extent and resolution, geographical- and environmental space), and the statistical methodologies used to test model fit and selection.

Methodological innovations have been recently proposed to improve the predictability of conventional SDMs in spatial modeling of animal-habitat interactions. These newer models incorporate explicit relationships between environmental conditions and organismal performance, which are estimated independently of current distributions. They include: (i) the integration of animal movement and resource-selection models to arrive at biologically-based definitions of available habitat (Fieberg et al. 2010), (ii) the use of state-space movement models (Patterson et al. 2008), (iii) linking species with their environment via mechanistic niche modeling (Kearney and Porter 2009), (iv) and combining resource-selection functions, residency-time and interpatch-movement analyses (Bastille-Rousseau et al. 2010). These emergent efforts have one common, unifying feature: the need to implicitly or explicitly incorporate mechanism; that is, the underlying physiological, behavioral, and evolutionary basis for animal movement and habitat use. The emphasis on improving the statistical fit of SDMs via the incorporation of more ecologically-relevant procedures highlights the multiple advantages when considering the mechanistic links between the functional traits of the organism and its environment. These are: (1) the understanding of the proximate constraints limiting distribution and abundance, (2) the examination of the ultimate consequences of species range effects and population persistence, and (3) the exploration of how organisms might respond to environmental change.

One of the challenges in incorporating mechanism into SDMs is that these models can be limited by the availability of data for model parameterization and because their success in predicting range limits relies on the identification of key, abiotic limiting processes, such as climatic factors, humidity, etc., that have both proximate and ultimate effects on species distributions (Elith et al. 2010). These limiting processes, or constraints, might not be the most important ones, or equally important, in all areas of a species' range. In addition, the interaction between different abiotic constraints and those between abiotic and biotic constraints could cause observed ranges to deviate from predicted ranges. In essence, emergent relationships between the organism and a changing environment cannot be captured by mechanistic SDMs. Lastly, few studies have explicitly incorporated geographic variation in animal traits or genetic variation across a range in mechanistic models, thus essentially ignoring that unique phenotypes may behave in significantly different ways. For a more comprehensive review of correlative versus mechanistic SDMs, we refer the reader to Buckley et al. (2010). In this paper, we present an alternative approach to conventional correlative and mechanistic species distribution modeling, called agent-based modeling that can be used as an effective tool for understanding and forecasting animal habitat selection and use. This methodology offers several advantages. First, it can accommodate ecological and evolutionary theory in the form of behavioral ecology. Second, it can be readily integrated with the concepts of spatial ecology. In doing so, agent-based models (ABMs) can redress the fundamental issues of mechanism, spatial representation, and statistical model evaluation. ABMs can thus enable the exploration of how wildlife might respond to future

changes in environmental conditions - an inquiry of utmost importance for wildlife conservation and management.

This chapter is organized as follows. First, we begin by discussing why animal behavior should be incorporated into studies of wildlife conservation, and how its oversight can lead to erroneous understandings and predictions of critical habitat. We then describe how behavioral ecology provides the basic understanding of the mechanisms driving animal habitat selection and dispersal/migration behaviors; and we argue that it should be incorporated with the concepts of spatial ecology and its geospatial tools. Next, we introduce agent-based modelling and demonstrate how it represents the ideal framework for assimilating behavioral mechanisms with temporal-spatial processes to drive animal movement and habitat selection, and to determine habitat suitability and species distribution. Based on this principle, we then show how the incorporation of spatial behavioral ecology in ABMs can address issues of scale commonly found with the more conventional species-distribution models with regards to extent and resolution, and geographical and environmental space. We also discuss the issues of statistic evaluation of best fit models. We conclude by summarizing the potential of ABMs for wildlife conservation planning, and by suggesting areas for improving their flexibility and performance.

2. Behavior as a key mechanism

2.1 The advantages of addressing behavioral mechanisms over choosing statistical empiricism

As mentioned above, statistical statistical SDMs perform poorly in identifying true habitat quality when the mechanisms driving habitat selection are not explicitly incorporated into the modelling process. This is because strong social interactions, temporally unpredictable habitats, post-disturbance crowding effects, non-ideal habitat selection, and ecological traps all lead to animals either under- or over-utilizing a habitat that produces greater or fewer fitness returns than others available on the landscape, respectively (Johnson 2007; Jonzén 2008). For instance, Mosser et al. (2009) found that density was a misleading indicator of lion (*Panthera leo*) habitat quality in the Serengeti, as this metric identified 'source', high-quality sites that were actually low-quality sites that merely provide refuges for non-reproductive individuals. Over a multi-year and multi-site study of yellow warbler (*Dendroica petechia*) nest microhabitat selection, Latif et al. (2011) found a consistently negative relationship between preferred microhabitat patches and nest survival rates, suggesting that maladaptive nest microhabitat preferences arose during within-territory nest site selection. The authors attribute this mismatch to the recent proliferation of the parasitic brown-headed cowbird (*Molothrus ater*), and/or anthropogenic changes to riparian vegetation structure as likely explanations. These behavioral phenomena will result in SDMs identifying habitats as being suitable foraging, breeding, or dispersing grounds, when in fact there has been a mismatch between habitat use and fitness, with serious ramifications for conservation planning.

Novel or disrupted environments can also violate the assumption of correlational SDMs that animal populations are at equilibrium. Ecological niches may expand or go extinct, affecting population demographics and species ranges via animal behavior in discontinuous or non-linear ways. Schtickzelle et al. (2006) studied how habitat fragmentation modified dispersal at the landscape scale in the specialist butterfly *Proclossiana eunomia*. They showed that

dispersal propensity from habitat patches and mortality during dispersal were the consequences of two different evolutionary responses of dispersal behavior. They concluded that evolutionary responses can generate complex nonlinear patterns of dispersal changes at the metapopulation level according to habitat fragmentation, making predictions of metapopulation effects challenging. Additionally, the success or failure of establishing populations, or altering animal distributions in different environments is mediated by animals that benefit from the presence of conspecifics or heterospecifics after settlement, or are governed by personality-dependent dispersal. In a long-term study of the range expansion of passerine birds, Duckworth and Badyaev (2007) concluded that the coupling of aggression and dispersal strongly facilitated the range expansion of western bluebirds (*Sialia mexicana*) across the northwestern United States over the last 30 years. As such, forecasting the responses of wildlife to changes in their environment without acknowledging the mechanisms involved can give potentially misleading predictions of range effects.

2.2 Conservation behavior as a discipline

Conservation behavior is a relatively new interdisciplinary field aimed at investigating how proximate and ultimate aspects of animal behavior can be of value in preventing the loss of biodiversity (Bushholtz 2007). Animal behavior is an important determinant in species persistence since how an animal behaves determines its survival and reproductive success. In particular, natural selection favors individuals who adopt life history strategies that maximize their gene contribution to future generations. Expression of these strategies typically manifests itself through the behaviors of the animal that possess a heritable component sufficient to allow natural selection to operate. Thus, the behaviors of animals attempting to maximize their lifetime fitness will affect survival, reproduction, and hence recruitment, ultimately scaling up to the population level and species persistence.

Indeed, many of the initial responses by animals to environmental change are behavioral i.e., changes in feeding location, prey selection, or movement responses to disturbance. Behavioral indicators can provide an early warning to population decline or habitat degradation before numerical responses are evident. Similarly, they can be used to monitor the effectiveness of management programs, or evaluate the success of a management program at its early stages, before population or ecosystem-level responses are evident (Berger-Tal et al. 2011). While these concepts may seem atheoretical and merely descriptive, there is a strong incentive to understand the underlying motivations involved in animal responses to anthropogenic impacts and their mitigation. As an illustrative example, when managers plan for critical habitat, it is imperative to ensure: (1) that enough cover is present so that the animal does not spend an excessive amount of time being vigilant at the expense of acquiring its energetic requirements, (2) that the food resources available will not cause the animal to spend excess time searching or assimilating their forage at the expense of other activities such as dispersing successfully, breeding or caring for young, (3) that animals are not crowded into habitats so that foraging-interference or -exploitative competition occurs, thereby reducing food intake and potentially affecting health and reproduction, and (4) that human-induced alterations in food availability do not cause animals to modify their foraging behavior to the extent that natural history traits are altered and potentially maladaptive. As is apparent, animals must constantly trade off competing strategies to try to find the optimal solution to successfully survive and reproduce in their environment. Using a conservation behavior approach, we can understand such relationships that are critical to survival of individuals and persistence of populations.

2.3 Behavioral ecology - providing the mechanism

Behavioral ecology is a field of animal behavior that can be used to investigate fitness impacts of organismal interactions with their environment, since it seeks to understand both the ecological and evolutionary basis of animal behaviors. There are three fundamental types of adaptation that allow individuals to adjust to the environment: phenotypic plasticity, learning, and genetic (Huse and Giske 2004). These adaptations partly determine individual behavior, and whichever is dominant will depend on the current circumstances and the different timescales on which they function. Adaptation functions by animals making tradeoffs between competing goals to try and find an optimal solution that maximizes their fitness. Behavioral ecology therefore attempts to understand how an individual's behavior is adapted to the environment in which it lives, and how a particular behavior pattern contributes to an animal's chances of survival and its reproductive success (Krebs and Davies 1996). Furthermore, because anthropogenic change can disrupt optimal decision-making and affect an animal's reproductive success and survival, behavioral ecology can be a key ecological indicator when assessing wildlife fitness impacts. Within the field of behavioral ecology, there are three key behavior domains that are central to the attainment of high fitness in individuals of all species and are therefore of key concern in habitat-suitability and species-range effects management: foraging and predator–prey related behaviors, social behavior and reproduction, and life-history strategies (Caro 1998, Gill and Sutherland 2000, Festa-Bianchet and Apollonio 2003, Berger-Tal et al. 2011).

2.4 Spatial behavioral ecology - one step further

Because most wildlife management directives occur *in situ*, these domains are inherently related to spatiotemporal variations in landscape, and indeed, behavioral ecologists can benefit by assimilating the tools and the concepts developed in spatial ecology (Valcu and Kempenaers 2010). The following section focuses on how behavioral ecology combined with spatial ecology can be used to explain and explore space-use and movement patterns in wildlife.

2.4.1 Habitat selection

Conservation of a species requires knowledge of the habitat use of both sexes in order to predict the population size and to protect the habitats that a species requires. Habitat selection is the behavioral process used by individuals when choosing resources and habitats. From a behavioral ecology perspective, habitat selection implies that individual organisms have a choice of different types of habitat available to them, and that they actively move into, remain in, and/or return to certain areas over others (Stamps 2009). When faced with a site in which to forage, rest, or mate, an individual will rely on abiotic and biotic cues that will help shape the behavioral rules (optimal group size, anti-predator tradeoffs, foraging efficiency) and tactics (e.g., natal home range cues, public information cues and conspecific attraction) to make an optimal selection at various spatial and temporal scales (Johnson 1980).

Investigating habitat selection with a behavioral-ecological focus and using local, fine grain spatial parameters is common practice. However, more behavioral ecologists are availing themselves to the data-capturing tools and techniques offered by geographic information science, such as telemetry, remote sensing, and sensor networks, and incorporating larger-scale analyses to understand the complexities involved in animal habitat choice and use.

Indeed, behavioral ecology often contributes to habitat-selection studies and 'confounds' analyses relying just on empirical relationships between an organism and its static environment. Using GPS telemetry monitoring, Fischhoff et al. (2007) examined variation in plains zebra (*Equus burchelli*) movements and habitat use in relation to danger from lions. They found predator avoidance and predation risk to be the main drivers of habitat choice and movement patterns, and concluded that individual variation in zebra responses can affect individual variation in survival. Willems et al. (2009) used a remotely sensed index of plant productivity as a spatially explicit and temporally varying measure of habitat structure and productivity for the study of vervet monkey (*Chlorocebus pygerythrus*) habitat preferences. Using both broad spatiotemporal scales and finer grained level of analysis, they were able to relate home-range use to food availability, and anti-predatory responses to changes in habitat visibility using their index of vegetation productivity. Durães et al. (2007) evaluated whether female hot spots can account for patterns of lek structure in the blue-crowned manakin (*Lepidothrix coronata*) by modeling female distribution patterns relative to lek locations using radio-telemetry. The authors found a lack of spatial correlation between males and females, and concluded that refutation of the hotspot hypothesis renews the debate on how leks evolve and are shaped, and emphasizes that spatial considerations are an important issue for lek evolution that likely involve multiple interacting mechanisms. Lastly, using a combination of animal- and environmental-GPS point locations and satellite imagery, Greisser and Nystrand (2009) studied the influence of large-scale habitat structure on the vigilance levels of kin- and non-kin Siberian jay (*Perisoreus infaustus*) groups to aerial predators. They found that different foraging habitats, differentiated by large-scale metrics, had different levels of predation risk, and these were partially mediated by whether or not jays were in groups with offspring. The authors surmised that large-scale habitat structure influences predator–prey interactions; and therefore antipredator allocation is crucial to understanding spatial variation in habitat use and individual jay mortality. The above examples showcase the need of interrelating spatial data at fine and broad scales with fitness-maximizing behaviors and demonstrate the applicability of this approach in elucidating the array of factors involved in habitat use.

2.4.2 Dispersal and migration

Non-foraging movements of animals within a heterogeneous landscape are recognized as the key process influencing meta-population dynamics, the coexistence of competitors, community structure, disease ecology, and biological invasions (Morales and Ellner 2002). It is not surprising then, that most effort by conservationists has focused on the dispersal and migration requirements of animals. Animal dispersal consists of two component behaviors: (i) emigration out of an original habitat patch and (ii) subsequent search for a new habitat patch. Emigration is assumed to depend on the chance rate of encounter with habitat boundaries, and dispersers are assumed to search for new habitat in the manner of a correlated random walk (Conradt and Roper 2006). The decision-rules of animal movement, however, have a very strong behavioral component that is influenced by both endogenous and exogenous factors. Physiological and motivational states, perceived travel costs in terms of predation risk, and the distance at which a dispersing animal can perceive remote habitat will determine whether an animal will cross habitat gaps formed by fragmentation (Zollner and Lima 2005). Susceptibility to competition as well as level of conspecific attraction will also play an important role in determining the movements of individuals (Bélisle 2005).

Whether an animal needs to migrate to find resources or exploits resources from a central place to which it periodically returns will also affect the degree of impact from sub-optimal habitat quality, size, and connectivity. In other words, the movement paths of wildlife result from the dynamic interplay of the internal state of the organism, its motion capacity, its navigation capacity, and the external environment (Holyoak et al. 2008, Revilla and Wiegand 2008).

As with habitat-selection studies, behavioral ecologists also employ GIS techniques to both represent the environment and collect wildlife movement data when studying animal dispersal and migration. For instance, Long et al. (2008) investigated emigration cues and distance of transitional movements in white-tailed deer (*Odocoileus virginianus*), and found that both inbreeding avoidance and mate competition ultimately underlie emigration of juveniles, and that, proximately, these patterns of dispersal are elicited by different social cues during different seasons. Using ruffed grouse (*Bonasa umbellus*), Yoder et al. (2004) tested the hypothesis that increased movement rates during dispersal bouts increases conspicuousness and hence predation-related mortality of individuals. Contradictorily, they found that movement rates and distance moved did not predict bird mortality; instead, it was the familiarity with the site itself which determined the birds' survival. Lastly, a study by Hebblewhite and Merrill (2009) investigated how trade-offs between predation risk and forage differ between migrant strategies in migratory elk (*Cervus elaphus*). Each strategy had its associated costs and benefits, with resident elk balancing increased predation risk with refugia caused by human activities. These examples again highlight that the success of managers and policy makers when planning critical habitat for species conservation depends on a spatial *and* mechanistic understanding of the species in question.

2.5 Behavioral ecology and the individual

On a final note, it is crucial to realize that behavioral ecology concerns itself with the adaptations of *individuals*. Although inter-individual variation in phenotypic traits is omnipresent, it has historically been considered to be noise superimposed on the evolutionarily important signal, the population mean (Careau et al. 2008). But a rapidly growing literature on animal personality, temperament, coping styles, and behavioral syndromes (Stampes and Groothuis 2010) reveals the increasing importance researchers place on inter-individual variation as an important ecological and evolutionary characteristic of wild populations. Individuals are the building blocks of ecological systems - the birth and death of individuals are the constituents of the birth and death rates of populations, and because these rates are the result of the assimilated effects of varying and different fitness-maximizing behaviors that are used by each individual, population structure, demography, and community structure can be significantly affected by variation in the behavior of individuals (Bradbury *et al.* 2001). The approaches explained so far describe the relationships existing between a given individual organism, which is influenced by its need for basic resources (e.g. water, food, security cover, space), and the spatial distribution of such resources. As explained above, individuals are spatially clustered around resources and the spatial distribution of animals and plants can therefore be predicted. However, most animals and plants also have the need to encounter conspecifics and to reproduce. Therefore, populations are formed comprised of multiple individuals that are associated to spatially distributed resources and to each other, and these are the units that survive or go extinct during the evolutionary process. Subsequently, population-level properties such as persistence, resilience, and patterns of abundance over space and time are

not simply the sum of the properties of individuals; instead, they emerge from the interactions of adaptive individuals with each other and with their environment (Figure 1). These links make models of spatial distribution of organisms and of populations relevant and crucial for the following conservation purposes: to predict spatial occurrence of populations, population sizes that resources can sustain, connectivity among populations, and their very chances of survival. As such, models of species distribution and habitat suitability should therefore consider individual mechanisms of habitat selection and movement coupled with spatially explicit representations of the animal's environment.

2.6 Behavioral ecology and SDMs

The call for integrating behavioral ecology into spatially explicit species distribution and range models is not new. Blumstein and Fernández-Juricic (2004) suggest that specific behavioral mechanisms should be the basis of bottom-up models that predict the behavior, movement, habitat use, and distribution of species of conservation concern. Morales and Ellner (2002) further posit that the challenge for scaling up movement patterns resides in the complexities of individual behavior, specifically behavioral variability between individuals and within an individual over time, rather than solely in the spatial structure of the landscape. Bélisle (2005) also advocates for the use of behavioral ecological resource-based
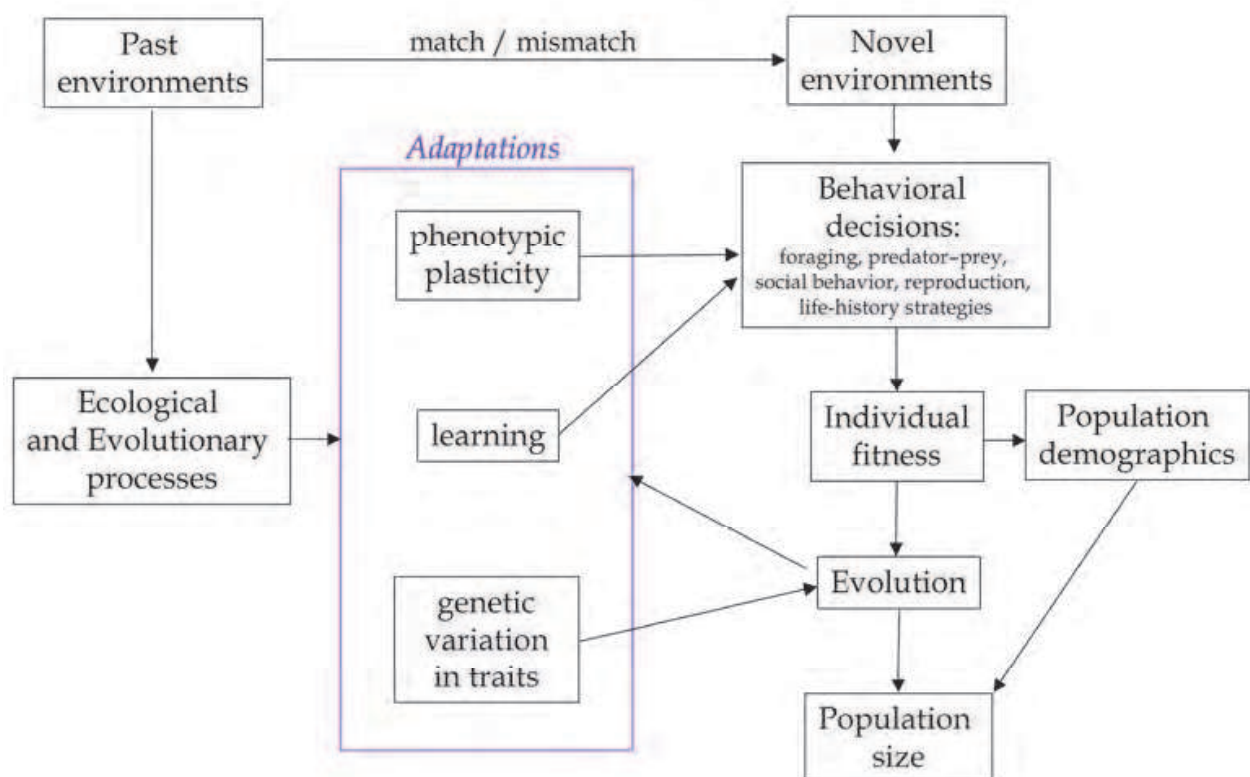

Fig. 1. Summary of how behavioral decisions, driven by animal adaptations that have evolved over time from ecological and evolutionary processes, can match or mismatch an animal to its environment. This process has cascading direct and indirect effects on population and species persistence via individual-fitness effects on population demographics and evolution of species' traits. Modified from Lankau et al. (2011).

models in judging habitat quality, travel costs, and hence landscape functional connectivity. Specifically, these latter types of models would be capable of addressing the distribution of individuals among resource patches at large spatial scales, among resource patches embedded within a hierarchy of spatial scales, and along smoothly changing resource gradients. Finally, Jonzén (2008) acknowledges that while habitat selection theory has a successful history in behavioral ecology, it can also be useful for understanding spatial population dynamics on a large scale. We propose here that the principles of behavioral ecology can be quite naturally and readily integrated with the tenets of spatial ecology in the alternative approach to SDM:

3. Agent-based models

Agent-based models (ABMs) are computational simulation tools that rely on a bottom-up approach that explicitly considers the components of a system (i.e. individual entities represented as agents) and attempts to understand how the system's properties emerge from the interactions among these components (Grimm 1999, Grimm and Railsback 2005). 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; Figure 2a), and additionally allows the use of ABMs for the exploration of complex phenomena that are ill-suited to analytic approaches (e.g., statistical models; Tang 2008).
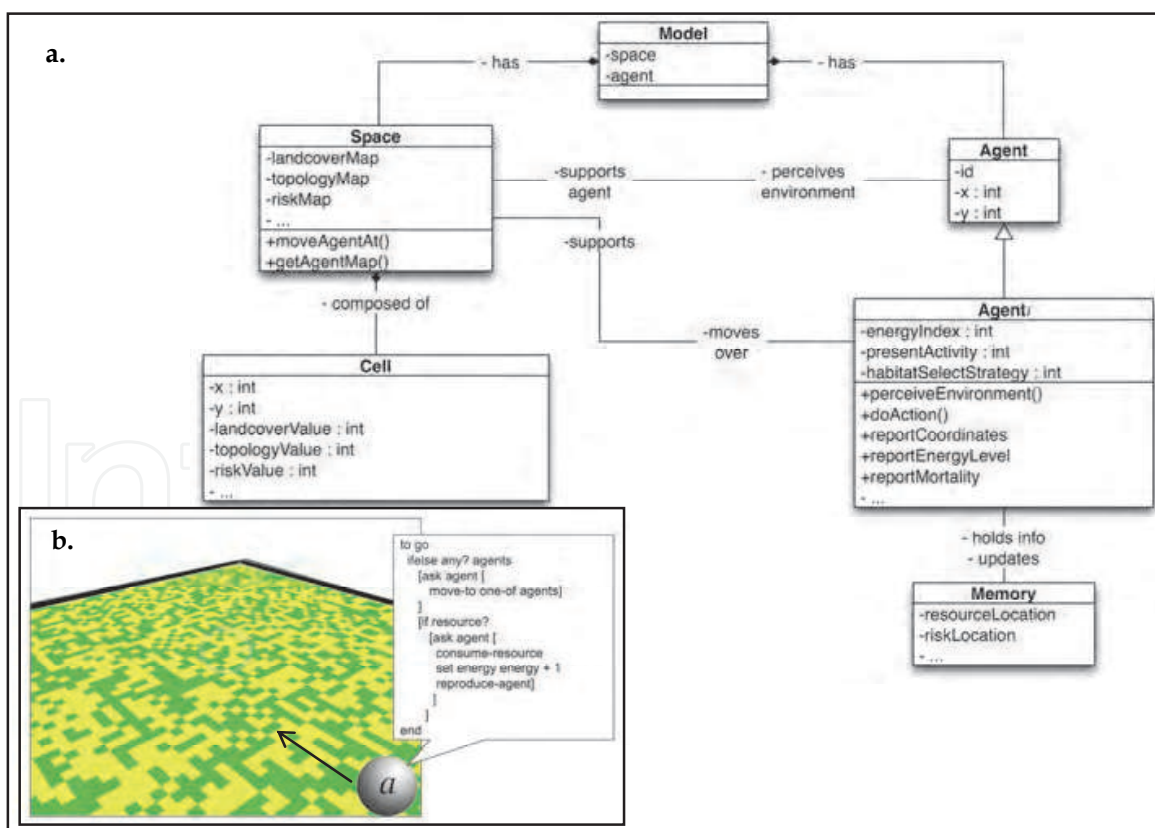

Fig. 2. ABM architecture. a) Example of an ABM conceptual diagram demonstrating how agents are tightly coupled to their environment. b) Generic programming language, giving rise to agent (*a*) autonomy and intelligence.

The concepts underlying ABM are similar to those of the object-oriented programming paradigm in computer science, and ABMs frequently employ object-oriented programming languages like C++ and Java (An et al. 2005; Figure 2b). Because of this architecture, the most critical feature of ABMs is their ability to reproduce artificial intelligence. Agents can explicitly execute decision-making heuristics - symbolic rules or numerical functions - that can be either predefined (e.g., expert knowledge or statistical inferences) or learned through their interactions and feedback with other agents or their environment (e.g., via memory or machine learning techniques like genetic and evolutionary algorithms; Russell and Norvig 1995, Tang 2008). These agents act 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 surroundings. It is these characteristics of ABMs that make their amalgamation with animal mechanisms of habitat selection and movement so ideal as they share the same principles of behavioral ecology: animal adaptation, individual variation, and fitness-maximizing tradeoff behaviors.

3.1 Behavioral-ecological ABMs and species distributions

ABMs have been developed to expressly evaluate wildlife habitat suitability and species range effects via habitat-selection and movement studies. These ABMs can be divided into categories depending on whether agents are given imposed, empirically-derived behaviors, or agents are allowed to choose the optimal strategy themselves based on decision-making tradeoffs (for a thorough review, see McLane et al. 2011). The latter category is the focus of this section, as it most closely represents the tenets of behavioral ecology (Figure 3). As one example of habitat suitability and its underlying habitat-selection behaviors, Kanarek et al. (2008) incorporated habitat selection in their ABM of environmental fluctuations on a barnacle geese (*Branta leucopsis*) population in Helgeland, Norway. The aim of each individual was to optimize fitness (survival and reproduction) by gaining enough food (energy reserves) to meet a threshold of energy necessary for successful reproduction. In their model, geese chose 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. Their findings revealed that different types of population dynamics and patterns of colonization occur, depending on the strength of site fidelity and degree of habitat loss. Duriez et al. (2009) investigated the decision rules of departure and stopover ecology of the migratory behavior of geese (*Anser brachyrhynchus*) between wintering grounds in Denmark and breeding grounds in Svalbard, Norway. They tested rules governed by energetics, time-related cues and external cues 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. They also found that by changing decision rules 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, they could improve ABM model predictions of site selection.
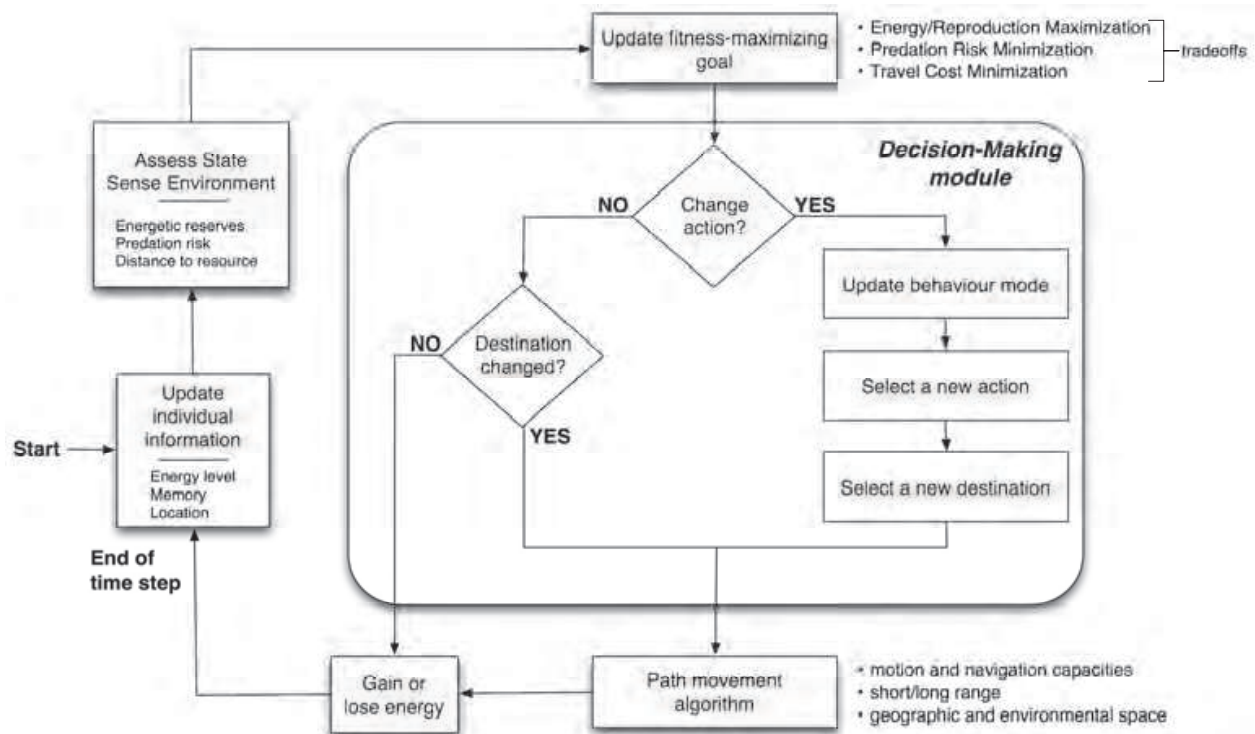
Fig. 3. An agent's decision-making heuristics in a behavioral-ecological ABM.

With respect to range-limiting effects and migration, Pettifor et al. (2000) used an agent-based approach to predict the response of goose populations to both natural and human-induced environmental changes. They used contrasting time-minimizing vs. energy-maximizing foraging strategies as well as a game theoretic approach of competitor density to determine year-round dynamics of the goose populations. Populations were predicted to decline following habitat loss in their winter or spring-staging sites, providing a clear illustration of the need for a year-round, individual-behavior approach to animal population dynamics. Lastly, Goss-Custard and Stillman's (2008) seminal work on oystercatcher (*Haematopus ostralegus*) management elegantly demonstrates how mechanistic ABMs can contribute to the conservation of local populations' occupancy and species persistence. The overall purpose of their ABM was to predict how environmental change (e.g., habitat loss, changes in human disturbance, climate change, mitigation measures in compensation for developments, and changes in population size itself) affects the survival rate and body condition in animal populations. The model does this by predicting how individual animals respond to environmental change by altering their feeding location, consuming different food or adjusting the amount of time spent feeding. The central assumption of the model is that animals behave in ways that maximize their chances of survival by using rate-maximizing optimization decision rules and game theoretic rules in that each animal responds to the decisions made by competitors in deciding when, where, and on what to feed. They found that even small reductions in fitness can substantially reduce population size of shorebirds since their "ecological food requirement" greatly exceeds the "physiological requirement".

As has been demonstrated, the use of behavioral-ecological based ABMs 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 mechanical,

empirically-derived traits can also provide a feasible 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 wildlife management such as ecological forecasting. In fact, SDM approaches may not reliably ascertain whether the empirical relationship upon which these models are based will hold under new environmental conditions

To have confidence in predictions, models need to operate on basic principles, underpinned by theory that will still apply in the new scenarios, rather than on present-day empirical relationships which may no longer hold in the scenarios for which predictions are required (Grimm et al. 2007). The allocation of behavioral strategies to individual agents allows researchers 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). Finally, with ABMs intra-specific relationships among individuals can also be modeled, thus allowing better understanding of population responses to the environment and to conspecifics as well as other organisms (e.g. competitors, predators, parasites).

4. ABMs and issues of scale

All types of animal-environment models need to allow for the determination of where the important interactions lie and to understand both the spatial scales and time scales on which the various processes operate (Bithell and Brasington 2009). This is particularly the case where the issues of conservation planning and ecological forecasting are concerned, as these typically involve spatial scales that can cross political borders, temporal scales longer than the organism's lifespan, and the need for long-term institutional policies to be effective. 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 at the adequate spatial and temporal scale can improve the effectiveness of wildlife management as it can highlight the causal links between organism movement and environmental change (Nathan et al. 2008; Figure 4).

4.1 Extent versus resolution

Although various approaches exist, there is as yet little consensus on how to deal with scale disparities - such as extent and resolution, when fitting SDMs (Barry and Elith 2006; Elith and Leathwick 2009). While there is no single scale at which ecological patterns should be studied (Levin 1992), mismatches between coverage and grain can be caused by the study goals, the system, data availability, and by extent to which a species perceives its environment. Some SDMs attempt to address these issues by incorporating hierarchical structures into the modelling process, either through the use of sub-models, through Bayesian approaches that operate across scales, or through models that allow nested structures of data (reviewed in Elith and Leathwick 2009). However, these different approaches remain untested both theoretically and practically, nor is it certain whether these scale-specific model predictors provide a clear advantage over traditional SDMs (Barry and Elith 2006).
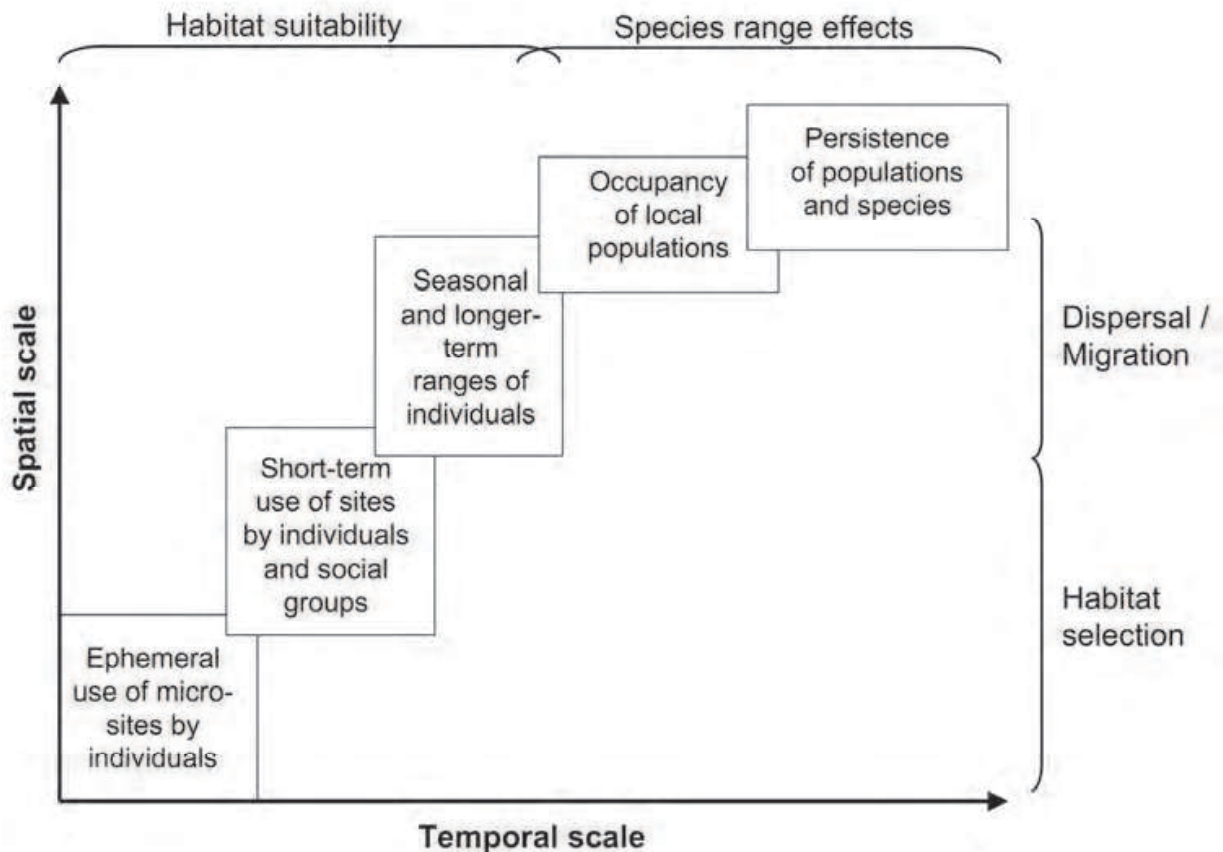
Fig. 4. The link between spatial and temporal scales of habitat selection and dispersal/migration and conservation planning of habitat suitability and species range effects. Modified from Mayor et al. (2009).

Agent-based models are particularly well suited to represent a virtual geographic environment within which entities and their interrelationships (e.g., spatial, temporal, and spatiotemporal) can be explicitly described, and provide contextual information to which agents sense and respond (Tang 2008). In agent-based modelling, the movement trajectory or pathway of an animal can be represented as a sequence of discrete time-stamped location variables, for example, geographic coordinates. Because environment representation in ABMs can be raster- or vector-based, the location variables can be further indexed by raster cells or vector-based patches (Tang and Bennett 2010; McLane et al. 2011). ABMs are not completely immune to issues of scale. Scale factors can affect the design and application of agent-based models particularly when temporal landcover changes are incorporated. To deal with spatial constraints, Evans and Kelley (2004) recommend that models be run at a range of spatial scales. Then modelers can choose the minimally-acceptable resolution by identifying the spatial resolution at which agents have sufficient partitions on their landscapes within which to make biologically-relevant decisions pertinent to the study goals (minimum change unit), and where the heterogeneity of the landcover and land suitability measures are adequately represented. The coarsest, or upper bound, resolution for model runs can be identified by the resolution at which appreciable data loss occurs (e.g., the disappearance of potentially relevant cover classes).

Despite the universal confounds of scale regardless of the modelling methodology used, ABMs are still more decoupled from scale issues than SDMs as the researcher can address the extent- and resolution-issues by developing a model that makes the best statistical use of information at the finest spatial and temporal resolution available; and then allowing large-scale behavior to emerge from the small scale via interaction between these model elements (Parker et al. 2003; Bithell and Brasington 2009). In addition, because ABMs incorporate ecological theory, and deal with processes and mechanisms at the level of the individual, the resultant hierarchical phenomena that emerge from agents' interactions with others and their environment can naturally accommodate issues of scale (Breckling et al. 2006). As an illustrative example, Bennett and Tang (2006) combined cell- and patch-based approaches to represent multi-scale environmental representation in their elk migration model. Agent elk performed local movement at the cell level, but were capable of perceiving and using greater scale, patch-level information to guide their long-distance winter migration. In the wolf (*Canid lupus*) ABM study of Musiani et al. (2010), their canid agents were able to perceive disturbance (i.e., bear and human agents) at a 200m scale, and able to detect prey (elk) at a 3km scale, travel accordingly, and allow pack home range dynamics to emerge from these interactions and behaviors.

Multiscale detection does not have to only be via the the agent's immediate perception of heterogeneous landscapes features and/or agents at different scales, but through its memory processes. In an ABM study of the effect of anthropogenic landscape change on disease of red colobus monkeys (*Procolobus rufomitratus*) populations (Bonnell et al. 2010), monkey agents were able to remember the location and quantity of past resource sites that contained a significantly higher amount of resources (i.e., spatial memory), allowing red colobus agents to estimate resource levels at these sites while not within their search radius. This allowed for a more biologically-relevant prediction of the optimal distribution of resources which could facilitate the spread of an infectious agent through the simulated population. ABMs, through a multi-scale environmental representation, can therefore support the investigation of scale issues and even facilitate our understanding of individual movement behavior in response to spatiotemporal heterogeneity on landscapes in ways in which traditional SDMs cannot (Figure 5).
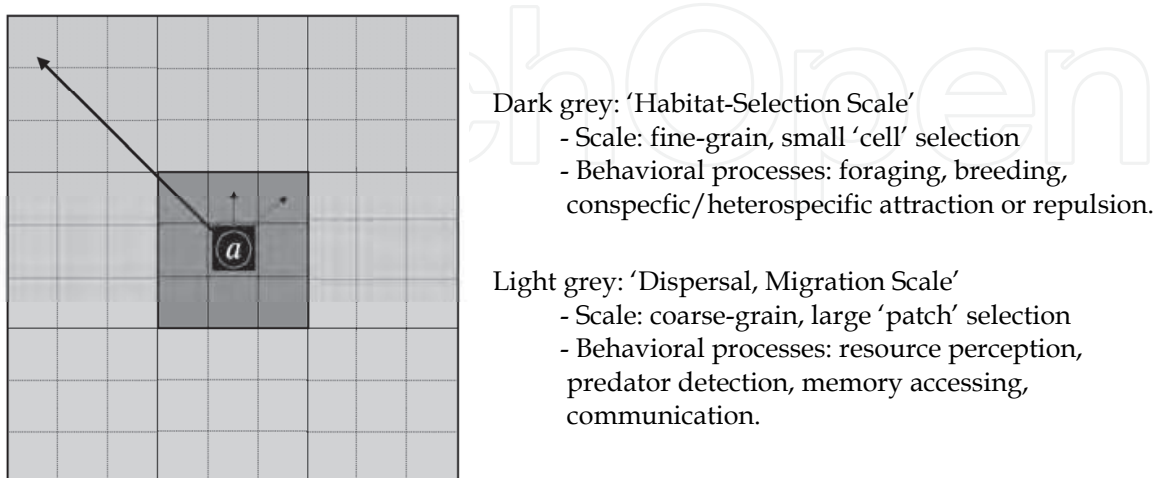

Dark grey: 'Habitat-Selection Scale'
- Scale: fine-grain, small 'cell' selection
- Behavioral processes: foraging, breeding, conspecfic/heterospecific attraction or repulsion.

Light grey: 'Dispersal, Migration Scale'
- Scale: coarse-grain, large 'patch' selection
- Behavioral processes: resource perception, predator detection, memory accessing, communication.

Fig. 5. Multiscale habitat selection of an agent (*a*) in a spatially-explicit space.

4.2 Geographic versus environmental space

Another issue in SDMs is the distinction between geographic and environmental space. For example, two animal locations may be very close in geographic space, but the two points may be in completely different habitats. Important geographic predictors include glaciation, fire, contagious diseases, and connectivity (Elith and Leathwick 2009). Environmental factors primarily deal with abiotic and biotic processes such as resource distribution, social factors, and predation risk. Purely geographic SDMs, when attempting to derive habitat suitability and extrapolate findings to predictive species-range modeling, may ignore important environmental predictors. Equally, SDMs that solely incorporate environmental variables have difficulty in mapping their predictions onto geographic space as species distribution simply reflects the spatial autocorrelation of the environment. Current methods using both geographic and environmental predictors in SDMs (examples include species prevalence, latitudinal range / marginality, and spatial auto-correlation), while a promising compromise, can affect modelling performance and species predictions, with contradictory results (Marmion et al. 2009). Furthermore, these combined-effects models are more difficult to implement than standard techniques so they are under-utilized, and the emerging recommendation is to simultaneously apply several SDM methods within a consensus modelling framework (Grenouillet et al. 2011).

ABMs are capable of representing both geographic and environmental space cohesively. This is accomplished by coupling ABMs to geographic information systems (GIS) that provide detailed abiotic and biotic characteristics of the environment (e.g., land cover, elevation models, resource distributions, risk), and having agents assign values to these geographic and environmental attributes either via a weighting function (like a friction map) or independently (Brown et al. 2005; Figure 6). The decision-making behaviors of agents therefore consider the spatiotemporal variation of the landscape itself; and the ABM accommodates how this variation feedbacks onto behavior in dynamic, non-predictable and non-linear ways. Specifically, an animal's location in space and time, the way it perceives the surrounding landscape, and its subsequent behavior all determine what resources are accessible to it and what it chooses among those resources (May et al. 2010). In ABMs, the scale and degree of heterogeneity within the landscape will be perceived in different ways by different species, and thus an animal's perception will influence its movement behavior, choice of search strategy and habitat patch choice (e.g. Lima and Zollner, 1996).

In essence, by allowing agents to explicitly interact with, modify, and respond to their environs, geographic and environmental predictors are both naturally incorporated into the agent's decision-making process. Any habitat-selection or movement patterns that then emerge will be more robust to the uncertainties involved in future predictions of species occupancy and range effects since specific geographical factors (e.g., barriers to movement, events) and spatial autocorrelation are directly represented and assimilated into the model. As an illustrative example, Rands et al. (2004) created a state-dependent foraging ABM for social animals in selfish (i.e., non-kin) herds. In the model, the agents tradeoff protective herding versus individual foraging behavior, with the individual basing its decisions upon its energy reserves, the distribution of foraging resources in the environment, and the perceptual range over which individuals are able to detect conspecifics, risks, and resources. The resulting behavior and energetic reserves of individuals, and the resulting group sizes were shown to be affected both by the ability of the forager to detect conspecifics and areas of the environment suitable for foraging, and by the distribution of energy in the environment. Both environmental (presence of conspecifics) and geographic (spatial

detection of resources) are considered independently of one another with this model. Grosman et al. (2009) developed an ABM to investigate management strategies that would reduce moose-vehicle collisions through salt-pool removal and displacement. The moose agents forage and travel in the Laurentides Wildlife Reserve, Quebec; and assess patches to visit and disperse through based on a weighted assessment of both geographic and environmental factors of food quality, cover quality (protection from predators and thermal stress), proximity to salt pools, proximity to water, and slope. The realistic patterns which emerged from the simulations revealed that the most successful management action was complete removal of salt-pools without any compensatory ones to ensure moose (*Alces alces*) survival.

The ABM examples used in this section either comprised behavioral mechanisms in a spatially-implicit environment, or incorporated and modeled empirically-driven behaviors of agents (e.g., probabilistic, mechanical 'decision-making') on spatially realistic landscapes. Each proved very capable of accommodating multiscale agent behaviors and multi-environmental factors in reproducing the desired results. We believe, however, that integrating multi-scale and -environs using more behavioral-ecological based mechanisms in spatially realistic contexts (of which explicit examples in the literature are not yet available) will prove to be even more beneficial. When combined with behavioral mechanisms, the realism and applicability of the model will increase multi-fold, and the capacity of these ABMs 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 will represent a powerful tool in conservation planning and ecological forecasting.
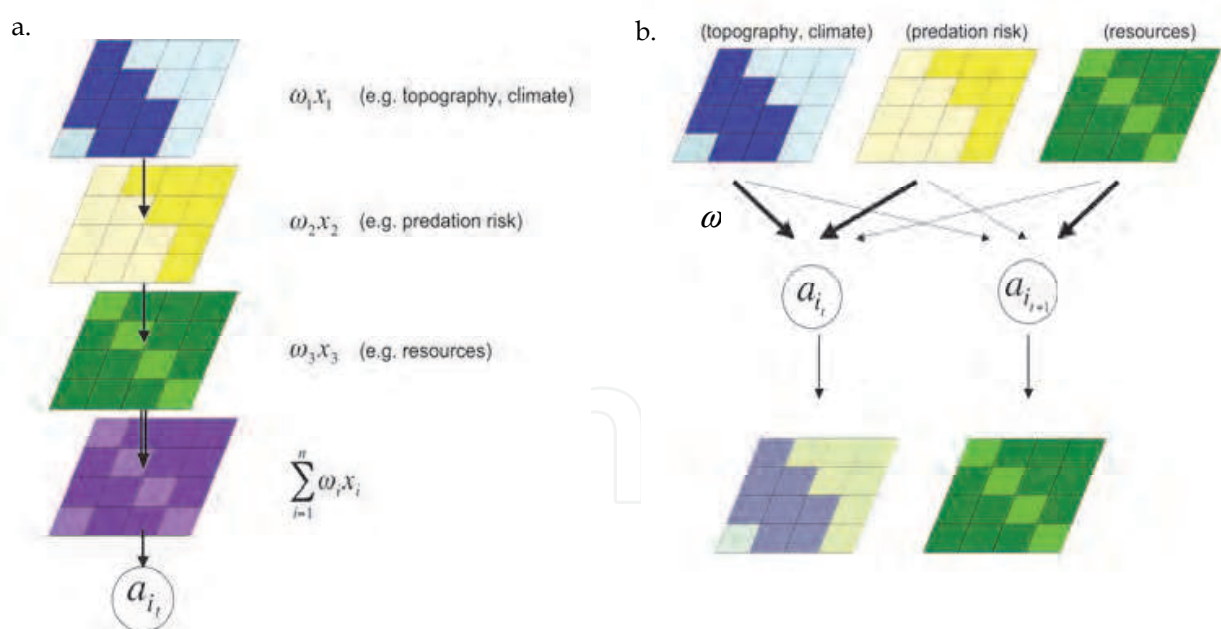

Fig. 6. Examples of how an agent perceives its environment. a.) Geographic and environmental variables are given specific weights (*w*) based on the agent's habitat preferences at the initialization of the model, and the agent assesses its environs based on the integration of these factors which remain unchanged throughout the simulation. b.) Geographic and environmental variables are independently assessed by the agent at each time step, and factors are weighted based on the agent's internal state, and/or fitness-maximizing goal at that time step.

5. ABMs and model evaluation

Because SDMs are essentially statistical models, it is necessary to consider the compatibility between statistical model evaluation and selection of predicted versus observed species distributions and the underlying ecological model. The principle of model selection is to formulate different verbal hypotheses, express these hypotheses mathematically as statistical models, evaluate a score of a goodness-of-fit indicator for each statistical model, and either strongly select one hypothesis or keep a set of plausible ones with different weights (Piou et al. 2009). There still exists a lack of agreement amongst SDM researchers about the most effective statistical methods to evaluate and predict the spatial distribution and habitat selection of animal species, and the degree of ecological realism inherent in the statistically 'best-fit' model (Keating and Cherry 2004; Guisan and Thuille 2005; Austin 2007; Elith and Graham 2009). The main reason is that different statistics are used for the various different models, each one measuring different aspects of performance, and as such, appropriate statistics relevant to the application of the model need to be selected.

ABMs use an altogether different approach, known as pattern-oriented modeling (POM). This protocol is based on the assumption that patterns are the defining characteristics of a system and are indicators of essential underlying ecological structures and processes. Patterns are defined by Grimm et al. (2005) as any observation made at any hierarchical level or scale of the real system that display non-random structure. Patterns are therefore particular expressions of a given comportment of the studied individuals, populations, or system. 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 et al. 2005).

POM capitalizes on both behavioral ecology and spatial ecology through the emergence of biologically- (and behaviorally-) relevant patterns at multiple scales to evaluate model results. For example, the emergence of a pattern generated by a tradeoff between the costs and benefits of a decision process could explain the selection pattern of certain habitats, leading to specific step length and turning angle distribution patterns, and allowing the reproduction of home range characteristics to emerge (Latombe et al. 2011). This modelling approach allows one to simultaneously filter combinations of parameter values and model structures in order to achieve the aims of testing the behavior of the agents in the model and of reducing parameter uncertainty. The greater the number of real-world patterns that can be simulated concurrently, the greater the confidence in the model, and typically the smaller the possible parameter space (Topping et al. 2009). By extension, the POM approach can additionally allow for rigorous statistical approaches. Information theory and information criteria have been recently developed for the POM method, and serves to further improve the agent-based modeling framework (Piou et al. 2009). The approach can be used to analyze separately the different patterns of focus, and analyze together an overall level of evidence of each model to all the patterns. This approach is more universal than the various methods of SDMs model evaluation, and can be applied to very different types of agent-based models.

POM has been used extensively and demonstrates a strong utility in addressing model complexity, unknown data requirements, variable parameterization, and model evaluation. As an example, Railsback and Harvey (2002) created an ABM to simulate habitat selection of

salmonid fish species in response to spatial and temporal variation in mortality risks and food availability. They used their ABM to draw conclusions about foraging theory by analyzing the ABM's ability to reproduce six patterns of habitat selection by contrasting three alternative habitat-selection objectives: maximizing current growth rate, current survival probability, or expected maturity. In the model, fish based their daily decision on the projection of current habitat conditions for a certain number of days into the future, as this strategy was capable of reproducing a set of six patterns observed in reality. Rossmanith et al. (2006) developed an ABM to test the impact of three behavioral scenarios on population persistence of the lesser spotted woodpecker *Picoides minor*: strict monogamy, polyandry without costs, and polyandry assuming costs in terms of lower survival and reproductive success for secondary males. Using a POM-approach where the model was simultaneously fitted to a set of four empirically observed patterns (adult sex ratio, ratio of old and new pairs, proportion of nest producing at least one fledgling, number of fledglings per successful nest) to produce a realistic population structure, the authors found that polyandry and in general flexibility in mating systems is a buffer mechanism that can significantly reduce the impact of environmental and demographic fluctuations that cause variations in the population's growth rate. Consequently, they suggested that rare, exceptional behavior should be considered explicitly when predicting the persistence of populations. Lastly, Tyre et al. (2007) explored behavioral mechanisms for home range overlap in a Scincid lizard, *Tiliqua rugosa*. The authors tested two mechanisms, one that used refuge sites randomly and one that included a behavioral component that incorporated refuge sites based on nearest neighbor distances and use by conspecifics. Comparisons between the simulated patterns and the observed patterns of range overlap provided evidence that the behaviorally-driven refuge use model was a better approximation of lizard space use. In sum, pattern-oriented modelling presents an effective method for identifying and evaluating behavioral mechanisms of habitat selection and animal movement underlying observed patterns.

6. Conclusion

In a recent paper, Caro and Sherman (2011) state that the field of behavioral ecology is at a key turning point in its history. While the discipline was originally created with the intent of developing explanatory theories of ecological and evolutionary adaptations of organisms, future studies should be designed to provide information for the protection and management of organisms that are increasingly being compromised in human-dominated landscapes because of species extinctions, habitat destruction, invasive species, pollution, and climate change. The authors posit that behavioral ecology and conservation biology can be linked by forecasting how anthropogenic ecological changes are liable to reshape specific aspects of behavioral ecology during the 21st Century. We would like to further add that Caro and Sherman's 'call to arms' can be accomplished in one manner by integrating behavioral ecology with spatial ecology in agent-based models for conservation planning.
As we have shown, ABMs have multiple advantages: they incorporate and embody individual variation, adaptation, emergence from interactions, geographic and environmental space, short- and long-range spatial scales, multiple processes, and hypothesis testing to identify the most influential mechanisms. In doing so, ABMs can reduce uncertainty and increase model fit in the identification of habitat suitability and in the prediction of long-term species responses to environmental change. In addition, ABMs

are ideally suited to work across spatial and temporal scales and on individuals and populations of organisms, thus reaching the most meaningful scale in conservation biology. ABMs also have the ability to incorporate dynamic interactions between individuals, whether they be competitors, predators, or even humans (e.g., hunters, recreationists). Since the models are not constructed to meet a set of equilibrium criteria, they can additionally produce discontinuous and nonlinear phenomena, such as species extinctions, range shifts, and exponential growth or decline of populations (Parker et al. 2003). And to reiterate, employing behavioral ecological concepts to reproduce the underlying mechanisms can aid in overcoming the issues typically associated with traditional SDMs.

Our intent here is not to suggest ABMs replace statistical SDMs. They simply represent a promising alternative approach. Spatially-explicit, behavioral-ecological based ABMs are still rare; most models found in the literature are empirical and/or are based in implicitly-structured spatial environs (see McLane et al. 2011 for a review). ABMs also need more testing and comparisons, of their own predictions and with those of other models, although there has been recent progress in this regard (Latombe et al. 2011). Nonetheless, while we perceive ABMs that encompass such a multidisciplinary approach as promising species distribution models for conservation research, the full potential of agent-based modeling in this domain still remains to be explored and fulfilled.

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Biodiversity

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Biodiversity is strongly affected by the rapid and accelerating changes in the global climate, which largely stem from human activity. Anthropogenic activities are causing highly influential impacts on species persistence. The sustained environmental change wildlife is experiencing may surpass the capacity of developmental, genetic, and demographic mechanisms that populations have developed to deal with these alterations. How biodiversity is perceived and maintained affects ecosystem functioning as well as how the goods and services that ecosystems provide to humans can be used. Recognizing biodiversity is essential to preserve wildlife. Furthermore, the measure, management and protection of ecosystem biodiversity requires different and innovative approaches. For all these reasons, the aim of the present book is to give an up-to-date overview of the studies on biodiversity at all levels, in order to better understand the dynamics and the mechanisms at the basis of the richness of life forms both in terrestrial (including agro-ecosystems) and marine environments.

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