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Spatially Explicit Models of Habitat Permeability for Mammalian Wildlife

by

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ABSTRACT
CENTRE FOR BIOLOGICAL SCIENCES and INSTITUTE OF COMPLEX SYSTEMS SIMULATION
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Least-cost and agent-based models present alternative approaches to modelling animal movements, at the population level and individual level respectively. This study introduces and tests a novel integration of adapted least-cost methods into agent-based simulations, in order to analyse connectivity and habitat preferences in two species of mammal. An initial proof-of-concept study built a set of empirically validated least-cost models of European hedgehogs (*Erinaceus europaeus*) into a simple agent based model. Agents most closely simulated natural behaviours of dispersing hedgehogs when their movements accounted for temporally-dependent habitat preferences in addition to least-cost pathways informed by the connectivity map. The fitness of these agents increased in more highly fragmented landscapes, in contrast to agents that took least-cost pathways without time-specific preferences. The integration of functional connectivity with individual behaviour combined the advantages of both modelling techniques. Quantitative analysis of the individual-level consequences of moving within different landscape scenarios provides a unique way of applying model outcomes to direct conservation action. A second conceptual study applied integrative methods to the construction of an agent-based simulation scaled for jaguars (*Panthera onca*) occupying fragmented landscape in Belize. This simulation tested alternative configurations of a wildlife corridor currently under development in Central Belize as part of the intercontinental Mesoamerican Biological Corridor. Six alternative corridor configurations and three control conditions differed substantially in their effectiveness at mixing agents across the environment, despite relatively little difference in individual welfare. Best estimates of jaguar movement behaviours suggested that a set of five narrow corridors may out-perform one wide corridor of the same overall area. The first two studies set the framework for developing a detailed simulation of jaguar behaviour and population dynamics in a mixed forest and farmland landscape in the south of Belize. This more complex model drew on empirical data on resident jaguars in the region to simulate typical movement, feeding, reproduction and mortality events within a stable natural population. An overview of the construction and application of the model precedes detailed descriptions of its calibration, sensitivity analysis and validation with empirical data. Agents located inside protected forest reserves exhibited higher fitness, expressed in higher fecundity and lower energy- and habitat-related mortality, than agents located outside these reserves. Model validation showed similar patterns to field data in landscape utilisation and the spatial distribution of individuals. This approach to spatial modelling of population dynamics can provide novel insights into effective conservation strategies for large carnivores. Application of the model to the fragmented central corridor region of Belize sets the context for real-world conservation planning. Under current conditions, simulated jaguars formed a small but stable population with various levels of immigration. Implementation of wildlife corridors showed the largest tracts of physically connected reserves increased connectivity between spatially-disconnected habitat patches but also increased vulnerability to environmental degradation.

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Declaration Of Authorship

I, Angela Watkins, declare that the thesis entitled Spatially-Explicit Modelling of Habitat Permeability for Mammalian Wildlife and the work presented in the thesis are both my own, and have been generated by me as the result of my own original research. I confirm that:

- this work was done wholly or mainly while in the candidature for a research degree at this University
- where I have consulted the published work of others, this is always clearly attributed

- where I have quoted from the work of others, the source is always given. With the exception of such quotations, and the items listed below, this thesis is entirely my own work

Chapter 2 of this work was developed in collaboration between A. Watkins and J. Noble, with C.P. Doncaster providing initial data and technical input on ecological and statistical aspects of the study. The chapter has been written by A. Watkins and submitted for publication in Oikos as:

Watkins, A., Noble, J., and Doncaster, C.P. (In Review) Integrating least-cost models into agent-based simulations: example of hedgehog responses to fragmented landscape. *Oikos.*

Chapter 3 of this work was developed in collaboration between A. Watkins and J. Noble, with C.P. Doncaster providing technical input on ecological and statistical aspects of the study. The chapter was co-written by A. Watkins and J.Noble, with J. Noble doing final edits in preparation for conference presentation. It has been published in Artificial Life conference proceedings as:

Watkins, A., Noble, J., and Doncaster, C.P. (2011) An agent-based model of jaguar movement through conservation corridors. In: Advances in Artificial Life, ECAL 2011: Proceedings of the Eleventh European Conference on the Synthesis and Simulation of Living Systems, pp. 846-853, MIT Press.

Chapter 4 of this work was developed primarily by A. Watkins, with technical coding and modelling input from J.Noble. Datasets and specialist jaguar/Belize input was given by

R.J. Foster and B.J. Harmsen and direction and technical ecological input given by C.P. Doncaster. The chapter was written by A. Watkins and has been published in Ecological Modelling as:

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only sad I didn't get to see a wild jaguar!

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Abbreviations and Definitions

ABM	Agent-Based Model
ALife	Artificial Life
BIC	Bayesian Information Criterion
C	Celsius
CAS	Complex Adaptive Systems
CBC	Central Belize Corridor
CBWS	Cockscomb Basin Wildlife Sanctuary
CO_2	Carbon Dioxide
GDP	Gross Domestic Product
GIS	Geographic Information Systems
GPS	Global Positioning System
GUI	Graphical User Interface
IBM	Individual Based Model
IUCN	International Union for Conservation of Nature
LCJCWC	Laboring Creek Jaguar Corridor Wildlife Sanctuary
LCM	Least-Cost Model
POM	Pattern Oriented Modelling
PVA	Population Viability Analysis
SEPM	Spatially Explicit Population Model

Agent Autonomous entities encoded with a set or rules that are able to independently learn and adapt their behaviour in response to stimuli over time

Complexity Science The study of the phenomena which emerge from a collection of interacting objects

Corridor Patches of linear habitat connecting larger blocks of habitat, surrounded by a dissimilar matrix that aims to enhance or maintain wildlife populations within the larger blocks

Emergent Property Pattern that arises out of a multiplicity of relatively simple interactions

Fitness Lifetime reproductive output per capita for an equilibrium population; otherwise net rate of population growth per capita

Home range An area over which an animal or group of animals regularly travels in search of food or mates, and which may overlap with those of neighbouring animals or groups of the same species

Jaguar Corridor Initiative A multi-partner on-going research project with the aim of demonstrating that a tract of wilderness habitat can sustain the function of a corridor between two protected forest areas, with minimum impact on economic development within the corridor strip, whilst giving priority to selected areas for formal protection from some or all development

Landscape Regional mosaic of habitat patches

Latin Square In experimental design, an $n \times n$ array filled with n different symbols, each occuring exactly once in each row and exactly once in each column

Mesoamerican Biological Corridor A large habitat corridor stretching from Mexico southeastwards through Central America, connecting several national parks, national and private refuges and private wild lands

Metapopulation Assemblage of populations each prone to extinction but connected by more or less frequent colonisation and re-colonisation events

Survivorship The number or proportion of individuals surviving at each age for a given species

Wildlife Conservation Protecting endangered plant and animal species and their habitats by maintaining the processes that underpin wilderness

Chapter 1

Measuring and modelling landscape connectivity

Wildlife species are under tremendous pressure from habitat loss and fragmentation that, together, constitute the biggest threats to global biodiversity (Baguette et al., 2013; Crooks et al., 2011; Fischer and Lindemayer, 2007; International Union for Conservation of Nature, 2013; Laurance, 2008; Pinto et al., 2012; Zanin et al., 2014). Some 38% of species are currently listed as vulnerable, endangered or critically endangered by the IUCN (International Union for Conservation of Nature, 2013), resulting from direct actions (e.g., utilisation, conversion, pollution, persecution) and indirect events (e.g., invasive species and climate change). Moreover, current estimates of a human population of over 7.1 billion generate expected increases to over 9 billion by 2050 (United States Census Bureau, 2014), increasing pressure on limited resources and forcing many species to cohabitate with humans in order to survive.

Thresholds for sustainable habitat loss for wildlife populations range from 1 to 99%, depending on the species (Fahrig, 2001), with 20% representing a broad minimum threshold below which fragmentation begins to affect population survival (Fahrig, 1998). Traditional reductionist approaches to conservation design and management comprise understanding dynamic ecosystem processes by using individual elements as representative indicators of the state of the system (Eiswerth and Haney, 2001; Hartvigsen et al., 1998). In contrast, this thesis demonstrates the application of the more modern complex adaptive systems (CAS) theory. Here, the focus is on the emergent macroscopic population-level behaviours that arise as a product of processes and interactions occurring at the microscopic-level, i.e. individuals (Holland, 2006; North et al., 2013). Effective conservation planning acknowledges the complexities of these microscopic processes, and anticipates that changes to species distributions in response to environmental or landscape changes will influence conservation design and management decisions (McLane et al., 2011). Computational modelling can provide an opportunity to explore the influence of these processes without the need for extensive experimental field sites and long-term data collection.

1.1 Habitat Loss versus Habitat Fragmentation

Definitions of fragmentation are generally confounded with habitat loss (the reduction in the amount of habitat in a given area) (Laurance, 2008). Seminal works on the effects of loss and fragmentation have often failed to dis-entwine the two effects (e.g., Andren (1994); Saunders et al. (1991); Wilcove et al. (1986)) and definitions of fragmentation have historically integrated habitat loss as a key component, either explicitly - e.g. ‘a large expanse of habitat is transformed into a number of smaller patches of smaller total area, isolated from each other by a matrix of habitats unlike the original’ (Wilcove et al., 1986), or implicitly - e.g. the process of subdividing habitat into smaller pieces (Andren, 1994). Whilst human-dominated landscapes mostly exhibit both loss and fragmentation of habitat, studies that attribute strong detrimental effects of fragmentation on biodiversity do so only when inseparable from that of habitat loss (Fahrig, 2003).

Computer simulation modelling provides a convenient method for experimentally controlling the landscape, a necessary step to detect the effect of fragmentation per se. Using these tools to control and manipulate habitat patches and their spatial pattern shifts the focus away from individual patches to that of the landscape-scale and facilitates quantification of the relative importance of fragmentation versus habitat loss (Laurance, 2008). The advantages of using computational tools for this purpose lie in their ability to distinguish between the four key processes of habitat loss and fragmentation (Fahrig, 2003):

1. reduction in habitat amount
2. increase in number of habitat patches
3. decrease in size of habitat patches
4. increase in patch isolation

Fragmentation per se refers to the breaking apart of habitat, where changes in habitat amount are controlled (Fahrig, 2003; Fischer and Lindemayer, 2007; Zanin et al., 2014). Reduction in the amount of habitat leads to an increase in patch isolation as patches are removed or reduced in size. Patch isolation is therefore a function of the amount of habitat rather than a measure of habitat configuration, despite the suggestion of it being a product of fragmentation per se (e.g. Fischer and Lindemayer 2007). Both habitat loss and patch isolation can therefore be excluded as independent components of fragmentation per se (Fahrig, 2003). This leaves two processes from which to derive an accurate description, concurring with early work by Bender et al. (1998) for example, and therefore constitute the meaning of fragmentation per se throughout this thesis - fragmentation occurs as a result of an increase in the number of habitat patches combined with a reduction in their individual size, Fig. 1.1. Despite the inherent difficulties, it's critical to understand both the isolated effects and the synergistic effects of habitat loss and fragmentation in order to better guide wildlife management strategies (Zanin et al., 2014).

1.2 Thesis objectives

The overarching goal of this thesis is to describe CAS and demonstrate its role in increasing our understanding of population resilience and robustness in a fragmented landscape. The jaguar, *Panthera onca*, comprises the chosen model system, set in a real-world neo-tropical region of Belize in Central America. The status of these cats as apex predators, combined with the vulnerability of large bodied species of high-trophic level with large home ranges to increasing fragmentation, make these an interesting and relevant case study. These studies can help us explore how disturbance disrupts

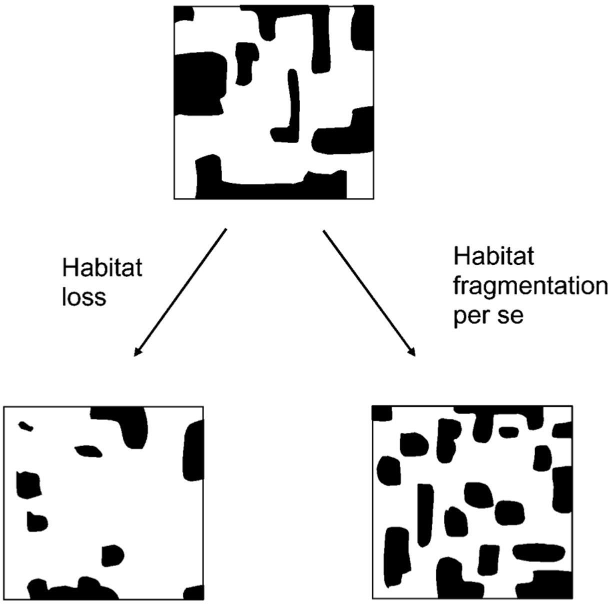


Figure 1.1: Both habitat loss and fragmentation per se result in smaller patches. Therefore, patch size is ambiguous as a measure of either process. Habitat fragmentation per se leads to reduced patch isolation. *Taken from Fahrig (2003).*

system-level properties, revealing the strength of system resilience and likely responses to external perturbation.

Chapter 1 introduces the subject of connectivity. I critically analyse established population dynamics theories, show the advantages and limitations of different approaches to understanding landscape-scale population behaviours and place this discussion in the context of our contemporary understanding of the processes involved in shaping current species distributions. I introduce the concept of connectivity of the landscape and discuss the potential functionality of habitat corridors in mitigating against habitat loss and fragmentation and in maintaining connections between locally isolated populations.

In this introductory chapter I also introduce modelling in ecology, and describe agent-based models (ABMs) and their role in modelling animal populations, whilst setting these in the context of alternative modelling and measuring approaches. Methodologies employed in this thesis aim to increase the exploratory power of computational tools by integrating modern simulation models with real-world geographical information and empirical datasets. The non-invasive nature of agent-based simulation models, and the inability to carry out large-scale long-term experimental work on long-lived large-bodied species, make this a novel, plausible and useful tool for exploring population-level dynamics of the jaguar. These models still require refinement and I later address the suitability of applying agent-based modelling techniques for this purpose along with their successful validation with empirical data.

I discuss the application of agent-based models as a tool in ecology in Chapter 2, with the objective of exploring the application of this type of simulation model to conservation issues, as well as the merits of integrating ABMs with least-cost models of landscape connectivity, that have, on their own merits, been applied to studies of species-landscape interactions. This chapter focuses on the hedgehog, where sufficient empirical data exists from which to undertake this initial investigation. Encouraging results from chapter 2 provide evidence of the benefits and potential usefulness of an integrated least-cost, agent-based model in understanding the interactions between individuals and the environment.

Chapter 3 introduces the jaguar, as an exemplar of an endangered large-bodied and long-lived mammal. Conservation efforts that focus on this species provide significant benefits to local wildlife by protecting extensive tracts of prime and corridor habitat (due primarily to the size of range of individuals), increasing connectivity and habitat permeability for a wide variety of species across the region. The Central Belize Corridor (CBC), a region in the centre of the country, is introduced in chapter 5. This area provides an excellent case study to explore the role of functional connectivity in facilitating the movement of individuals between protected reserves to the north and south of the country, and constitutes a key link in the intercontinental Mesoamerican Biological Corridor (Rabinowitz and Zeller, 2010). By using computational methods this thesis aims to provide evidence that can be used by field researchers and policy makers to contribute to the long-term conservation of jaguars in Central America. The specific study area is described at the end of the chapter.

Chapter 3 takes the first step at using the integrated model methodology to explore landscape-scale population dynamics of the jaguar in a fragmented landscape, albeit in an abstract reality. I discuss the validity of using corridors to increase the connectivity of a landscape by connecting locally isolated populations.

Chapter 4 signifies a move away from the abstract model, to one based on geographical information and empirical data collected in Belize. I show how empirical data from camera traps can be used to explore and define model parameters and validate the movement of jaguars in a real-world landscape. This constitutes a novel approach to understanding the movements of animals and highlights the potential for using computer simulated data in real-world ecological problems. I discuss the need for validated simulation models and their potential for helping us explore real-world conservation problems.

Having now obtained a validated model of jaguar movements in Belize, chapter 5 links the abstract landscape structure investigation of chapter 3 with the real-world context of chapter 4, shifting the focus of the investigation to the CBC study area as described in chapter 5. This chapter investigates the resilience of jaguar populations under current conditions and the effects of a number of conservation corridor designs, both in terms of increasing connectivity and movement between spatially-disconnected protected reserves and in mitigating increased human disturbance and habitat degradation across this corridor area.

The final chapter discusses the content and implications of the novel work contained in earlier chapters, and sets it in the context of current work in the field. I outline the potential future use of ABMs as tool for conservation and ecology, the implications and limitations of my work and describe where this research could be developed in the future.

1.3 Understanding and Measuring Connectivity

The permeability of a landscape to an animals' movement depends on structural characteristics of the landscape as well as the mobility of the individual. To effectively understand how animals respond to changes in their environment, we need to quantify landscape connectivity and its relationship with individual movement and decision-making. For this we need to understand how a species perceives the permeability of its landscape and the range of interacting factors that may influence the distribution of individuals and populations in space and time. Here I review the evolution and development of landscape-scale population and conservation research to place connectivity in historical context, show its origins in island biogeography and the importance of species-specific characteristics that define connectivity measures.

1.4 Origins of connectivity theory

Island biogeography, 'one of the most elegant and important theories in contemporary ecology' (Laurance, 2008), sets the groundwork for modern conservation biology. Through a framework of single reserve and reserve system structural characteristics, along with distance-dependent colonisation and area-dependent extinctions, the MacArthur and Wilson (1967) theory predicts the slope of the species-area relationship and determines the abundance and diversity of species within habitat patch 'islands (Gravel et al., 2011; Ricketts, 2001; Rosindell et al., 2011; Saunders et al., 1991). Its elegance lies in its simplicity, but this explains its limitations in explaining variation in community structure and/or population dynamics (Fletcher et al., 2007; Gravel et al., 2011). Despite the widespread application and discussion of island biogeography theory, its single-patch focus misses important landscape-scale processes that reduce the strength of this approach to solving modern conservation problems, and are outlined below (Laurance, 2008):

Limitations:

1. Non-random conversion of habitat in real landscapes
2. No distinction between the effects of habitat loss and fragmentation
3. Correlates of extinction pressures
4. Community-level changes
5. Altered ecosystem processes

6. Environmental synergies

Omissions:

1. Edge effects
2. Matrix effects

A shift in focus away from individual habitat patches to that of entire landscapes extends island biogeography theory. Doing so corroborates the importance of individual patch size, but highlights the influence of landscape structure and habitat patch spatial pattern, as well as matrix quality in understanding the relationship between habitat loss and fragmentation and population persistence. Species-specific responses to these processes complicate matters: generalist species may be better able to use heterogeneous landscapes whilst specialist species may be far more susceptible to changes in habitat structure and quality (Bailey, 2007; Ewers and Didham, 2006; Laurance, 2008; Lyra-Jorge et al., 2008; Schtickzelle et al., 2006). Furthermore, resource patchiness, population density, body size, home range size, trophic level and dispersal distance may also influence species' sensitivity to habitat loss and fragmentation (Ewers and Didham, 2006; Lyra-Jorge et al., 2008; Opdam and Wascher, 2004; Riley et al., 2006; Skov et al., 2011).

The size and shape of individual habitat patches influences the extent that edge effects penetrate into the patch itself, and Figure 1.2 shows the extent and variety of processes that can act at typical forest habitat edges (Laurance, 2008). Animals located within smaller patches, or in those with a larger surface area to volume ratio, are more vulnerable as the proportion of edge habitat compared to internal habitat is relatively high. Local environment changes (light, temperature, wind, moisture content), and bottom-up effects of subsequent plant community structural and compositional changes can dramatically alter the functional characteristics of these edge zones, changing interactions, composition and abundance and causing some species to avoid these areas altogether (Ewers and Didham, 2006; Fletcher et al., 2007).

Beyond individual patches, the size and spatial distribution of patches in the landscape affects the movement of animals. More isolated patches increase the likelihood of single patch occupancy, limit the potential of individuals of reaching alternative patches or neighbouring populations, and increase vulnerability to local extinction events (Ewers and Didham, 2006; Riley et al., 2006; Schtickzelle et al., 2006). However, landscapes will be more or less permeable to movement, and individual habitat patches more or less isolated, given the dispersal dynamics of a species. Defined as the movement of individuals from their site of birth to their site of reproduction, or between sites of reproduction (Coulon et al., 2004; Massot et al., 2008; Schtickzelle and Baguette, 2003; Schtickzelle et al., 2006), dispersal describes the probability of movement between locally isolated populations. Given its importance in connecting and maintaining links between subpopulations of a metapopulation, dispersal plays a vital role in determining the species-specific connectivity, or connectedness, of a landscape (Coulon et al., 2004; Ewers and Didham,

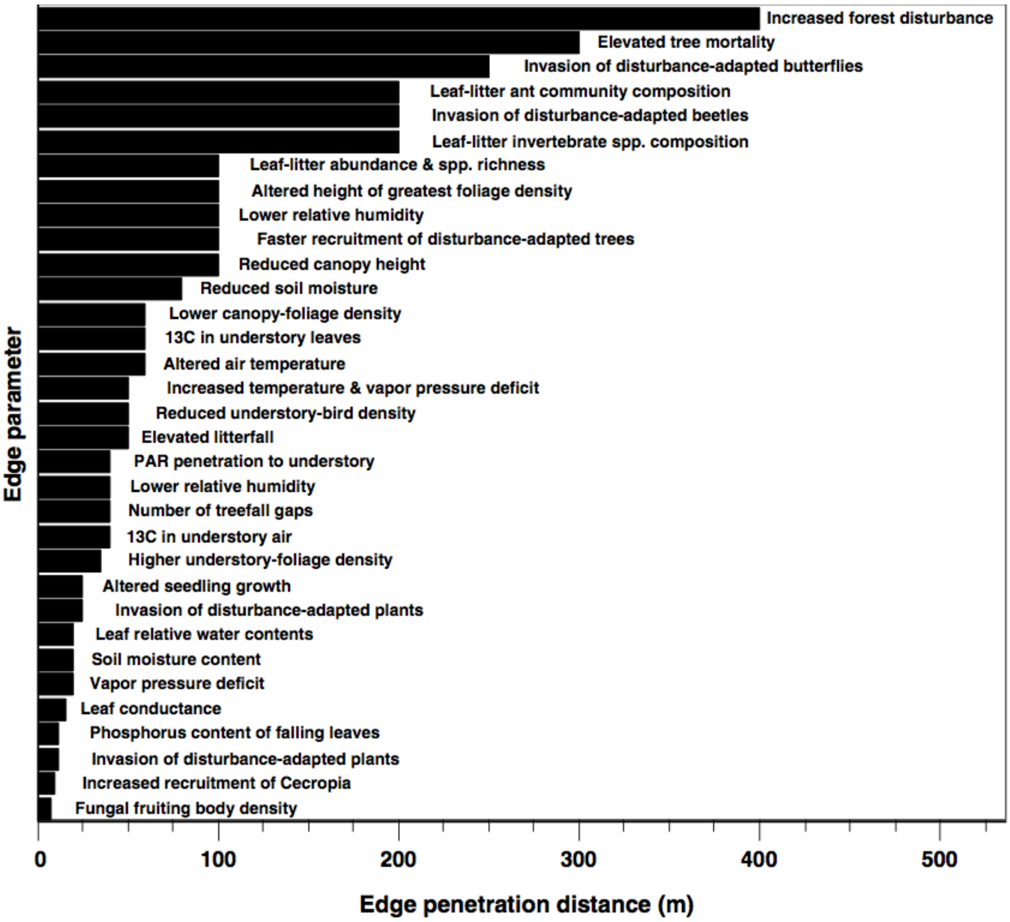


Figure 1.2: The diversity and strength of edge effects documented in Amazonian rainforest fragments. *Taken from Laurance (2008).*

2006; Massot et al., 2008; Travis and Dytham, 1998; Watts and Handley, 2010). This is demonstrated through the mapping of connectivity described in chapter 2. High dispersal rates can act to reduce the effective isolation of habitat patches by maximising colonisation and emigration rates (Crooks, 2002; Laurance, 2008; Schtickzelle et al., 2006; Wilson et al., 2009).

Increasing habitat loss and fragmentation affects species differently and there is increasing evidence that habitat quality plays a substantial role in determining species distributions (Mortelliti et al., 2010). The level of heterogeneity, as well as the quality of the intervening matrix can inhibit dispersal and movement by some species, but enhance it in others (Ewers and Didham, 2006; Zobel et al., 2006). Movement inhibition of this nature is demonstrated in an abstract landscape in chapter 3. The influence of matrix tolerance in estimates of species persistence is demonstrated in figure 1.3 (Laurance, 2008). Those species that are better able to exploit heterogeneous landscapes should therefore be less vulnerable to local extinctions. In fact, the quality of the matrix can outweigh the effects of patch size and spatial arrangement and can directly impact the direction and density of dispersal movements (Fletcher et al., 2007; Jules and Shahani, 2003; Opdam and

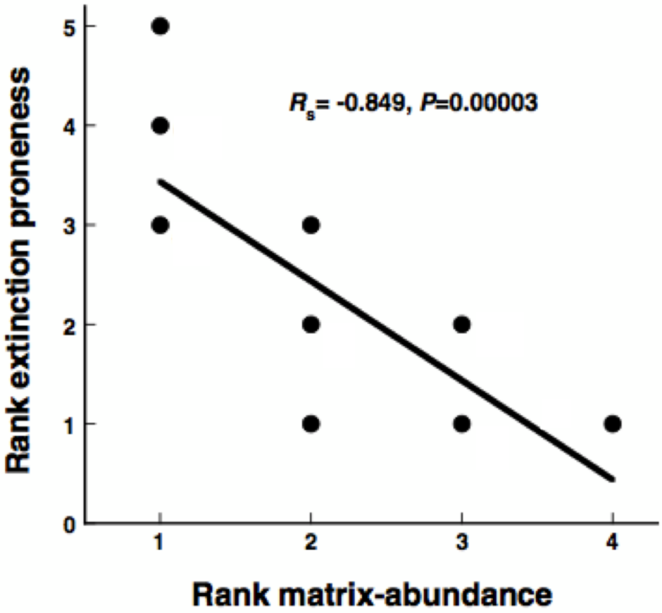


Figure 1.3: Relationship between the matrix tolerance (abundance of a species in matrix habitats) and local extinction vulnerability in 16 mammal species of Australian rainforest fragment. The greater the matrix-abundance of a species, the better able it is to use the matrix habitat and the less vulnerable it is to extinction. *Taken from Laurance (2008)*

Wascher, 2004). The adaptive capacity of a species will ultimately define its response and resilience to landscape change and increased fragmentation; more generalist species should be better able to adapt and will be less negatively affected by increasing edge effects (Ewers and Didham, 2006; Jules and Shahani, 2003).

Shifting the emphasis to the landscape-scale enables us to consider the long-term viability of the metapopulation rather than that of locally isolated populations. Metapopulation dynamics and capacity has been a popular theory and metric for quantifying the potential of a landscape to support a viable community of populations (Baguette et al., 2013; Hanski and Ovaskainen, 2000; Ricketts, 2001), where a metapopulation refers to a collection of spatially separated but interacting local populations of the same species (Baguette et al., 2013; Moilanen and Hanski, 1998). These metapopulations can overcome critical minimum size thresholds for single patch population viability (Hanski and Ovaskainen, 2000; Opdam et al., 2006) through colonisation and re-colonisation of spatially connected habitat patches. However, studies of metapopulation dynamics largely ignore the influences of patch shape, habitat quality, matrix quality and environmental disturbances on population interactions (Moilanen and Nieminen, 2002; Opdam and Wascher, 2004; Ricketts, 2001).

Connectivity is considered a critical factor in ecology and conservation for determining species viability and persistence (Crooks et al., 2011; Kool et al., 2013; McRae et al., 2008; Moilanen, 2011; Pe'er et al., 2011; Rayfield et al., 2011; Stevens et al., 2006) and is defined as the ‘degree to which the landscape facilitates or impedes movement among resource patches (Taylor et al., 1993). This has evolved over recent years to describe the connectedness of ecological processes at multiple spatial scales, as a process for maintaining continuity of ecological processes (Fischer and Lindemayer, 2007) and to facilitate the flow of genetic material and/or the transfer of information or behaviour (Kool et al., 2013; McRae et al., 2008). High connectivity is also advocated to allow natural shifts in pattern and range of species distributions in response to environmental and land-use change (Crooks et al., 2011).

Connectivity can be further separated into two distinct forms: *structural connectivity* the physical relationship between habitat patches; and *functional connectivity* an organisms’ behavioural response to the landscape structure and matrix composition (Baguette et al., 2013; Stevens et al., 2006). Conservation calls for functional ecological networks that support viable metapopulations and will therefore require high quality habitat patches that are efficiently linked to allow individuals to transfer between these patches (Baguette et al., 2013). Measures of connectivity therefore depend on metapopulation ecology, within-patch dynamics, matrix composition and habitat spatial pattern and need to encapsulate the relationship between landscape quality and structure and species-specific responses. Figure 1.4 shows the place of connectivity in spatial ecology and conservation and demonstrates its importance in understanding population distribution and persistence over time (McRae et al., 2008).

Despite the recent drive for the quantification of connectivity (McRae et al., 2008), calculations and measures are complicated by the presence of non-linear patterns and the scale-dependent nature of species-responses to changes in fragmentation (D’eon et al., 2002; Ewers and Didham, 2006; Turner, 2005). This makes connectivity a species-specific measure that demonstrates the difficulty of a ‘one size fits all’ plan for conservation. Multiple measures of connectivity therefore exist, specific to each species present in the landscape (Coulon et al., 2004; Tischendorf and Fahrig, 2000; Watts and Handley, 2010). Uncertainties in connectivity measures also make it a potentially inefficient primary conservation tool. These uncertainties stem from difficulties in measuring and validating dispersal distributions (described in chapter 2 and critical for measuring functional connectivity), immigration/emigration rates, and spatially correlated environmental stochasticity (Hodgson et al., 2009; Kool et al., 2013). Landscapes that measure high in connectivity may also not capture the species-specific responses of some species that are highly specialised or have low dispersal and that may still be unable to cross habitat boundaries (Heller and Zavaleta, 2009). The quantification and measurement of connectivity is discussed in more detail in section 1.5.

Higher connectivity measures occur with increases in suitable habitat, but the role of physical connections, or corridors, is not clear. Corridors are defined as linear habitats embedded in a dissimilar matrix connecting two or more larger blocks of habitat (Beier and Noss, 1998). They serve to increase physical connections between habitat patches and

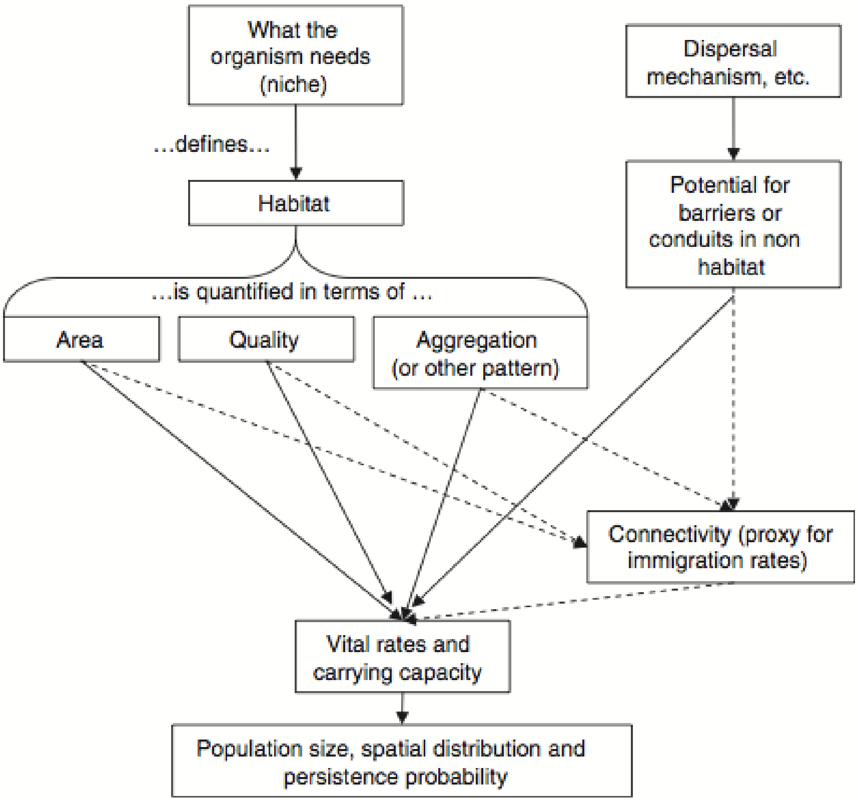


Figure 1.4: A schematic of the place of connectivity in spatial ecology and conservation. *Taken from Hodgson et al. (2009).*

are generally thought to increase biota movement and provide additional foraging or refuge space (Baguette et al., 2013; Saunders et al., 1991). Corridors may therefore exist as additional tracts of habitat or as conduits of movement, or both (Noordijk et al., 2011), and need not consist of high quality habitat to function effectively (Haddad and Tewkesbury, 2005). However, the ability of small, narrow linear features to promote recolonisation or provide population subsidisation remains in doubt (Cushman et al., 2013a). Chapter 3 demonstrates the role of corridors in extending, and increasing movement between, habitat patches, and they constitute a popular strategy for widespread conservation of biodiversity (Beier and Noss, 1998; Bennett, 2000; Haddad and Tewkesbury, 2005; Hilty et al., 2006; Petracca et al., 2014; Pouzols and Moilanen, 2014; Pullinger and Johnson, 2010). Despite the recognition of the role corridors can play in maintaining and increasing connectivity, rigorous approaches for building corridors, as an integrated part of spatial conservation strategies, are currently limited and are made more problematic given the diverse spatial scales and resolutions at which corridors may function (Pouzols and Moilanen, 2014).

Species-specific ecology regarding social structure, diet, foraging patterns and home range size inform predictions of the minimum corridor area required for successful movement between patches (Lindenmayer and Nix, 1993), investigated in an abstract reality in chapter 3 and a real-world landscape in chapter 5. Habitats may be connected through either some combination of discrete patches or a continuous corridor that may serve as a movement route or also provide some of the resource requirements of the species in question (Pullinger and Johnson, 2010). Where relatively large distances between patches occur, species may require wider and better quality corridors to reduce potential edge effects, particularly where crossing requires multiple generations (Haddad and Tewkesbury, 2005).

However, the effectiveness of corridors per se is not clear when comparing across taxa and spatial scales (Gilbert-Norton et al., 2010) and complications arise when considering conservation for multiple species or communities (Pouzols and Moilanen, 2014; Rudnik et al., 2012). There are also few scientifically-based guiding principles for the evaluation and design of connected habitat systems (Lindenmayer and Nix, 1993; Pouzols and Moilanen, 2014) and corridors can also serve to increase the spread of catastrophic disturbances (wildfires for example), invasive or exotic species, and could facilitate the movement of animals into areas where they suffer a greater mortality risk (Beier and Noss, 1998). The conservation value of corridors therefore only accrues when animals are able to successfully traverse these areas.

Species responses to climate change

Observed increases in atmospheric CO_2 and predicted increases in average temperatures, of between 1 and 3.5 °C by 2100 (Brooker et al., 2007; Heller and Zavaleta, 2009; Opdam and Wascher, 2004), make climate change one of the most important drivers of global biodiversity loss. However, the scale-dependent nature, and the influence of connectivity and disturbance, on species responses to climate warming, make predictions of the effects of increased temperatures on ecosystems problematic (Bailey, 2007; Brooker et al., 2007; Massot et al., 2008; Opdam et al., 2006; Opdam and Wascher, 2004). Figure 1.5 shows observed shifts in species distributions in response to global temperature increases, ranging from 10 to over 100 km, and demonstrates the need for species to adapt, genetically or physiologically, in situ, or by moving to find a more suitable climatic location to enable persistence of a population (Brooker et al., 2007; Heller and Zavaleta, 2009; Hickling et al., 2006; Massot et al., 2008; Opdam and Wascher, 2004; Parmesan, 2006; Parmesan and Yohe, 2003; Thomas et al., 2006; Vos et al., 2008; Wilson et al., 2009).

Changes in landscape connectivity may severely inhibit, or enhance, a species' ability to disperse to new climatic zones (Vos et al., 2008; Walther et al., 2002; Watts and Handley, 2010; Wilson et al., 2009), aggravating the effects of climate change in more fragmented or disturbed landscapes (Ewers and Didham, 2006; Parmesan, 2006; Vos et al., 2008). Observed independent shifts in local populations also create a complicated interaction between geographical range shifts and compositional changes in species communities driven by species-specific physiological tolerances, life-history strategies, dispersal capabilities and resource availability (Parmesan, 2006; Walther et al., 2002). Dramatic range shifts can lead to regional declines in populations, and potentially, to global extinctions for rarer or more specialised species where no available alternative habitat exists (Thomas et al., 2006). Mitigating conservation measures therefore focus on reducing these declines by increasing landscape connectivity to enable adaptation to climate change in the face of increasing loss and fragmentation of habitats (Heller and Zavaleta, 2009; Hodgson et al., 2009).

1.5 Modelling in Ecology

Ecology, as a science, concerns itself with the abundance and distribution of organisms in time and space (Kokko, 2007) and ecological models must capture underlying causalities to understand how and why populations fluctuate. Progress in the field of landscape ecology over the last 25 years has demonstrated the importance of landscape pattern and spatial heterogeneity for many species as well as a better understanding of how these processes vary with scale (Turner, 2005). Early modelling techniques, such as Lotka-Volterra, predate the field of landscape ecology and comprise non-linear, deterministic, population-level models that focus on short-term scenarios (Wangersky, 1978; Zhu and Yin, 2009). Despite their extensive application to biodiversity dynamics and co-evolution, limitations in their application to modern conservation issues lie in the exclusions of important stochastic effects that are critical components of understanding the relationship between spatial heterogeneity and species responses', and includes

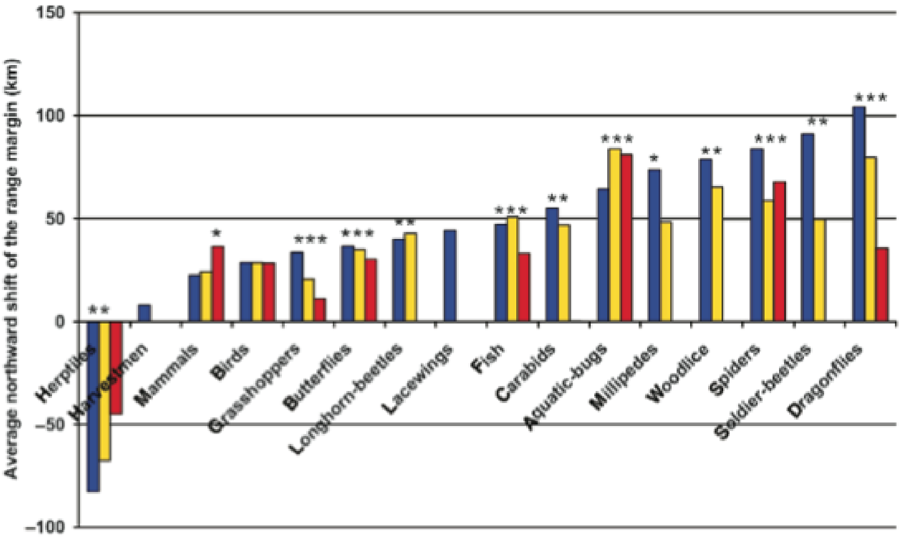


Figure 1.5: Latitudinal shifts in northern range margins for 16 taxonomic groups during recent climate warming. *Taken from Hickling et al. (2006).* Results are given for three levels of subsampling (recorded, blue; well-recorded, yellow; heavily recorded, red). Asterisks indicate significant range shifts.

connectivity, spatial correlations in the environment or population and individual heterogeneity (Wangersky, 1978).

There is a need for efficient and reliable tools that relate landscape composition and pattern to connectivity for ecological processes (McRae et al., 2008). The permeability of a landscape to animal movement depends strongly on the structural characteristics of the landscape as well as aspects of the mobility of the organism in question and captures the two component parameters of connectivity: structural connectivity encompassing the shape size and relative location of habitat patches; and functional connectivity encompassing the response of individuals to landscape structural characteristics (Stevens et al., 2006).

Common approaches to quantifying spatial connectivity include the derivation of landscape pattern indices, analytical measures of network connectivity such as graph theory or least-cost paths, and individual-based simulations (McRae et al., 2008). Metrics for landscape pattern and composition describe what is present and in what quantity, and how this is configured (Mas et al., 2010; Turner, 2005). Popular software packages that output measures of landscape connectivity include FRAGSTATS (McGarigal and Marks, 1995), and specific metric tools in Geographical Information Systems (GIS), e.g. Arc Map or GRASS. Limitations of this approach become quickly clear, when different results can be obtained by analysing the same data, when results depend on the resolution of the landscape and where single calculations of landscape pattern exist regardless of the species in question (Mas et al., 2010; Turner, 2005). The question of whether these metrics actually estimate connectivity has been explored, with limited success (e.g., Schumaker (1996); Tischendorf (2001)). Continuous spatial statistics advance on these categorical calculations, but the relationship between processes that create patterns and the patterns themselves cannot be deduced through either type of calculation (Turner, 2005).

Graph theory, and electrical circuit theory have been used extensively in studies of connectivity (Cushman et al., 2013b; Hanks and Hooten, 2013; McRae et al., 2008; Rayfield et al., 2011) and can be applied to both structural and functional connectivity (Minor and Urban, 2008). Graphs represent the landscape as a set of nodes (habitat patches or local populations), connected in pairs to some degree by edges (connections via dispersal for example), Fig 1.6. Most popular in geography or computer sciences, this flexible method has been applied to ecological connectivity and metapopulation theory to assess the relative importance of patches in a landscape to overall connectivity (e.g., Urban and Keitt (2001); Urban et al. (2009)) and for identifying patches most resilient to human development, or most suitable for conservation (e.g., Minor and Urban (2008)). Dispersal movements and observed movement patterns of individuals can be used to define links between nodes (Rayfield et al., 2011). However, these methods are fundamentally limited given the requirement for habitat quality thresholds and that the focus on emigration-immigration processes means they are unable to answer questions regarding population persistence, resilience or distribution in heterogeneous landscapes

(Moilanen, 2011).

Using the basic concepts of electrical currents, circuit theory comprises resistance, conductance, current and voltage, and is applied to ecological systems to quantify the expected movement of organisms through specific habitat types, nodes and edges and for calculation of the likelihood of an organism moving from any point in a landscape to a given destination. Similar to least-cost path calculations, effective distances between two locations is represented by the resistance distance between the nodes in the network (Hanks and Hooten, 2013; McRae et al., 2008). These methods can be useful as simple movement models and for predicting dispersal patterns between populations to parameterize metapopulation models (McRae et al., 2008), or for use in analysis of ecological flows between populations (Hanks and Hooten, 2013; Urban and Keitt, 2001). Limitations of these approaches centre around the lack of species-specific biological parameters to quantify movement decision-making, temporally-, and spatially-explicit habitat preferences, including knowledge of behaviours, mortality and fecundity (Minor and Urban, 2008), and also intra-specific and inter-specific interactions and environmental feedbacks.

Least-cost models are an alternative analytical measure of connectivity have much in common with graph theory (McRae et al., 2008). They describe the functional

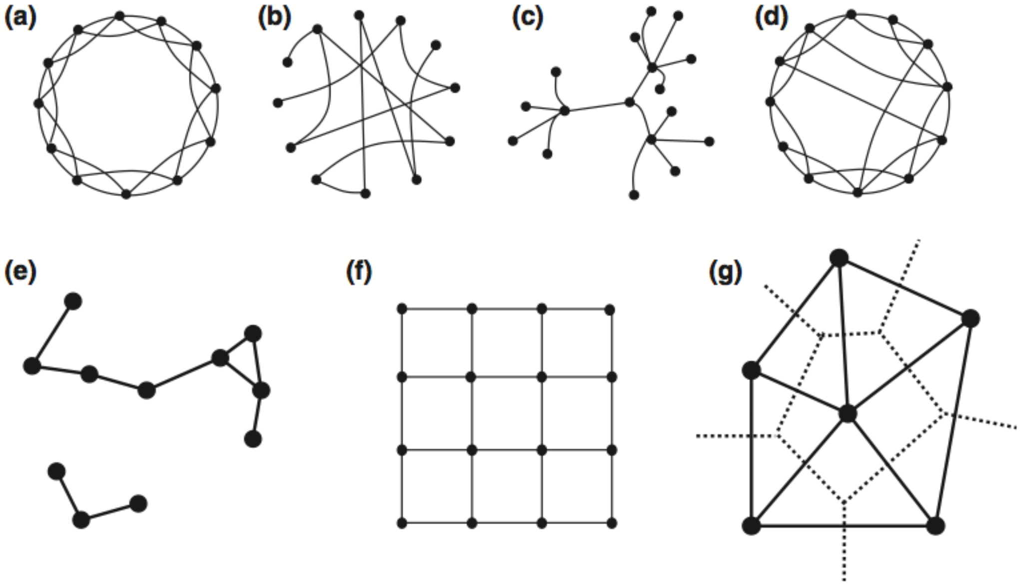


Figure 1.6: Examples of graphs, taken from (Urban et al., 2009). Top line represents theoretical graphs: a) regular; b) random; c) scale-free; and d) small-world. Bottom lines represents more typical landscapes: e) nodes are linked if they are less than some threshold distance apart; f) a regular planar graph representing a raster grid; g) a minimum planar graph defined by a Delaunay tessellation. f) and g) are common landscape configurations originating from GIS data analysis of underlying habitat maps.

connectivity of a landscape (using real-world geographical information) by identifying resistance values for each land cover type based on the facilitating or impeding impact on species movement (Cushman et al., 2013b; Stevenson-Holt et al., 2014). They work on the basis that dispersing organisms are more likely to use a route of least resistance when traversing their environment (Pinto and Keitt, 2009). However, whilst these resistance maps can provide the foundation for applied analyses of population connectivity, sufficient information cannot be gained to allow evaluation of the existence, strength and location of movement barriers and corridors (Cushman et al., 2013b). The output of a single least-cost path through the landscape is a common evaluation methodology for quantifying the success of moving across the landscape and yet, despite the recent development to a more informative estimate of multiple potential movement routes (Pinto et al., 2012), these methodologies continue to focus only on dispersal as the key mechanism influencing the ability of a species to maintain connections across a landscape (Cushman et al., 2013a; Pinto et al., 2012). Described in chapter 2, these models can be useful in conservation planning and for identifying potential corridors that link populations and metapopulations (e.g., Cushman et al. (2013a); Rabinowitz and Zeller (2010)) but often lack biological realism and are unable to assess if these corridors actually provide functional links between patches and populations (Kanagaraj et al., 2013).

Population viability analyses (PVA) extend simple connectivity models and focus on the balance of individuals into and out of a population (Coulson et al., 2001; Ellner et al., 2002; McCarthy et al., 2003; Morris et al., 2002; Zanin et al., 2014), determining the extinction probability of the population, and the efficacy of proposed conservation policy and management (Ellner et al., 2002; McCarthy et al., 2003; McCarthy and Possingham, 2013; Pe'er et al., 2013). They advance upon methods of landscape metrics with their species-specific approach and facilitate the evaluation of individual species' responses to a range of environmental scenarios (Zanin et al., 2014). The computational software programme VORTEX has been a popular choice to simulate population dynamics and estimate species persistence probabilities (e.g., Bruford et al. (2010); Zanin et al. (2014). Their broad application across conservation biology and inclusion of habitat characteristics with demographics data, via spatially-explicit population models (SEPMs), enables useful evaluation of the relationship between connectivity and patch occupancy (Carroll et al., 2003; Dunning et al., 2006). However, they offer a limited technique, and do not account for individual heterogeneity, decision-making, or interactions between individuals and the environment, nor do they enable changes in model parameters, learning or adaptation: factors fundamental to effectively understanding long-term landscape utilisation and spatial and temporal population distributions.

However, differences in species responses to changing levels of connectivity require us to understand and describe landscapes from the perspective of the individual in order to measure and conserve functional habitat connectivity as a tool for providing effective conservation management (Driezen et al., 2007; Fahrig, 2001; Pe'er et al., 2011; Rabinowitz and Zeller, 2010; Rayfield et al., 2010; Skov et al., 2011; Zanin et al., 2014).

Empirical data on species biology and movement is often available and obtainable, but behavioural responses and decision-making processes have not been widely studied (Pe'er et al., 2011). There is therefore a need to develop tools that allow estimates of functional connectivity, i.e. whether a patch or landscape actually functions as connected from the perspective of a population or a species, across landscapes and species (Pe'er et al., 2011).

Predictive systems ecology is defined as the integrated analysis of interactions and feedbacks across different components of biological and ecological organisation and scale, and their relationships with their abiotic and biotic environments, to understand and predict the properties and behaviour of ecological systems (Evans et al., 2013). This new wave of ecological modelling calls for an embrace of the need to forecast the likely impacts of environmental change but is particularly challenging given their complex nature and non-linearity (Grimm and Railsback, 2011). Further challenges of this field centre on the requirement for predictive models to generate accurate and realistic projections; not possible with simple models that contain few parameters (such as the simplified connectivity models described above) that are so removed from real-life systems that its near impossible to test meaningfully against empirical data (Evans et al., 2013). Whilst simplifying assumptions will be necessary, more complex and realistic models have the ability to include heterogeneity, between individuals and at a variety of levels (Evans et al., 2012).

This new realm of predictive ecology focuses on the potential for process-based models that are able to capture the important underlying biological processes and mechanisms that drive the behaviour of the system (Evans et al., 2013, 2012). In this way, forecasting and exploring of future behaviours comes from the emergent properties of these models. Simulation models can be used to deliver useful predictions, but progress in this area has three main obstacles (Grimm and Railsback, 2011):

1. It's not possible to develop a separate model for every specific species/region, but generic models become harder to match to data
2. How do we decide if our model has the right level of complexity?
3. How do we expand out from the traditional single pattern focus of ecological theory and modelling?

Pattern-oriented modelling (POM) has been suggested as a strategy for developing models that are able to address these barriers: facilitating a multi-scope approach that links model outputs to multiple observed patterns at a variety of scales, and therefore providing some measure of finding the right level of complexity (Grimm and Railsback, 2011). The POM approach is demonstrated in chapter 4 for calibration of a number of model outputs to empirical field data.

Agent-based models (ABMs) capture the fine-scale effects of individual movements and the spatial distribution of individuals in driving dynamics within populations.

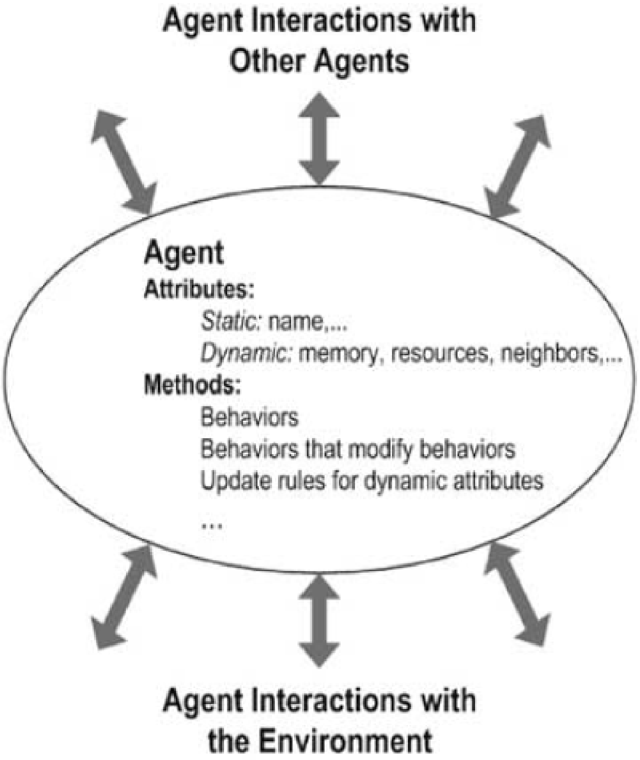


Figure 1.7: Properties of an agent in a typical agent-based simulation model. *Taken from Macal and North (2010).*

Socio-ecological modellers already use ABMs that are well adapted to integration with process-based ecological models (Evans et al., 2012). These models are often referred to as individual-based models in ecology, but I refer to a specific type of individual-based model (IBM) and therefore retain the term ABM throughout the thesis. Despite the ambiguity in terminology, IBMs tend to incorporate much more detail than other connectivity models, and thus present greater realism in process and output (Cushman et al., 2013b). ABMs, specifically, take a bottom-up approach to predicting system-level properties as an emergent product of the interactions between agents, that act independent to any central controlling factor (Grimm, 1999; Macal and North, 2005; Matthews et al., 2007; McLane et al., 2011; North et al., 2013; Railsback, 2001). In this respect they provide a mechanism for modelling CASs and have been used for this purpose across many different disciplines (e.g., archaeology, ecology, biology, economics, military planning) (North et al., 2013).

Despite the simplification of real-world behaviours, agent behavioural characteristics and rules (Figure 1.7) allow them to learn and adapt in response to other agents and changes in the environment (Matthews et al., 2007; Nonaka and Holme, 2007). The integration of empirical knowledge in this process enables direct comparisons between model output and real-world data, making these models particularly suited to investigate animal movement dynamics (Tang and Bennett, 2010).

The flexible nature of ABMs (in terms of species, behavioural rules and model landscapes that can be incorporated) make experimentation through simulation a plausible alternative to empirical data collection where direct manipulation of the landscape is rarely feasible (Bennett and Tang, 2006; Brown et al., 2005; Grimm, 1999). However, the complexity of model design makes interpretation of system-level behaviour problematic necessitating some level of compromise between complexity and ecological realism (Grimm et al., 2005): too simplistic and the model may omit essential mechanisms and dynamics of real systems; too complex and the ambiguity in deriving cause and effect mechanisms may fail to improve our understanding of important system dynamics (Grimm et al., 2005). Achieving a good balance strengthens our interpretation of model outcomes whilst increasing credibility and application to real-world problem, whilst appropriate validation, sensitivity analyses and calibration of ABMs to field data where possible will be crucial in getting computational techniques more widely accepted; discussed in more detail in chapter 4.

Previous simulation modelling studies have addressed conservation issues (for example, Kanagaraj et al. 2013; Kramer-Schadt et al. 2004; Palmer et al. 2011) and population-level dynamics (for example, Cramer and Portier 2001; Imron et al. 2011; Travis and Dytham 1998), but these comprise individual-based models (where a population of individual animals are modelled) that can be separated from the more specific subset of simulations termed agent-based models, due to the lack of explicit representation of variation, adaptation, interaction and feedbacks. The spatially-explicit agent-based nature of the work presented in chapters 2, 3, 4 and 5, the detailed behaviour and life histories described in chapters 4 and 5, the long-term exploration of chapters 4 and 5, and the calibration and validation with empirical field data presented in chapter 4 set the work presented in this thesis apart from other individual- and agent-based models of large felids (Ahearn et al., 2001; Cramer and Portier, 2001), large carnivores (Musiani et al., 2010; Pitt et al., 2003) and those that explore responses to perturbation (Burton et al., 2012; Parry et al., 2006, 2012; Topping et al., 2003, 2005).

Although others have used individual-based models (including those referred to here as ABMs) in the study of animal foraging and movement (e.g., Bernardes et al. 2011; Brooker et al. 1999; Nonaka and Holme 2007; Pitt et al. 2003; Stevens et al. 2006; Tang and Bennett 2010; Topping et al. 2003) but they have not been extensively employed to ask questions of direct conservation value. Furthermore, studies that integrate the two concepts we discuss here (least-cost methodologies within an individual-based model) for these purposes are limited. As with most models that tend to address specific components of connectivity, Palmer et al. (2011) focused on the role of dispersal in long-term population growth and spread across the landscape. The subsequent RangeShifter model extended this and now allows for much greater realism in modelling dispersal capabilities as well as allowing for inter-individual variability (Bocedi et al., 2014). In an alternative approach, the FunCon model (Pe'er et al., 2011) addresses how animal-landscape interactions determine functional connectivity and how this in turn affects the functioning of species in fragmented landscapes. What is clear from this modelling developments is that effective conservation planning requires understanding how individual movement choices inform landscape utilisation and adaptation in response to dynamic environmental change (McLane et al., 2011). Chapters 2 and 5 describe and implement ABMs to understand population-level behaviour and responses to landscape change that demonstrate direct relevance to modern conservation issues.

Chapter 2

Integrating least-cost models into agent-based simulations: example of hedgehog responses to fragmented landscapes

Some parts have been included in previous chapters, but are re-presented here as this chapter has been submitted for publication as "Watkins, A., Noble, J., and Doncaster, C.P. (In Review) Integrating least-cost models into agent-based simulations: example of hedgehog responses to fragmented landscape. Oikos".

Abstract

Least-cost models attempt to quantify the impacts of landscape elements on dispersal dynamics by modelling the landscape in terms of its functional connectivity for a dispersing species. Model validation, however, is rarely achieved due to difficulties in collecting dispersal data. Agent-based simulations provide an alternative approach to modelling ecological systems by simulating the behaviour of individual animals. Empirical knowledge of individual behaviours can be set in a spatial context to improve understanding of the link between individual-level mechanisms and system-level behaviour. This study presents an agent-based simulation of animal movements that incorporates a novel integration of a validated least-cost model. Our reference species is the European hedgehog (*Erinaceus europaeus*), dispersing through fragmented agricultural habitat that has previously been subjected to least-cost modelling. A comparison of the fitness of agents revealed that the addition of a simple behavioural rule to distinguish refuge from foraging habitat dramatically improved the permeability of the landscape for agents, and more closely replicated observed trajectories. Agents without the behavioural rule always prioritized least-cost habitats and were less able to occupy preferred woodland habitats when feeding habitats were fragmented into small and isolated patched. This study demonstrates that integrating models of functional connectivity into those describing individual behaviours combines the advantages of both modelling techniques and provides a unique way of applying model outcomes to direct conservation action.

2.1 Introduction

Landscape connectivity refers to the degree to which an animals interactions with its environment and conspecifics impede or facilitate its movement and acquisition of resources (Coulon et al., 2004; Ewers and Didham, 2006; Fahrig, 2001; Janin et al., 2009; Pe'er et al., 2011; Rayfield et al., 2010). The permeability of a landscape to animal movement depends strongly on the structural characteristics of the landscape as well as aspects of the mobility of the organism in question and captures the two component parameters of connectivity: structural connectivity encompassing the shape size and relative location of habitat patches; and functional connectivity encompassing the response of individuals to landscape structural characteristics (Stevens et al., 2006). However, differences in species responses to changing levels of connectivity require us to understand and describe landscapes from the perspective of the individual in order to measure and conserve functional habitat connectivity as a tool for providing effective conservation management (Driezen et al., 2007; Fahrig, 2001; Pe'er et al., 2011; Rabinowitz and Zeller, 2010; Rayfield et al., 2010; Skov et al., 2011). Empirical data on species biology and movement is often available and obtainable, but behavioural responses and decision-making processes have not been widely studied (Pe'er et al., 2011). There is therefore a need to develop tools that allow estimates of functional connectivity, i.e. whether a patch or landscape actually functions as connected from the perspective of a population or a species, across landscapes and species (Pe'er et al., 2011).

A challenge in studying the relationship between species movements and behavioural responses and landscape connectivity arises from the lack of consensus on how to actually measure landscape connectivity (Belisle, 2005). Graph theory has much to offer the field and provides a mathematical estimation of habitat connectivity through exploration of the likely dispersal patterns of a species (Ernst, 2014; Laita et al., 2011; Urban and Keitt, 2001). As an example of a cost-benefit analysis, this method facilitates the merging of population process with landscape patterns. However, the primary focus on emigration-immigration components of spatial population dynamics means these tools are unable to answer questions about local population size, resilience or persistence and are poorly applicable in landscapes with habitats of varying quality (Moilanen, 2011).

Least-cost models have much in common with graph theory and have been used to describe the connectivity of a landscape for dispersing organisms. Here, land cover types are assigned a resistance, or permeability, score based upon the facilitating or impeding effects on species movement. The resultant connectivity map assumes that animal's take a route of least resistance when traversing their environment (Adriaensen et al., 2003; Pinto and Keitt, 2009; Stevenson et al., 2013). These permeability costs allow for the evaluation of effective distances - distances corrected for the costs involved in moving between habitat patches. However, preferred landscape components do not systematically relate to those components of lowest resistance and preference costs have been shown to more strongly correlate with dispersal rates and movements than Euclidean distances or patch specific resistances (Stevens et al., 2006).

Agent-based models (ABMs), in contrast to the population-level focus of these connectivity models, capture the fine-scale effects of individual movements and the spatial distribution of individuals in driving dynamics within populations. As an example of an individual-based model, ABMs provide an excellent framework for studying connectivity (Pe'er et al., 2011) and can integrate known biological processes (taken from empirical data) into parameter settings. These models take a bottom-up approach to predicting system-level properties that emerge from interactions between individuals (Grimm, 1999; Macal and North, 2005; Matthews et al., 2007; McLane et al., 2011; Railsback, 2001). Agents represent individuals that can learn and adapt their behaviour as they respond to other agents and changes in their environment (Matthews et al., 2007; Nonaka and Holme, 2007). The ABM approach has a major advantage over top-down approaches in enabling extensive exploration of the effects and implications of future landscape changes, including potential degradation or fragmentation of a landscape and mitigating conservation management strategies (Grimm et al., 2006; McLane et al., 2011). ABMs have the potential to work synergistically with least-cost models by integrating least-cost behaviours into individual and activity-specific behaviours.

Although others have used individual-based models (of which ABMs are one variety) in the study of animal foraging and movement (e.g. Bernardes et al. (2011); Brooker et al. (1999); Nonaka and Holme (2007); Pitt et al. (2003); Stevens et al. (2006); Tang and Bennett (2010); Topping et al. (2003)) but they have not been extensively employed to ask questions of direct conservation value. Furthermore, studies that integrate the two concepts we discuss here (least-cost methodologies within an individual-based model) for these purposes are limited. As with most models that tend to address specific components of connectivity, Palmer et al. (2011) focused on the role of dispersal in long-term population growth and spread across the landscape. The subsequent RangeShifter model extended this and now allows for much greater realism in modelling dispersal capabilities as well as allowing for inter-individual variability (Bocedi et al., 2014). In an alternative approach, the FunCon model (Pe'er et al., 2011) addresses how animal-landscape interactions determine functional connectivity and how this in turn affects the functioning of species in fragmented landscapes. This study highlights that populations are comprised of individuals that carry out daily movements as well as dispersal events, and so both movements can be regarded as components of functional connectivity, although the relative contributions of each have yet to be determined. Therefore, focusing on connectivity from the dispersal perspective only, may lead to overlooking important effects of functional connectivity on meta-population dynamics (Pe'er et al., 2011).

Here we test an adapted least-cost model integrated into an ABM of hedgehogs (*Erinaceus europaeus*) dispersing through environments of diverse landscape structure, where we were able to identify and separate dispersal movements from home range behaviours. We limit ourselves to a proof of concept model for quantifying the influence of habitat fragmentation on fitness, in lieu of attempting to represent real-world events or to make quantitative predictions of hedgehog movements. We discuss ways to elaborate this technique for more predictive applications encompassing a suite of stochastic parameters for the full behavioural repertoire. Our purpose is not to argue against other approaches already in use, but rather to present an additional integrated option that has much to offer to studies of the relationship between connectivity and population dynamics.

We first re-implement and develop an analysis of proposed least-cost models previously carried out by Driezen et al. (2007). This study comprises one of the few examples that attempt least-cost model validation with field data, which is hard to accomplish in practice due to the inherent difficulties of collecting dispersal data. In this study, the authors tested and validated a set of twelve potential least-cost models (each providing a different suite of habitat costs) with empirical dispersal data of hedgehogs to derive the best fit least-cost model. Following the identification of a best fit least-cost model, we adapt modelling costs to base them on general daily movements rather than specific dispersal movements, in order to facilitate easy integration into an agent-based simulation model. These costs then determine localised and individual daily movements within our ABM, rather than long-term population-level dispersal movements. We find this a plausible application of least-cost modelling as the principles behind individual movement decision making is the same in both contexts: dispersing animals make small-scale movement decisions in an unfamiliar environment; agents make individual movement decisions per time-step based on nearest neighbour information and are not presumed to know information about the wider landscape. The use of a landscape-based connectivity model within an ABM allows us to use a single parameter cost, to represent individual movement decisions based on a combination of a number of complex environmental and species-specific factors, such as food resource, water and mating opportunities.

2.2 Methods

2.2.1 Calibration and validation of least-cost models

We adapted the analysis of Driezen et al. (2007), which evaluated the alternative least-cost models against dispersal data from 48 translocated hedgehogs (see Appendix A for more details of this study). We present an improved method of validating empirically-based least-cost analyses prior to integrating it into the decision-making of agents in an ABM. The original study by Driezen et al. (2007) tested 12 least-cost models against empirical data to find a single best-fitting model that most closely represented the way in which dispersing hedgehogs moved through the landscape. They evaluated each least-cost model against empirical data on dispersal movements of hedgehogs through five areas in and around Oxford, UK, as reported in Doncaster et al. (2001). These data were collected from individuals translocated to an unfamiliar site and released with a radio tag.

Locations were taken twice daily, once during the day and once during the night. Recordings stopped once the individual appeared to have settled into an area: identified by occupation for at least five consecutive days.

Maps in ArcMap format distinguished a total of 22 land cover types including both linear and non-linear features (provided by F. Adriaensen). This landscape encompassed a total of 48 dispersal paths, each taken by a different hedgehog. We developed new criteria for including paths (based on expert opinion of author CPD) prompted by ambiguity in the method of data point elimination in the previous Driezen et al. (2007) study. Included paths comprised those that met the following criteria: > 7 observations, each within > 2 non-linear land-cover types, taking the individual > 600 m from the release site while staying within the confines of the map. Any cluster of points at the end of a path was also excluded in order to separate the dispersal component from home-ranging behaviour.

From the 21 paths that met the criteria, ten randomly assigned dispersal paths constituted the calibration set following methodology described in (Driezen et al., 2007). These data compared the initial performance of each least-cost model (named resistance set in Driezen et al. (2007)) and identified models that best matched empirical data. The remaining eleven dispersal paths comprised the validation set and validated results from the training set, identifying the single model that best captured a representation of hedgehog dispersal movements.

The 12 least-cost models proposed by (Driezen et al., 2007) represented the estimated cost to an individual of traversing or utilising each habitat within the landscape in terms of resource availability, predation risk or physiological cost. Driezen et al. (2007) compiled each least-cost model to test and validate each suite of relative cost values against empirical data. Most models allocated water, arable and synthetic land-cover types as the highest cost habitats, and ley, pasture and managed grasslands the lowest cost habitats. Two models proposed alternative costs, one allocating the lowest costs to wood and scrub habitats and relatively high costs to ley and pasture; the second inverting the relative costs of all habitats to create a completely contrasting model. This study also developed a method of comparing the cost of an animals location to alternative locations equidistant from the source cell: the z-score, with low z-scores indicating an animal was located in a cell with lower than average cost, or a better than random route through the landscape.

2.2.2 Agent-Based Simulation: The model

The model was constructed with the freely available agent-based modelling software NetLogo (`http://ccl.northwestern.edu/netlogo/`). Model description employs the protocol of ODD (Overview, Design concepts and Details: Grimm et al. 2006).

2.2.2.1 Purpose

The model integrates a least-cost model of connectivity into an ABM with the aim of demonstrating the potential of this approach to explore the relationship between an organism, its population and the environment. Setting three agent types, each with a different behavioural repertoire, in environments with varying levels of fragmentation and with two contrasting models of connectivity (set of habitat costs derived from a validated least-cost model) produced a suite of test cases for evaluation.

State variables and scales

Landscape entities: Model architecture comprised a square grid of 33 × 33 cells, giving 1089 in total. The model runs with an 8-neighbour system. Grid-cells belong to a certain habitat type, one of 7 described in table 2.1. Habitat types in the model landscape had the same proportional representation as in real habitats, estimated from aerial coverage of habitat maps used in Driezen et al. (2007). Habitat costs matched those from the two best least-cost models identified in each of the original Driezen et al. (2007) study and the re-implementation described here.

Basic entities: Individual hedgehogs comprised the basic entity of the model and occupied a single cell in the grid. The location and behavioural type defined hedgehog agents: Type-1 agents had random movement; type-2 agents had simple least-cost movement; and type 3 agents had time-dependent least-cost movement (see submodels).

Source of fragmentation: Landscape structure developed from a random-walk process with habitat types assigned to cells that allowed variation in levels in fragmentation (see Appendix B for full details of the fragmentation algorithm). Lower fragmentation levels created a higher likelihood of the same habitats being clumped together, whilst higher levels had a higher likelihood of small and isolated habitat patches (Figure 2.1). This process represents fragmentation per se, avoiding the confounding effects of habitat loss.

Process overview and scheduling

With each time-step, agents completed their required processes one at a time, in random order. Agents moved to any one of the 8 neighbouring cells according to their behavioural rules set at simulation initialisation. The overall process is not intended to mimic a real process of hedgehog movement and decision-making, but rather to emulate the movement patterns that typify dispersal and home-range establishment.

Table 2.1: The seven habitat types used in agent-based simulations. These are representative of the natural habitat types identified during the field-based least-cost analysis. Costs are given for environments underpinned by the original and new least-cost models.

Habitat	Original cost values	New cost values	Real land-cover types incorporated	Percentage cover of the landscape	Colour in the model
Wood	2	1	Woodland, scrub	13	Brown
Pasture	1	10	Ley, pasture	30	Green
Garden	2	5	Allotments, gardens, playing fields, mown grass	10	Lime
Arable	100	150	Arable	30	Yellow
Urban	5	15	City, farm	10	Grey
Road	100	150	Small, medium and large roads, railroads	5	Black
Water	150	300	Streams, rivers	2	Blue

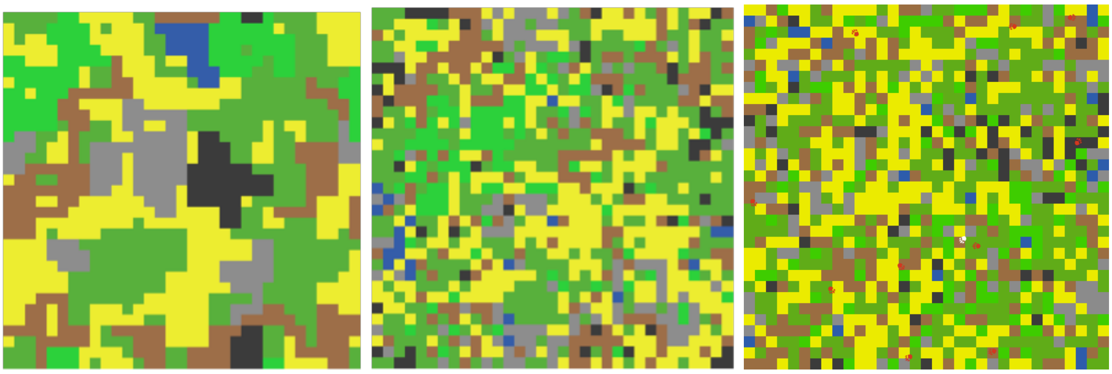

(a) (b) (c)

Figure 2.1: NetLogo model display showing landscape of three fragmentation levels: (a) value of 0; (b) value of 25; and (c) value of 50, representing maximum fragmentation. Colours represent each of the seven habitat types as shown in table 2.1.

2.2.2.2 Design concepts

Emergence and Adaptation. Spatial patterns of landscape structure and connectivity developed uniquely with the initialisation of each simulation. Agent behavioural types imposed hedgehog behaviour, but the distribution of individuals emerged from the specific animal-landscape interactions. Consequently, model outputs can be related to observed patterns of movement and distribution.

Fitness. Agent movement included an implicit measure of fitness, represented by two model outcomes: total path cost; and cost per step. The model did not include any natural life history events of hedgehogs: no mating, no feeding and no mortality.

Sensing and Interaction. The movement of hedgehogs and their response to the environment depended entirely on the information available within their 8-cell neighbourhood, i.e. habitat type and cost. Movement represented potential displacement in any direction for the next time-step. Individuals did not interact at any time during the simulation.

Observation. The Netlogo graphical user interface (GUI) enabled instantaneous updating and visual observation of agent movement and behaviour.

Initialisation

For each new run, the model cleared and reset parameters, agents and environmental data. Runs began with a population of 300 agents, each located in a random grid-cell and assigned at random to one of the three agent types. Each simulation run comprised 480 time-steps that represented the 20 days of empirical data collection in Driezen et al. (2007). Data comprised two sets of 1530 simulations, each of which constituted 30 runs at each level of fragmentation from 0 to 50 inclusive, all underpinned by each of two least-cost models.

Submodels

Moving An agent moved to one of the eight neighbouring grid-cells with every time-step. Three different behavioural rules differentiated agent types: type-1 agents moved to a random neighbouring grid-cell regardless of habitat type; type-2 agents moved in least-cost pathways, specifically choosing a neighbouring grid-cell of lowest, or equal lowest, cost; type-3 agents moved in a time-dependent manner, choosing to prioritise movement in woodland habitat during the day and pasture or ley habitats during the night, and otherwise moving through least-cost pathways. Type-3 agents aimed to improve the ecological realism of ABM agents by using a behavioural rule that better represented how real hedgehogs execute both temporally- and spatially-motivated movements.

2.2.3 Statistical Analysis

Empirical Data

Successive concentric circles, with an individual hedgehog release point at their centre, passed through every hedgehog path observation point in each landscape (Fig. 2.2). The spatial analyst' extension in ArcMap facilitated the calculation of summary statistics for the cost value of each cell lying on each circle circumference, allowing the computation of a standardised value of the relative cost of the observed location in the landscape compared to all other locations equidistant from the release point. This z-score equalled [cost of observed location - mean cost of all locations on the circle] / [standard deviation of the total cost of all locations on the circle]. The z-score thereby measured the cost of a location relative to all other equidistant locations, with negative scores, indicating a better than area location for the individual. Full methodology is detailed in Driezen et al. (2007).

The performance of each least-cost model was compared against alternative models and against empirical data. Individuals with a negative average z-score did not move randomly but rather chose a preferred route through the landscape (Driezen et al., 2007). The model that consistently provided the lowest z-scores therefore constituted the best representation of hedgehog dispersal movements. One-sample z tests quantified the difference of observed mean z-scores per least-cost model from zero, where zero indicated random movement. The greater the difference from zero, the better the fit to empirical data, given the assumption that dispersing hedgehogs move along least-cost pathways.

A second analysis, using a linear mixed effects model in R, tested the effect of least-cost model and dispersal distance on the distribution of observed z score. This consisted of calculating z-score, assigning model and distance as cofactors, distance from release cell as a fixed factor co-variate, and repeated measures on individuals nested in regions (model code in R: z-score $\sim$ model $*$ distance, random $= \sim$ 1|region/individual) (Crawley, 2005; Doncaster and Davey, 2007; Faraway, 2005).

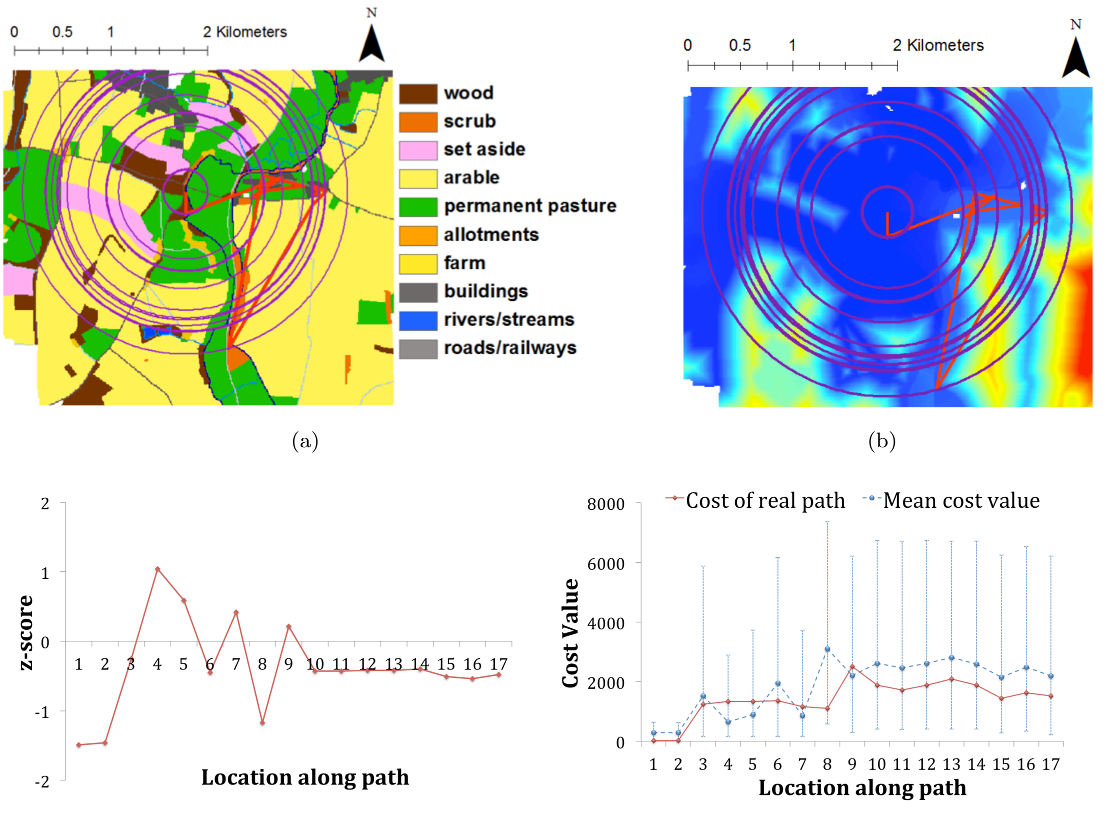
Simulated Data

A wides III analysis, in R, allowed us to compare the habitats selected by agents against their proportional representation in the landscape and followed methodology outlined in Aebischer et al. (1993). Outputs from ABMs comprised both the use and availability of habitats, facilitating calculation of the *Khi2L* resource selection ratio, a log-likelihood statistic describing a test of random resource use. A subsequent chi-square test compared observed *Khi2L* values with random resource use. Following calculation of Shannon-Wiener diversity indices, a gls (Generalised Least Squares) in R then tested for the effect of least-cost model and fragmentation on the diversity of habitats used by agents, using a linear model constructed with generalized least squares methodology that accounted for the observed unequal variances in the data.

2.3 Results

2.3.1 Calibration and validation of least-cost models against empirical data

Analysis with the training set of hedgehog paths provided only three least-cost models suitable for inclusion within the validation analysis: a contrasting set of the two best performing models (5 and 10) and the worst performing model (12). Least-cost model 10 comprised the best-fit to empirical hedgehog data, exhibiting the lowest mean z-scores, lowest z-test values and largest difference from zero (Table Table 2.2) in both analyses. This model also performed well in the original Driezen et al. (2007) study but ranked behind least-cost model 6 (ranked fifth here). Least-cost model 10 therefore comprised



(a) (b)

(c) (d)

Figure 2.2: Illustration of the method of scoring an individual hedgehog path within the one of the five study sites, Rousham, using least-cost model 10. Dispersal path shown in red, concentric circles, in purple, with centre at the release site and edge reaching each observed location. (a) shows the habitat map and (b) the cost layer based on least-cost model 10, colours turning blue through to orange as cost increases; (c) shows z-scores, for difference of cost from zero, for observed locations; summary statistics for (d) were obtained from all grid cells transected by each circle and show cost of observed location, mean cost for all cells with vertical dotted lines extending to maximum and minimum costs.

our best representation of the way in which cost-minimising hedgehogs disperse through the landscape and, together with least-cost model 6, informed habitat costs of ABM simulations.

The type of least-cost model strongly influenced the distribution of observed log-transformed z-score values (linear mixed effects model, $F_{11,1139} = 5.94$, $p < 0.0001$) but distance from the source cell had no influence either as a main effect or interaction. Using distance from release point as a categorical factor rather than a co-variate (following conversion to three categories of distance, < 800m, $800 - 1500$m and > 1500m) did not change model outcomes (no effect of distance: $F_{2,1139} = 2.45$, $p = 0.12$; and no interaction between distance and least-cost model; $F_{11,1139} = 1.18$, $p = 0.30$). Least cost models 10 and 12 produced a better and worse set of mean z-scores respectively than all other models (linear mixed effects model, $t_{1139} = -2.707$, $p = 0.007$ and $t_{1139} = 2.101$, p

Table 2.2: Summary information from scoring locations along each hedgehog dispersal path using each proposed least-cost model. Least-cost models 1-12 calculated using the training set of hedgehog paths, validation models 5, 10 and 12 calculated using the validation set of hedgehog paths. Values of z and p represent the difference from zero and are calculated from one-sample z-tests, with values of $p < 0.05$ shown in bold. Where possible, comparative values obtained in Driezen et al. (2007) are shown in italics.

Proposed least-cost model	**Mean z-score**	**Minimum z-score**	**Maximum z-score**	**Standard deviation**	***Z* test**	***p*-value**
Training Data						
1	-0.19	-1.50	3.54	0.876	-2.12	**0.034**
	-0.47	*-20.89*	*2.73*			*<0.0001*
2	-0.28	-2.30	2.12	0.882	-3.17	**0.002**
	-0.35	*-2.35*	*2.37*			*0.001*
3	-0.29	-1.23	2.36	0.691	-4.11	**<0.0001**
	-0.45	*-1.34*	*2.84*			*<0.0001*
4	-0.17	-1.44	2.51	0.831	-2.03	0.042
	-0.41	*-9.34*	*5.16*			*0.007*
5	-0.33	-1.64	2.12	0.707	-4.59	**<0.0001**
	-0.34	*-2.64*	*2.24*			*0.001*
6	-0.29	-2.04	1.91	0.738	-3.94	**<0.0001**
	-0.47	*-6.35*	*2.38*			*0.0001*
7	-0.29	-1.49	2.12	0.712	-4.10	**<0.0001**
	-0.45	*-7.71*	*2.34*			*0.0006*
8	-0.24	-1.74	2.12	0.778	-3.08	**0.002**
	-0.27	*-2.46*	*1.94*			*0.002*
9	-0.06	-2.55	2.12	1.12	-0.50	0.620
	-0.316	*-20.89*	*2.80*			*0.002*
10	-0.44	-1.49	1.79	0.627	-7.02	**<0.0001**
	-0.42	*-3.28*	*2.30*			*0.0001*
11	-0.22	-1.99	1.68	0.758	-2.92	**0.003**
	-0.21	*-1.69*	*2.14*			*0.05*
12	0.36	-1.61	3.69	1.171	3.12	**0.002**
	0.15	*-1.64*	*7.22*			*0.2*
Validation Data						
5	-0.43	-7.54	2.84	1.119	-4.18	**<0.0001**
10	-0.48	-4.54	2.51	0.883	-6.22	**<0.0001**
12	0.06	-19.16	7.80	2.403	0.26	0.793

= 0.04 respectively). The removal of several strong outliers and log transformation of z-score and distance values reduced the observed skewness of residual plots.

2.3.2 Agent-Based Simulations

Two least-cost models informed ABM habitat costs: least-cost model 6, identified as the best-fit in the original study and henceforth called the original least-cost model; and least-cost model 10: identified here as the best-fit to empirical data and henceforth called the new least-cost model.

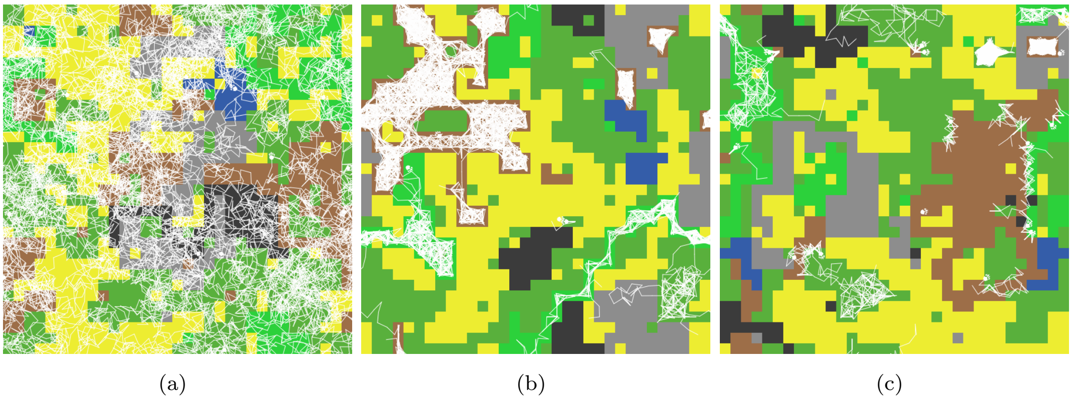


Figure 2.3: Example model visual for movement of all three agent types. a) Type-1 agents; b) Type-2 agents; c) Type-3 agents

Habitat Use and Agent Movements

Figure 2.3 illustrates agent movements, with type-1 agents using habitats in proportion to their availability (original least-cost model: $Khi2L = 147.93$, d.f. $= 9180$, $p = 1.0$; new least-cost model: $Khi2L = 147.47$, d.f. $= 9180$, $p = 1.0$) and showing pathways independent of habitat type or cost. Other agents preferentially selected favoured habitats and avoided habitats of higher cost (type-2 agents: original least-cost model: $Khi2L = 58013.59$, d.f. $= 9137$, $p < 0.01$; new least-cost model: $Khi2L = 69537.26$, d.f. $= 9131$, $p = < 0.01$; and type-3 agents: original least-cost model: $Khi2L = 53706.99$, d.f. $= 9116$, $p < 0.01$; new least-cost model: $Khi2L = 54338.33$, d.f. $= 9124$, $p < 0.01$). Initial movement of type-2 agents away from higher costs habitats preceded their settlement in low-cost pasture or woodland, depending on the least-cost model underpinning the environment, and representing up to 80 times more use than other habitats, as illustrated in Fig. 2.4. Woodland comprised the most-used habitat in both sets of simulations for type-3 agents, and increased use of garden habitats demonstrates the higher availability of these habitats in more fragmented landscapes and reflects their suitability as foraging areas by hedgehogs in the wild.

Higher Shannon-Wiener index values indicated agent movements encompassed a greater number of habitats. Least-cost model did not affect movement of type-1 agents ($F_{1,3056} = 0.00$, $p = 0.69$) but the smaller and more scattered patches of habitats observed with increased fragmentation caused less variation in the diversity of habitats used by these agents ($F_{1,3056} = 5$, $p = 0.02$), as illustrated in Fig. 2.5. Higher fragmentation caused an increase in the diversity of habitats used by type-2 agents ($F_{1,3056} = 15604.49$, $p < 0.0001$), which depended on the least-cost model ($F_{1,3056} = 294.19$, $p < 0.0001$). A change in dominant use of habitats from pasture to woodland generated higher diversity of habitat used across all simulations underpinned by the new least-cost model ($F_{1,3056} = 3184.38$, $p < 0.0001$). The relatively low proportional representation of woodland in simulation landscapes increased the likelihood of these agents traversing multiple habitats

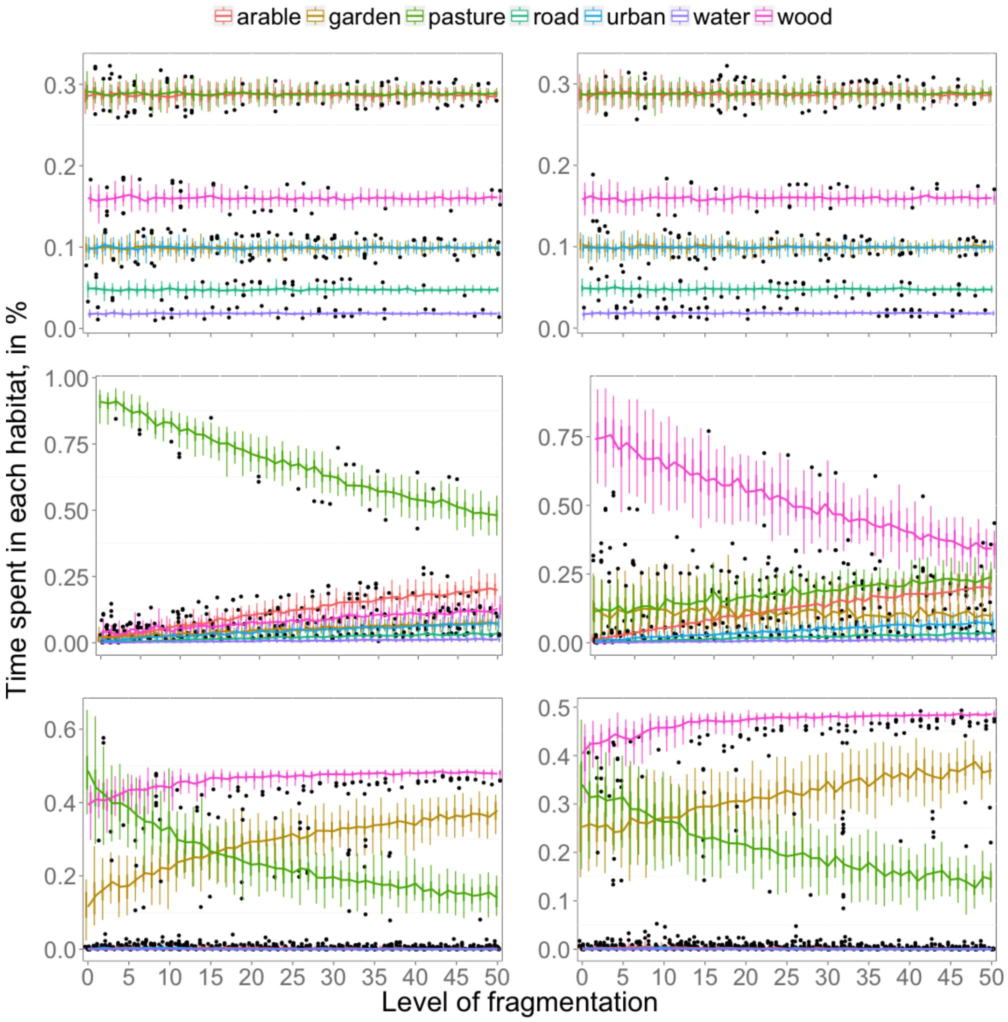


Figure 2.4: Habitat use for all agent types in environments underpinned with both original (left column) and new (right column) models, showing boxplots with mean values and 95% confidence limits. Dots represent outliers. Type-1 agents (top); Type-2 agents (middle); Type-3 agents (bottom).

before reaching a patch of this low-cost habitat. The use of both pasture and woodland by type-3 agents counteracted these effects and least-cost model alone did not cause any changes in the diversity of habitats used by these agents ($F_{1,3056} = 2.42$, $p = 0.12$). However, Figure 2.5 reveals diversity increased in line with increasing fragmentation ($F_{1,3056} = 19335.27$, $p = < 0.0001$), but acted independently of least-cost model ($F_{1,3056} = 1.97$, $p = 0.16$).

Agent fitness

By comparing the average step cost of agent types 2 and 3 against the averages of type-1 agents, we enumerated how well an agent's decision-making matched its fitness in the landscape. We assumed that if agents exhibited a lower than random cost then they preferentially selected more suitable habitats and better reflected the complex movement

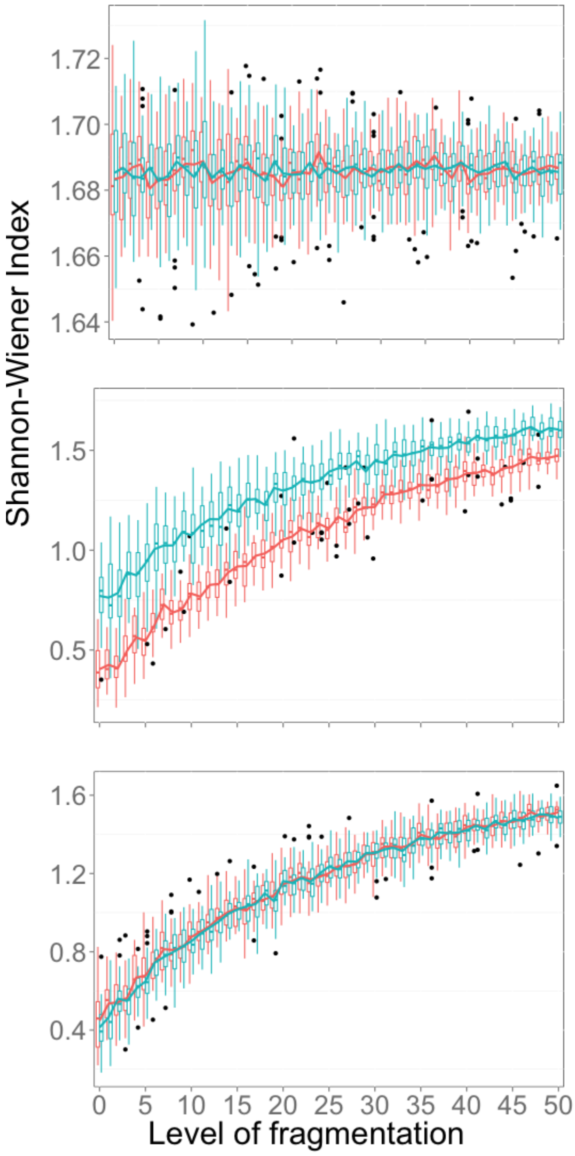


Figure 2.5: Diversity of habitat use for all agents with increasing fragmentation, calculated with the Shannon-Wiener Index, and showing boxplots with mean values and 95% confidence limits. Dots represent outliers. Diversity provided for each agent type in simulations using both least-cost models: the original least-cost model shown in red; the new least-cost model in blue. type-1 agents (top); Type-2 agents (middle); Type-3 agents (bottom).

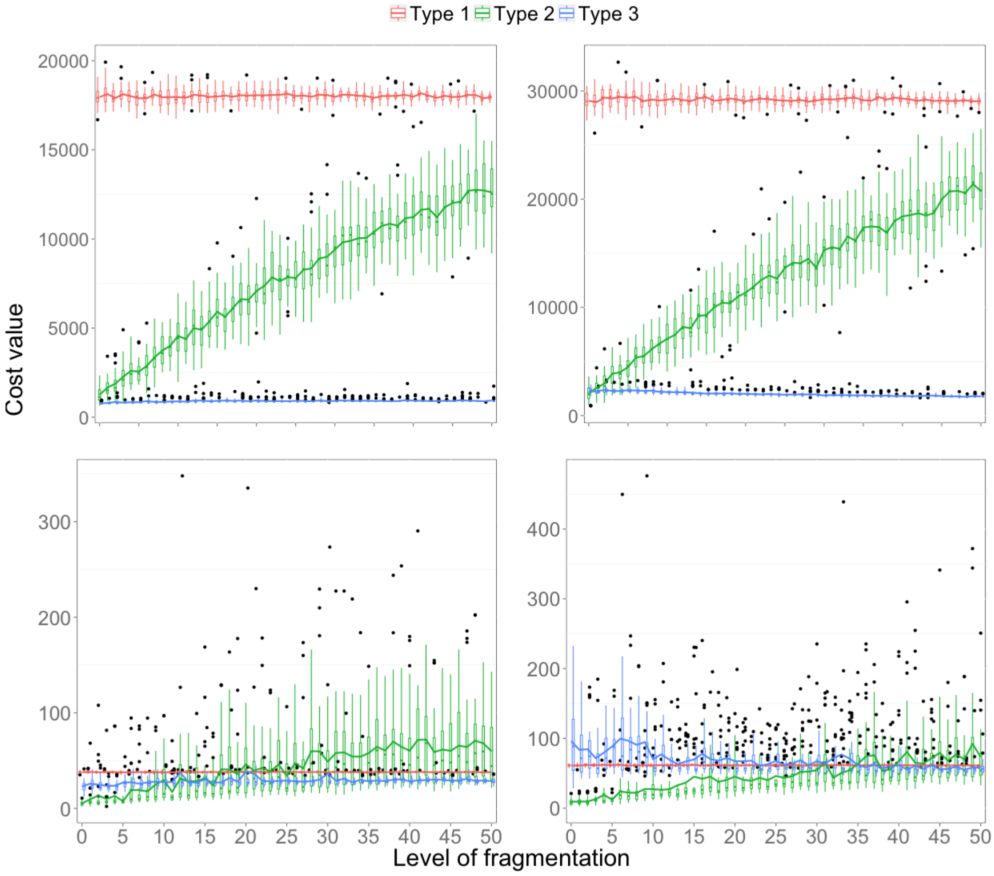


Figure 2.6: Fitness measures for all three agent types. Total path cost in top row; step cost in bottom row, for simulations using the original (left column) and new (right column) least-cost models. Showing boxplots with mean values and 95% confidence limits. Dots represent outliers.

and behaviour of real animals than those agents that exhibited higher than random costs. Type-3 agents consistently maintained the highest overall fitness, in terms of total path cost, independent of the level of fragmentation and least-cost model (blue in Figure 2.6). However, their temporally-motivated habitat preferences gave type-3 agents a fitness disadvantage in less fragmented landscapes compared to the less behaviourally complex type-2 agents (type-3 agents showed higher step costs than both other agents, particularly using the new least-cost model).

Figure 2.7 shows the original least-cost model produced type-1 agents of higher fitness than those in simulations with the new least-cost model, independent of fragmentation (path cost: $F_{3,3056} = 1.70$, $p = 0.19$; step cost: $F_{3,3056} = 1.693$, $p = 0.19$). Lower fitness of type-2 agents correlated with increasing fragmentation (path and step cost increased with increasing fragmentation: $F_{3,3056} = 119441.8$, $p < 0.0001$; $F_{3,3056} = 917.31$, $p < 0.0001$; respectively), but the type of least-cost model confounded this effect enabling type-2 agents to obtain higher fitness in simulations using the original least-cost model (path cost: $F_{3,3056} = 5909.1$, $p < 0.0001$; step cost: $F_{3,3056} = 7.02$, $p = 0.008$), Fig. 2.7.

The type of least-cost model influenced the response of type-3 agents to changes in

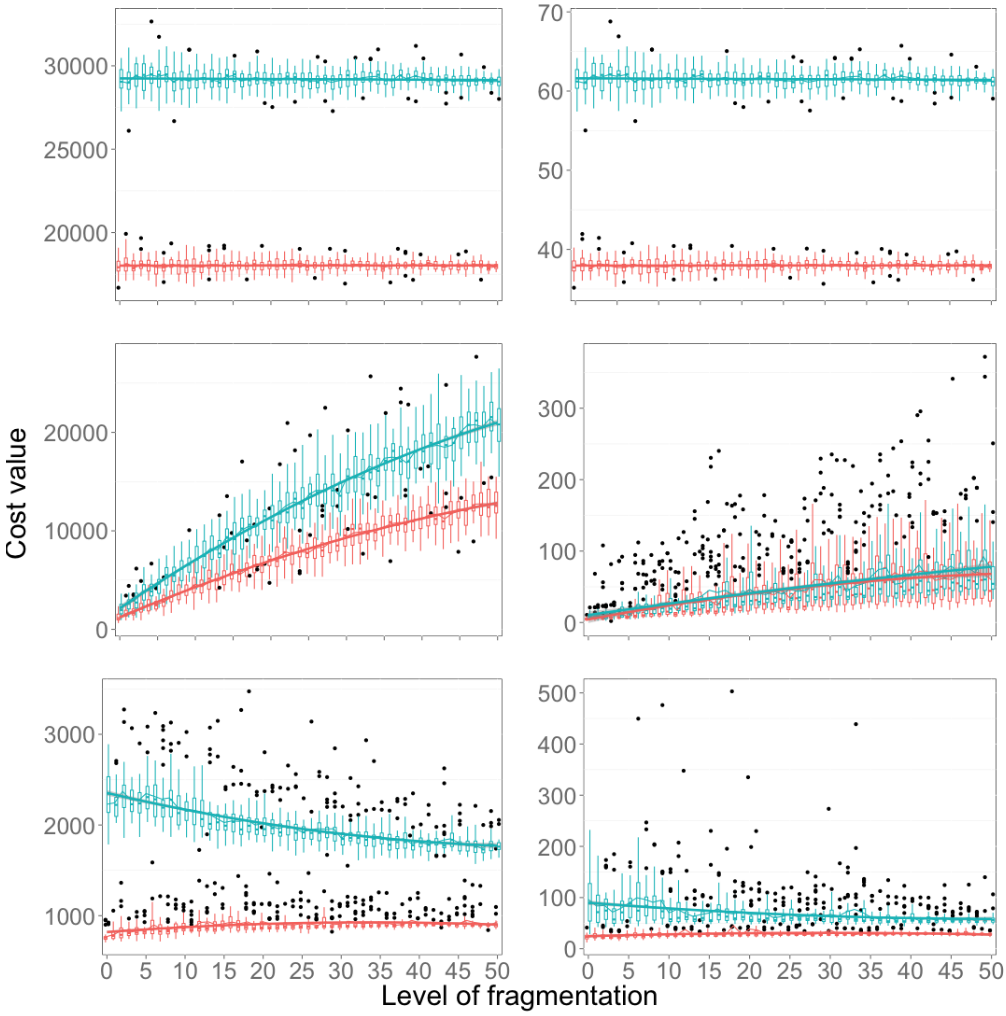


Figure 2.7: Total path cost, left column, and mean cost per step, right column. for the original least-cost model (red) and new least-cost model (blue). type-1 agents in top row; type-2 agents in middle row; and type-3 agents in bottom row, showing boxplots with mean values and 95% confidence limits. Dots represent outliers.

fragmentation (fragmentation and least-cost model strongly interact: $F_{3,3056} = 1052.9$, $p < 0.0001$), indicating least-cost model choice is non-trivial when considering quantitative estimates of fitness. Increased path and step costs showed these agents decreased in fitness in simulations with the original least-cost model (Pearson correlation = 0.22, $t_{1528} = 8.68$, $p < 0.0001$), but increased in fitness with the new least-cost model (Pearson correlation $= -0.63$, $t_{1528} = -32.05$, $p < 0.0001$): the only agent to do so (see path cost and step cost for type-3 agents in Fig.2.7 (bottom row)). Lower variation around mean path and step cost values for these agents also improved our ability to predict individual fitness responses to landscape fragmentation (F tests original model path cost: $F_{1529,1529} = 1096.51$, $p < 0.0001$; original model step cost: $F_{1529,1529} = 4.24$, $p < 0.0001$; new model path cost: $F_{1529,1532} = 483.12$, $p < 0.0001$; new model step cost: $F_{1529,1532} = 1.63$, $p < 0.0001$).

2.4 Discussion

Using the integrated model described here, we assessed the contribution of species-specific habitat preferences to resistance on calculations of functional connectivity and the associated impact on individual fitness. By distinguishing between theses components of connectivity we contribute to a better understanding of the relationship between landscape structure and species responses to changes in fragmentation; an essential factor when using indices of structural connectivity as surrogates for functional connectivity (Pe'er et al., 2011).

Least-cost models can capture many aspects of the connectivity of the landscape relevant to a dispersing individual but for most species are a poor representation of movement behaviours (Palmer et al., 2011). ABMs, however, can model differences in individual fitness within the population and better capture more complex and biologically significant movement behaviours. Integrating a least-cost model with an ABM allowed individuals to make decisions that captured some element of the interaction between connectivity and movement on individual- and population-level fitness. Our results clearly show that different behavioural repertoires yield qualitatively and quantitatively different results and highlight the complex relationship between landscape structure and functional connectivity. More highly fragmented landscapes favoured the more complex movement of type-3 agents, which offered a higher probability of finding suitable foraging and resting habitats. This contrasted with the fitness declines observed in the less behaviourally complex type-2 agents that relied purely on least-cost pathways informed by our connectivity models. This finding highlights a major value of landscape modelling: alternative habitats can be constructed that differ in patch size and isolation, but not in proportional representation, facilitating separation of fragmentation from habitat loss - rarely possible in a real-world context where the two processes are usually intertwined (Ewers and Didham, 2006; Skov et al., 2011).

We have not focused our efforts on cost-distance modelling as a primary connectivity calculation as it is implicitly assumed that individuals have completed knowledge of the landscape structure (Stevens et al., 2006). We have allowed hedgehog agents to carry out individual decision-making on limited knowledge about their environment (their 8-neighbour cells) and so provided greater biological relevance in agent behaviour. Whilst conservation managers desire simple connectivity indices that can inform selection of sites for reserves (Palmer et al., 2011), we have shown that much greater biological realism is necessary to better understand behavioural and fitness responses to changes in landscape structure. Whilst our study has focused on abstract approaches to representing habitat structure and fragmentation, the framework upon which our model is based facilitates individual movement behaviours to be modelled at different scales and under various landscape scenarios, making it an adaptable and flexible approach to modelling connectivity. The consideration of biological details, individual-level behaviour and landscape heterogeneity show how utilising a model that can incorporate such complexities is crucial for improving the reliability of exploring and projecting as a basis for conservation (Bocedi et al., 2014).

We have presented a methodology and tool for firstly, validating potential least-cost connectivity maps and secondly, integrating these with powerful individual-based models that can allow for dispersal movements and day-to-day home ranging behaviours to be separated, to aid better exploration of the relationship between functional connectivity and individual fitness. Studies thus far have focused primarily on dispersal as a main process maintaining connectivity, and frequently utilised a single measure, often the probability of inter-patch movements, for quantifying connectivity (Pe'er et al., 2011). By separating the two aspects of functional connectivity we can begin to explore the relative importance of, and relationship between, these important aspects of functional connectivity and therefore the response of species to changes in landscape structure (Pe'er et al., 2011).

2.4.1 Validation of connectivity model

Differences between z-scores obtained in this and the original Driezen et al. (2007) study suggests that validation of connectivity (least-cost) model is not trivially affected by path elimination criteria, with the different sets of criteria leading to only two models performing well under both conditions. Such ambiguity in statistical outcomes indicates that the method of analysing least-cost models is sensitive to empirical data and larger validation data sets may be required to provide greater confidence in model results. The importance of relative habitat costs contained within each connectivity model, in determining our understanding of the effect of connectivity on animal populations, was clear; in simulations with the new connectivity model, type-3 agents exhibited increasing fitness with fragmentation, compared to the decreasing fitness observed for same agents, under the same conditions, in simulations using the original connectivity model.

We have shown that the type of connectivity model influences agent fitness and that this effect can be confounded by the fragmentation of the landscape. Updating type-3 agents with an additional behavioural rule better captured the dynamics of individual movement decisions by dispersing hedgehogs. This relatively simple change yielded agents of higher fitness (lower path cost) across most landscapes in spite of them consistently travelling in habitats of non-minimum cost (temporally-motivated habitats choices did not consists solely of lowest cost habitats). The simpler least-cost pathway movements of type-2 agents could not capture such activity-specific habitat costs. Results from the agent-based simulations clearly show how fitness calculations, fragmentation effects and representations of landscape connectivity may be influenced to a large extent by this behaviour.

2.4.2 Limitations and future developments

Clearly, simulations could have incorporated many additional aspects of behaviour, including interactions with other agents of the same species, competing species or prey/predator species, as well as more realistic feeding behaviour and distribution of food resources. Also, a number of features inherent to the design of the simulation may have influenced the individual- to system- level relationship. Known sensitivity of least-cost models to changes in data resolution (Corry and Lafortezza, 2007) could similarly affect our agent-based simulations and further tuning of grid-cell size to length of time-step would likely improve robustness. The incorporation of real GIS habitat data into agent-based simulations is the logical next step for future models, and will go some way to addressing these concerns and maximising the applicability of using agent-based simulations to help tackle real-world projects. Whilst these additions will improve our ability to draw conclusions about system-level behaviours in realistic environments, they come at the cost of not being able to experiment with different habitat structures, as we have done in this paper. We recommend, therefore, minimising the number of rules and maximising the simplicity and interpretation of agent decisions with respect to the issue under investigation.

2.5 Conclusion

The study presented here constitutes an analysis of the added value obtained by integrating models of landscape connectivity into models of individual decision-making. The strength of least-cost modelling lies in its application to real-world conservation projects whilst agent-based simulations can increase exploratory power of complex system behaviours. The integration of least-cost modelling with agent-based simulations captures behavioural responses to landscape characteristics in an individual's view of the landscape. This process demonstrates the ability of connectivity measures to directly focus conservation action in a way that has not been explored previously and increases our understanding of processes that might influence and direct long-term population persistence. The inherent flexibility of agent-based simulations given the wide range of available software packages and programming languages provides much scope to develop models further to address sensitivity issues. Incorporating real spatial data into these models will improve our ability to draw conclusions about complex ecological systems in realistic environments, improving the validity of using such models to inform direct conservation action. Future models will therefore focus on understanding model parameters, integrating real GIS data into model simulations and extending models to incorporate multiple patterns of landscape dynamics.

Acknowledgements

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Appendix A: Outline of previous least-cost model validation study by Driezen et al. (2007).

This study presents a method of validating the results of a least-cost analysis by comparing realised movement paths of hedgehogs in unfamiliar areas. Observed during a previous study (Doncaster et al., 2001) and obtained via radio-tracking of 48 individuals for ± 20 days, real hedgehog locations informed calculations of the correspondence between empirical movement trajectories and least-cost paths. Calculated z-scores quantified this correspondence and allowed least-cost models to be statistically compared.

To test the full repertoire of relative cost values, this study developed a set of 12 least-cost models and shown below:

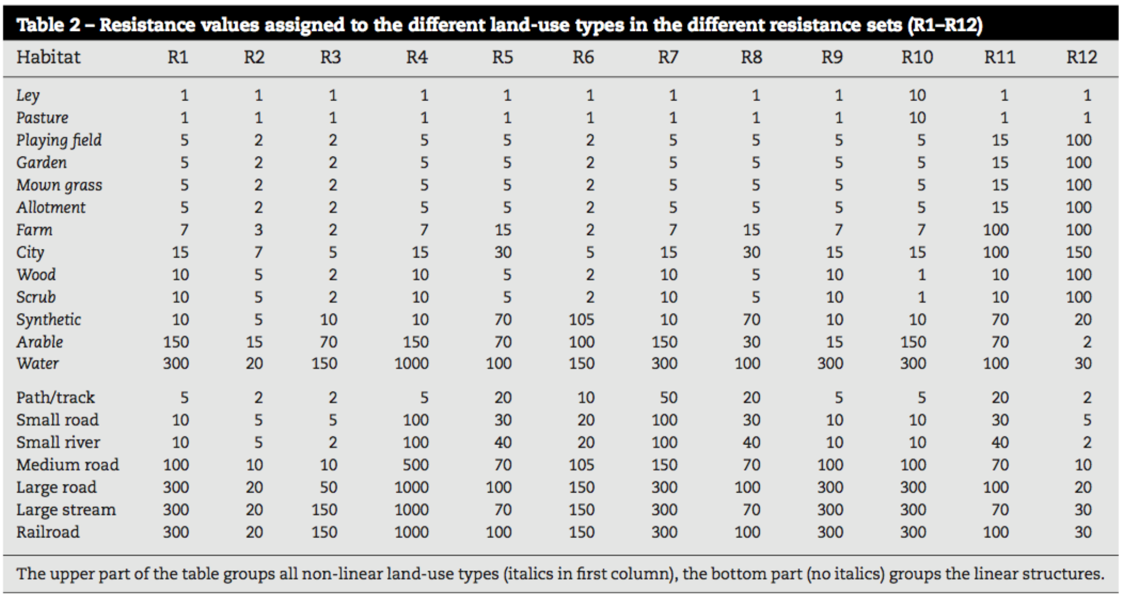


Table 2 – Resistance values assigned to the different land-use types in the different resistance sets (R1–R12)

Habitat	R1	R2	R3	R4	R5	R6	R7	R8	R9	R10	R11	R12
Ley	1	1	1	1	1	1	1	1	1	10	1	1
Pasture	1	1	1	1	1	1	1	1	1	10	1	1
Playing field	5	2	2	5	5	2	5	5	5	5	15	100
Garden	5	2	2	5	5	2	5	5	5	5	15	100
Mown grass	5	2	2	5	5	2	5	5	5	5	15	100
Allotment	5	2	2	5	5	2	5	5	5	5	15	100
Farm	7	3	2	7	15	2	7	15	7	7	100	100
City	15	7	5	15	30	5	15	30	15	15	100	150
Wood	10	5	2	10	5	2	10	5	10	1	10	100
Scrub	10	5	2	10	5	2	10	5	10	1	10	100
Synthetic	10	5	10	10	70	105	10	70	10	10	70	20
Arable	150	15	70	150	70	100	150	30	15	150	70	2
Water	300	20	150	1000	100	150	300	100	300	300	100	30
Path/track	5	2	2	5	20	10	50	20	5	5	20	2
Small road	10	5	5	100	30	20	100	30	10	10	30	5
Small river	10	5	2	100	40	20	100	40	10	10	40	2
Medium road	100	10	10	500	70	105	150	70	100	100	70	10
Large road	300	20	50	1000	100	150	300	100	300	300	100	20
Large stream	300	20	150	1000	70	150	300	70	300	300	70	30
Railroad	300	20	150	1000	100	150	300	100	300	300	100	30

The upper part of the table groups all non-linear land-use types (italics in first column), the bottom part (no italics) groups the linear structures.

Appendix B: Landscape fragmentation algorithm.

The random walk process first assigned a random single cell from across the entire landscape to each of the seven habitat types. From these seven cells, neighbour cells are assigned to the same habitat type until there are no unassigned neighbour cells. At this point, a random unassigned cell from those remaining is assigned to the same habitat type and the process of assimilating neighbours starts again. This process repeats for each habitat type, until all cells in the landscape have an assigned habitat type. Sample code from Netlogo is shown below for a single habitat:

```
to expand-habitatarable
ask arable [
if all? patches [pcolor != black] [stop]
if Harable = 0 [stop]
ifelse all? neighbors [pcolor != black]
[move-to one-of patches with [pcolor = black]
set pcolor color
reduce-colours]
[ifelse all? neighbors4 [pcolor != black] [
move-to one-of neighbors with [pcolor = black]
set pcolor color
reduce-colours
][
move-to one-of neighbors4 with [pcolor = black]
set pcolor color
reduce-colours]
]
]
end
```

Following the initial setup of habitats across the landscape, fragmentation occurred through the swapping of habitat type between cells. Here, higher levels of fragmentation caused more cells to be swapped. Sample code from netlogo outlines the method used in this study, where patches represent each cell in the landscape and fragmentation-of-habitats represents the user-inputter fragmentation value from 0 to 50:

```
ask patches [
if random 100 ¡= fragmentation-of-habitats
[swap self one-of patches]
]
```

Chapter 3

An agent-based model of jaguar movement through conservation corridors

This work has been presented at the European Artificial Life Conference 11, held in Paris, 4-8th August 2011, and is published as "Watkins, A., Noble, J., and Doncaster, C.P. (2011) An agent-based model of jaguar movement through conservation corridors. In: Advances in Artificial Life, ECAL 2011: Proceedings of the Eleventh European Conference on the Synthesis and Simulation of Living Systems, pp. 846-853, MIT Press."

Abstract

Wildlife corridors mitigate against habitat fragmentation by connecting otherwise isolated regions, bringing well-established benefits to conservation both in principle and practice. Populations of large mammals in particular may depend on habitat connectivity, yet conservation managers struggle to optimise corridor designs with the rudimentary information generally available on movement behaviours. We present an agent-based model of jaguars (*Panthera onca*), scaled for fragmented habitat in Belize where proposals already exist for creating a jaguar corridor. We use a least-cost approach to simulate movement paths through alternative possible landscapes. Six different types of corridor and three control conditions differ substantially in their effectiveness at mixing agents across the environment despite relatively little difference in individual welfare. Our best estimates of jaguar movement behaviours suggest that a set of five narrow corridors may out-perform one wide corridor of the same overall area. We discuss the utility of ALife modelling for conservation management.

3.1 Introduction

One of the most obvious effects of our own species on the planet has been the clearing of forests to make way for agriculture. In many parts of the world this means that the natural vegetation that remains tends to be divided into isolated patches (see figure 3.2 for an illustration) with disruptive consequences for the local wildlife. The establishment and maintenance of "corridors" connecting otherwise isolated areas of habitat have therefore been put forward as important tools in conservation biology (Bennett, 2000; Hilty et al., 2006). The idea of a corridor is to connect local sub-populations into a single meta-population and thereby reduce the risk of local extinctions due to human activity (hunting, land development, etc.) and, more importantly, to improve the species' long-term survival chances by increasing the size of the gene pool.

Bennett (2000) shows that evidence for the effectiveness of habitat corridors is mixed: they have been more helpful for some species than others. Indeed, habitat fragmentation is itself a concept that depends on the details of the behavioural ecology of the species concerned (consider, for example, the difference between a bird and a snail in their ability to move between habitat patches). The current paper puts forward a simulation model to help assess the effectiveness of different corridor policies for the jaguar, *Panthera onca*.

The jaguar (figure 3.1) is an apex predator that stalks and ambushes its prey. It is the third-largest of the big cats and the largest big cat species in the Western hemisphere. Its range extends from the southern United States to northern Argentina. Jaguars are stealthy and elusive, and thus there is still much we do not know about their behaviour. However, one of the better-studied jaguar populations is in Belize, on the Carribean coast of Central America. In particular, the Cockscomb Basin Wildlife Sanctuary (CBWS), a 425 square-km reserve in southern Belize, has been a productive jaguar fieldwork site for several decades (Harmsen et al., 2010a; Rabinowitz and Nottingham, 1986). Biologists working there have been instrumental in setting up the Jaguar Corridor Initiative (Rabinowitz and Zeller, 2010), a cooperative effort between scientists, conservation groups, and regional governments to establish corridors connecting known jaguar populations.

Assessing the usefulness of a corridor initiative is difficult when we do not fully understand the behaviour of the species involved. Two of us (AW and CPD) are conducting ongoing fieldwork at the CBWS in Belize, but we recognize that data on jaguar numbers and movement, collected through means such as stealth cameras and radio-tracking, will not be sufficient on its own. Such data collection efforts need to be combined with modelling in order to improve our understanding of jaguar behaviour. There has been some recent progress on statistical, data-driven modelling in this regard (see for example the Bayesian approach of Colchero et al., 2011) but we believe there is also utility in the agent-based modelling approach characteristic of work in artificial life.

Agent-based models explicitly represent the behaviours of individual organisms, allowing us to simulate both the interactions between individuals, and those between the individual

Figure 3.1: A jaguar photographed using a stealth camera. Image courtesy of the Jaguar Corridor Initiative, Belize.

and the environment (Grimm, 1999). For our purposes, the advantages of these types of models are the ability to integrate individual behaviours with landscape dynamics, to model individual-level adaptive processes such as learning and memory, and to study collective responses to changes in landscape composition. The potential to explore many alternative scenarios also provides distinct advantages over classical ecological models.

Agent-based modelling approaches have been widely used already, of course, under the banners of both artificial life and of ecology, to study the movement of animals through their environments. Examples include Nonaka and Holme's (2007) model of optimal foraging in clumpy environments, Wheeler and de Bourcier's (2010) work on the evolution of territorial signalling, and Hemelrjik's (1998) model of the spatial aspects of dominance hierarchies in chimpanzees.

In constructing a model of jaguars moving around in their habitat and using (or *not* using) corridors, we will need a way to model their decision-making about where to go next. This is an opportunity to integrate the "least-cost modelling" paradigm from landscape ecology (Adriaensen et al., 2003) with the agent-based approach. The idea behind least-cost modelling is simple: it is a species-specfic calculation based on the assumption that dispersing organisms are more likely to use a route of least resistance when traversing a landscape. In other words, whenever they are faced with a choice while moving around their spatial network, they will choose the lowest-cost option. Cost estimates are themselves derived from data on how frequently the animals are observed in particular landscape types, and their preference for one type over another in choice tests.

Least-cost modelling techniques are standard in many GIS (Geographical Information System) packages which offer built-in cost and distance functions that allow for rapid model construction (Rayfield et al., 2010). A raster-based grid of the landscape is generated with a cost assigned to each cell that represents the lowest cumulative cost from that cell to the source cell. This cost is the inverse of the degree of functional connectivity of the landscape according to the species in question (Driezen et al., 2007) and thus the end product of the calculation can be seen as a probability distribution across the landscape describing the likelihood of the animal settling at any given position. Rabinowitz and Zeller (2010) developed an ambitious least-cost model of jaguar dispersal across their entire range in Central and South America.

Validating least-cost models is not easy, however Driezen et al. (2007) produced one of the only studies to successfully compare the output of least-cost models with empirical data on animal movement. They used statistics on landscape-wide cost values and compared these to real hedgehog paths, constructing and presenting a novel approach to matching empirical movement trajectories with generated least-cost maps. Chapter 2 demonstrated that this approach could be taken further through integration with agent-based modelling.

The aim of the current project is to build a simple agent-based model of jaguar behaviour, employing a least-cost view of movement, in order to look at how the spatial structure of corridors intended to connect disjoint forest habitats could affect conservation goals. In short, we ask the reader to imagine two separated expanses of forest (as occurs in many locations in Belize) and enough resources to protect a few tens of square kilometres of remnant forest from further disturbance and human development. What would be the best corridor design policy? One wide corridor? Multiple thin corridors? A series of small “islands” between the two forests? How much could we expect of such a corridor once constructed, i.e., what effects would it have on individual welfare and on genetic mixing at the population level? We contend that the answers to these questions will be an emergent function of jaguars’ preferences for different landscape types and their territorial interactions with each other.

This work is intended to be the first in a series of increasingly detailed models of jaguar ecology. The integration of real GIS data into the model is beyond the scope of the current study — we think there are basic questions to ask of an abstract model first — but is the logical next step for future models. Basing simulated models in real landscapes can only improve our ability to draw conclusions about system-level behaviours in realistic environments.

3.2 The Model

The first step in constructing our model is devising a map layout that reflects the essentials of the problem. Figure 3.2 shows a typical Belizean landscape and illustrates the fragmentation of forest habitat that occurs due to road construction, tree-clearing for farming, urban development, etc. The key feature of our simulation will thus be two separated blocks of forest, surrounded by cleared farmland. Each forest section will hold an initial population of jaguars; the question is how easy or difficult it will be for them to

Figure 3.2: An aerial view of a typical landscape in Belize. Note that regions of ideal jaguar habitat (i.e., forest) are separated by roads and cleared farmland. Image: Google Earth.

travel from one forest zone to another.

Figure 3.3 shows the potential corridor designs that we will investigate. We begin with the basic two-forest layout in the top left corner. Note the blue edges where the forest meets farmland; we assume that these transitional zones are of intermediate appeal to the jaguars. The next design (top centre) features a corridor connecting the two forest sections. We also consider (top right) a layout with additional area added to the forest sections: this is equivalent to a control condition in which we spend the conservation budget on extending each forest rather than connecting them. Next we consider whether corridor width is more or less important than the number of corridors by looking at three- and five-corridor designs. In each case the same total area is devoted to the connecting corridors. These are followed by one- and three-island designs — alternatives to a direct corridor — and a design made up of many randomly placed islands. Again, the total area devoted to corridor is a constant. Finally we also look at a "contiguous forest" layout where the entire map is forested: this is another control condition in that it allows us to compare jaguar ecology in a modern fragmented habitat with what it might have been before human colonization.

The map is not meant to be a precise rendition of any particular location, but we do need to establish a scale in order to incorporate what is known about jaguar population density, movement rates, and territory size (our primary references in this were Harmsen et al., 2010a; Schaller and Crawshaw, 1980). The map is represented as a 100 × 100 grid of squares, with each square being 500 metres on a side. This means that the entire map covers 50 × 50 km, with each of the basic forest sections measuring 15 × 40 km and with a 10 km expanse of farmland between them. For comparison, the 2500 square km area of

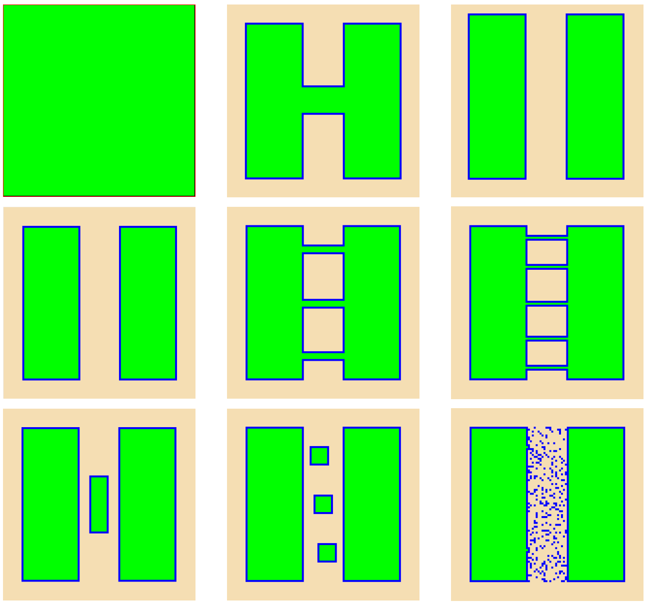


Figure 3.3: Map layouts investigated in the simulation. Core forest is in green, forest edges are blue, and farmland is khaki. First row: contiguous forest, one corridor, no corridor but equivalent area added to the forest. Second row: no corridor, three corridors, five corridors. Third row: one island, three islands, random islands.

the map represents about 10% of the land area of Belize.

In most layouts the map includes 1275 square km of forest (the exceptions are the no corridor layout with 1200 square km and the contiguous forest condition with 2500 square km). Each run of the simulation begins by placing 100 jaguars into randomly chosen forest squares, which corresponds to a density of 7.84 jaguars per 100 square km. This is consistent with Rabinowitz and Nottingham (1986) who found a minimum home range size of 10 square km per animal, and also with Harmsen et al. (2010a) who estimated densities of 3.5 to 11.0 individuals per 100 square km in the CBWS, which is itself thought to be a “hot spot” for jaguar numbers. Our simulated population of 100 jaguars thus represents a medium to high population density.

Edge effects are known to be important in landscape ecology, and so we added an edge-detecting routine to the initialization of our map. Any forest square that borders a farmland square (in any of 8 neighbouring positions) is labelled as an edge square. These are shown in blue in figure 3.3.

What about temporal scale? Schaller and Crawshaw (1980) recorded daily travel of between 1 km and 3 km straight-line distance for jaguars, with males travelling further than females. In our model male jaguars move one grid square every timestep; if all eight surrounding squares have equal cost, the movement will be in a random direction. In order to get plausible straight-line daily travel distances we therefore set one timestep to be 4 hours. This gives 6 timesteps per day, and 2190 timesteps in a year — the standard length of one of our simulation runs.

The least-cost movement algorithm for the jaguars is as follows: they look around their neighbourhood — 8 surrounding grid squares plus their current location — and assess the cost of moving into each square. Lower cost numbers mean a more attractive destination. The jaguar chooses the lowest-cost option 95% of the time, with ties being settled at random to avoid systematic movement bias in any one direction. The other 5% of the time they choose a random square; this modest level of randomness was introduced in order to disrupt any implausibly symmetrical movement patterns that might arise. The difference between male and female movement rates is reflected by females only actually *moving* to their chosen square 70% of the time, whereas males always move.

At this point we need to start fleshing out the least-cost model with specific numbers describing the preference of the jaguar for the map's three habitat types: forest, forest edge, and farmland. We set the preferred forest habitat's cost value at 1.0 as a reference. Previous least-cost models (Driezen et al. (2007) and chapter 2) suggest that non-preferred habitat such as farmland will have values many times higher. The correct cost value for farmland for the jaguar is not yet known; we have chosen a value of 25.0. The forest edge is intermediate but still relatively low-cost at 5.0. At this stage these numbers are arbitrary as their rank order is more important than their specific values: the effect is that jaguars in the model will prefer forest to edge to farmland.

Jaguars are known to be largely solitary except when mating. Our model does not explicitly include mating and so we added a cost of 100.0 for entering a square currently occupied by another jaguar, making this a very unlikely event.

Jaguars are territorial and their behaviour varies markedly by sex. Males range across bigger territories than females, and males and females seem to be territorial towards others of the same sex but not the opposite sex, e.g., male territories can overlap with female territories but not with each other. Simply having our simulated jaguars avoid direct contact with each other is not enough to reflect this complexity.

We model sex-specific territoriality using a pheromone system, as used by many artificial life models looking at social insects (e.g., Nakamura and Kurumatani, 2008). Each jaguar is assumed to mark its territory by leaving 100.0 pheromone units behind in every grid square that it traverses. The pheromone level then decays at a rate of 2% per timestep. A pheromone trace deposited by a jaguar of the opposite sex has no effect. Pheromone deposition is additive, so if a second jaguar comes along before the first deposit has decayed, the pheromone level can rise to even higher levels. This will not happen unless the jaguars are extremely over-crowded though, as the pheromones of other same-sex individuals are repellent: a pheromone deposited by another jaguar of the *same* sex adds to the cost value of the grid square in a 1:1 ratio, i.e., a freshly deposited same-sex pheromone trail in the forest will massively raise the cost of that square from the baseline 1.0 to 101.0.

All pheromone deposits decay over time at 2% per timestep. For computational

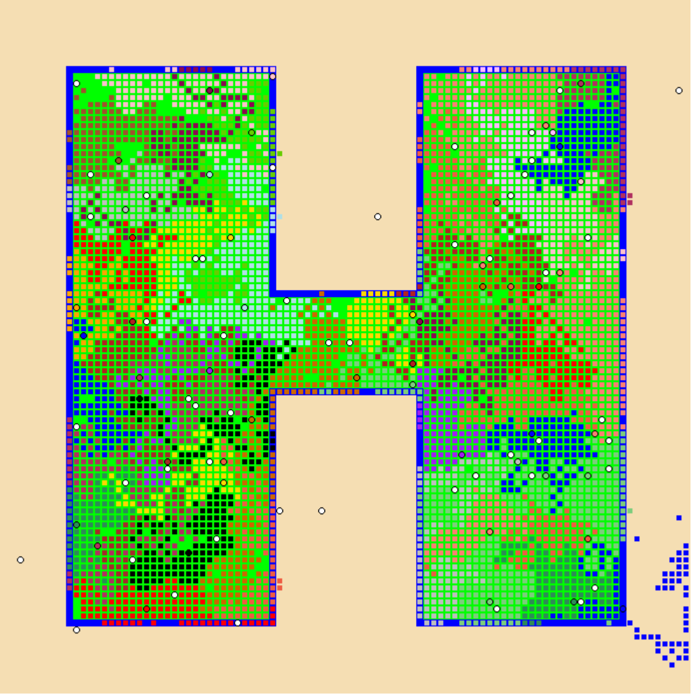


Figure 3.4: A representative screenshot of the simulation after 500 timesteps. Jaguar locations are represented as circles, with females in white and males in a random colour. Male and female pheromone trails (i.e., territories) overlap so, for clarity, only male territories are shown. Pheromone trails are in the same colour as the male that produced them. Note the variation in territory size, and the fact that a few animals have been "pushed out" into the less desirable farmland.

simplicity, pheromone levels lower than 5.0 are reduced to zero. This decay rate means that a jaguar's pheromone trail has less and less effect until finally becoming undetectable around 150 timesteps (25 days) after it passed through a grid square. Thus we can imagine each jaguar trailing out behind it a "scent cloud" that dissipates over several weeks. Figure 3.4 is an example screenshot of the simulation in action and shows what this looks like in practice.

There is a finely tuned balancing act involved in deciding just how strong the repellent effect of other jaguar's territories should be. If we take the landscape cost value of 25.0 for pasture as a reference point, our parameters for pheromone cost and decay rate mean that a jaguar will be ambivalent between entering a farmland grid square and entering a forest grid square that had seen another same-sex jaguar pass by around 12 days earlier. Clearly there is some guesswork going on here: jaguars are not well-studied enough for us to know the exact values that should be plugged in. The point is not to make a precise predictive model but to see whether it is possible to explain the basics of jaguar movement with some simple rules. In this regard, we do have circumstantial evidence: jaguars have occasionally been observed in pastures both in Belize and Brazil, and we know that jaguars are somewhat territorial. If we chose much higher values for the landscape cost of farmland, the jaguars would not leave the forest at all, even under extremely crowded local conditions. Conversely, if we make the cost of encountering another jaguar's pheromone too high, the animals will spill out into the farmland in great numbers in an effort not to encroach on each other's territory.

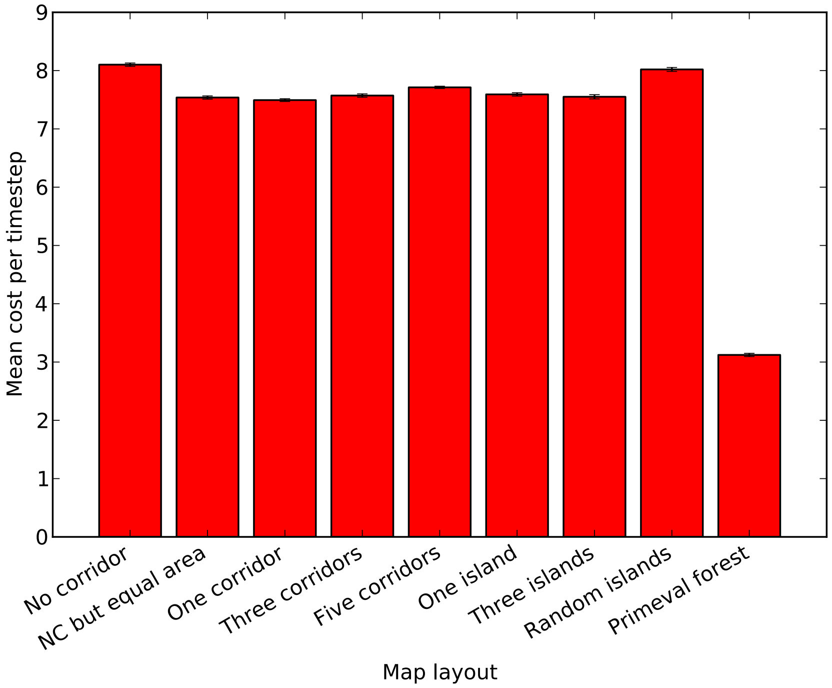


Figure 3.5: Mean cost figures per jaguar per timestep compared across the nine different map layouts. Standard errors are calculated across 25 replications of each condition with different random seed values.

Our simple pheromone mechanism is actually a reasonable model of how jaguars maintain their territorial boundaries in the real world. Jaguars are not as likely to mark their passage with urine or scat as other felids are (Harmsen et al., 2010a; Schaller and Crawshaw, 1980) but they are known to scent-mark by scraping trees in their territory (Harmsen et al., 2010a).

There is one more cost to be considered: we also made the jaguars sensitive not just to pheromones deposited by others but also to their *own* pheromone trails. The cost of entering a grid square where you were the last occupant is equal to 15% of the pheromone level (i.e., the effect is about 7 times weaker than for the pheromones of others). This reflects the fact that a section of forest where the animal has not hunted recently is a better prospect for prey than the same grid-square they occupied the day before. The effect is to stop the jaguars back-tracking on their own path. A solitary jaguar in a large expanse of forest will therefore perform a random walk strongly biased towards yet-unvisited grid squares, in effect carving out a territory of maximal size for itself.

Unlike much ALife work, there is no genetic algorithm in our model: our central question is not evolutionary but ecological. In the same vein as Hemelrjik (1998) we are not asking

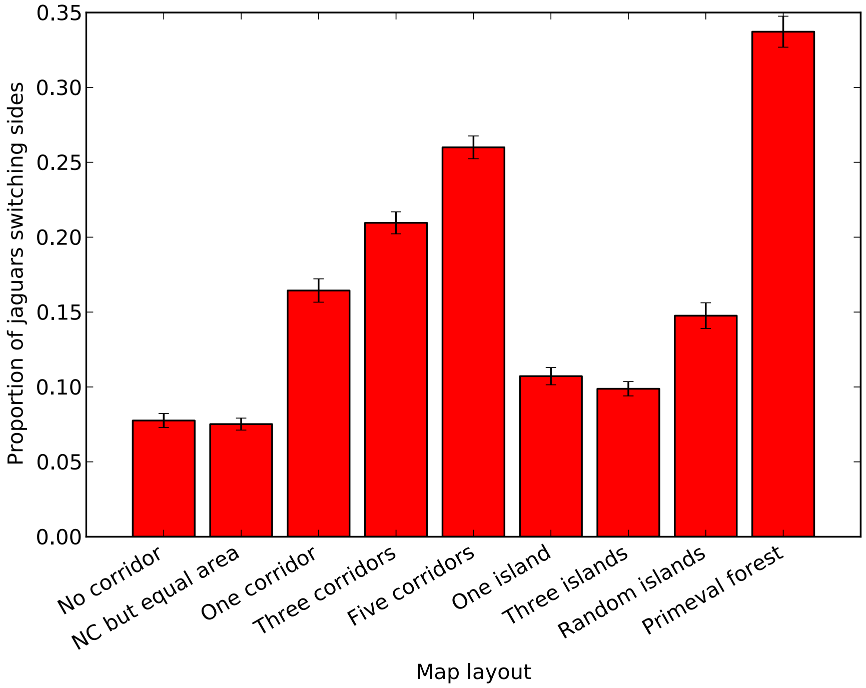


Figure 3.6: Proportion of jaguars that move from one side of the map's centre-line to the other by the end of the simulated year, compared across the nine different map layouts. Standard errors are calculated across 25 replications of each condition with different random seed values.

about the evolution of the animals' strategies, but about the implications of how a hypothesized behavioural program would play out when followed by multiple animals in a simulated spatial world.

The goal is to use our model of jaguar movement behaviour to evaluate the effectiveness of different corridor layouts — but what can we measure in order to do that? The jaguars' behavioural strategies are not evolving, so we cannot measure "fitness" per se. Instead we look at the average cost level for the grid squares each jaguar chooses to enter over the course of the run. This is effectively a measure of "jaguar welfare". Low cost grid squares (i.e., what jaguars want) are places in the forest that have not recently been visited by other jaguars. The low cost ultimately reflects the fitness benefits of being in such places: these are areas with high prey availability, low risk of being killed by farmers, low risk of costly fights with other jaguars, etc. Higher values on the average-cost measure will therefore be associated with stress or over-crowding. If one corridor layout can reduce this value compared to another, this is evidence for its jaguar-conservation effectiveness.

We are not simulating enough detail of the jaguar's lifestyle to look at mating behaviour directly, but we can look indirectly at whether different corridor layouts would encourage a larger breeding population as opposed to isolated sub-populations. We have done this simply by recording the proportion of jaguars that finish the year on the opposite side (east-west) of the map compared to where they started. A value of 0% indicates two isolated sub-populations, whereas 50% would indicate random mixing.

3.3 Results

Figure 3.4 shows a typical screenshot from the simulation. We can see that the model has been successful in reproducing male territories of a plausible size of 10 to 20 square km, and that a minority of jaguars have resorted to hunting in farmland. When watching the animation over time it is very easy to interpret the jaguar movements as "patrolling" a territory and avoiding conflicts with each other; the forest edges are used as "pathways" around territories; established core territories shift only gradually; and the jaguars that are forced out into farmland eventually get back into the forest when they are lucky enough to find an undefended edge section. Figure 3.4 shows the "one corridor" layout, and we can see that the corridor is certainly occupied by jaguars and thus might be leading to genetic mixing between the two sub-populations.

However, we can also see a threat to this exchange: note that the brown and the yellow territories in the centre of the corridor act as barriers to the transit of any other (male) jaguars. Our qualitative impressions when watching the simulation run with different corridor layouts were that the geography of the corridor could certainly make a difference as some layouts, notably the five-corridor map, led to "channeled" movement back and forth across the corridor, whereas other layouts such as the one in figure 3.4 led to blockages.

Figure 3.5 shows the comparison of the average-cost values across all 9 conditions. The obvious pattern here was that the layout did not seem to make a great deal of difference to the average cost experienced by each animal, except in the "contiguous forest" case. It is obvious that the contiguous layout will lead to lower average costs, however, as the same number of jaguars are distributed across about twice as much forest, giving larger territory sizes and fewer encounters with the pheromones of others.

The "no corridor" and "random islands" conditions lead to slightly higher costs than in other conditions. In the former case this is simply because there is less forest territory available; in the "equal area" control condition this difference disappears. The "random islands" condition leads to most of the corridor squares being edge squares, and there is a concomitant increase in average cost. On this evidence it would seem that corridor design does not make much difference to jaguar welfare, and that the critical thing is simply to have as much favourable habitat available as possible.

What of the genetic mixing results? If we look at figure 3.6 we see the mean level of movement across the centre-line of the map, over the different conditions. The differences here are much more dramatic. The "contiguous forest" condition is again the most favourable for the jaguars, with 34% mixing (approaching the 50% level that would you would get if the jaguar locations were shuffled at random). This contrasts with the "no corridor" conditions that support only 7 or 8% mixing. The island-based corridor designs perform very badly as well, although things are not quite so bad with the "random island" design. The striking finding from figure 3.6 is that corridor-based designs perform best, and that the more corridors and/or the thinner the corridor, the better. Observation of these runs suggests that the strong performance of the five-corridor design (26% swapping) is because the thin pathways promote rapid movement, often through the edge squares if another animal has recently passed through the forest squares, and the very thin strip of core forest (just 500 metres wide) is not big enough to support a territory. Wider corridors (the three-corridor and the one-corridor cases) were better than island-based designs, and certainly better than no corridor at all, but did not match the mixing levels of the five-corridor case due to the tendency for the corridor to become blocked by an established territory.

3.4 Conclusions

We were pleased with the qualitative results of the model in that we managed to replicate plausible territorial behaviour in jaguars using the least-cost paradigm and only a few assumptions. The model has brought novel aspects of the corridor design problem to light, notably the possibility that some corridor layouts could be counter-productive due to being large enough to support internal territories that then acted as obstacles to travel by other animals. We feel that the agent-based modelling approach we have begun here has the potential to be extremely useful in drawing out the implications for different theories about jaguar behaviour and thereby helping to determine which of those theories is a better match for the multi-faceted and incomplete observational data we have on the real animals (see Di Paolo et al., 2000, for an account of how this process can work). There are many parameters in the model for which we have had to guess at an appropriate value, but the idea is to take these values as a starting point and use them in an iterative process of model refinement in future comparisons with empirical data from Belize.

We began our modelling with a hypothetical question about the best corridor design to choose if you had the resources to reforest a few tens of square km of Belizean farmland separating two forests. We can answer that question unequivocally: of the corridor layouts we explored, the five-corridor layout was the most effective. We had expected that we might see significant differences in the average landscape cost value experienced by the jaguars across the different corridor designs, but this turned out not to be the case. Average landscape cost, given a constant population of jaguars, seems to be explained almost entirely by the availability of core forest grid squares. This suggests, for example, that constructing a new conservation corridor in Belize would not lead to a big boost in the landscape's carrying capacity for jaguars. Instead, the key difference observed between our corridor designs was their capacity to promote migration from one side of the map to the other, and thus to promote genetic mixing at the whole-population level. The five-corridor case achieved levels of cross-map migration that were almost comparable to the "contiguous forest" condition, which is a great outcome from a conservation perspective.

Having established that this agent-based least-cost modelling approach is viable, there are several ways in which we could improve the model. Incorporating real maps of the Belizean landscape using GIS packages is an obvious way of increasing the model's fidelity, although we believe it is important not to rush this process: we need to understand the dynamics of how our simulated jaguars behave in simplified environments first. Still, using GIS data would also allow us to build a richer least-cost model, incorporating data on jaguar preferences for entering or avoiding terrain such as hills, differing densities of forest, roads, and urban areas.

In terms of the corridor design problem, a weakness of the current model is that we only compared six specific corridor layouts with three control conditions. If we settled on a way to represent the spatial layout of a corridor, e.g., as a bitmap, we could use a genetic algorithm or other optimization technique to search for the best *possible* layout for the connecting corridors. This is perhaps slightly premature at this stage as the model is in an exploratory mode; we do not yet know enough about jaguar movement behaviour to be sure that such an optimized layout would be accurate enough to serve as a reliable conservation policy recommendation. Nevertheless we would at least be in a position to say *why* we believed a certain corridor design was optimal.

In conclusion: jaguars are rare, elusive, and hard to study. In coming years, we expect that improvements in radio- and GPS-tracking technology should see an increase in the data we have available on how they move around their environment. However, as that data comes in, it will be important to be able to evaluate it in the light of competing theories about how jaguars make decisions about hunting, mating, territory defence, etc. The agent-based simulations of artificial life can clearly help in doing this.

Chapter 4

A spatially explicit agent-based model of the interactions between jaguar populations and their habitats

This chapter has been published as:
"Watkins, A., Noble, J., Foster, R. J., Harmsen, B. J. and Doncaster, C.P. (2014) A spatially explicit agent-based model of the interactions between jaguar populations and their habitats. Ecological Modelling".

Abstract

Agent-based models can predict system-level properties of populations from stochastic simulation of fine-scale movements. One important application to conservation lies in their ability to consider the impact of individual variation in movement and decision-making on populations under future landscape changes. Here we present a spatially explicit agent-based simulation of a population of jaguars (*Panthera onca*) in a mixed forest and farmland landscape in Central America that demonstrates an application of least-cost modelling, a description of the way that agents move through their environment, to equilibrium population dynamics. We detail the construction and application of the model, and the processes of calibration, sensitivity analysis and validation with empirical field data. Simulated jaguars underwent feeding, reproduction, and mortality events typical of natural populations, resulting in realistic population dynamics and home range sizes. Jaguar agents located inside protected forest reserves exhibited higher fitness (fecundity, energy reserves, age and age of mortality) as well as lower energy- and habitat-related mortality than jaguar agents located outside these reserves. Changes in fecundity directly affected the dynamics of simulated populations to a larger degree than either mortality or agent-agent interactions. Model validation showed similar patterns to camera traps in the field, in terms of landscape utilisation and the spatial distribution of individuals. The model showed less sensitivity to socially motivated and fine-scale movements, apart from those directed towards feeding and reproduction, but reflected the interactions and movement of naturally occurring populations in this region. Applications of the model will include testing impacts on population dynamics of likely future changes in landscape structure and connectivity.

4.1 Introduction

As the largest cat in the western hemisphere, the jaguar, *Panthera onca*, can reasonably form the basis for large-scale conservation. Their large home ranges, adaptability to a wide variety of environmental conditions and presence in any countries throughout Central and South America encourage landscape-scale approaches at conservation of the species that will likely lead to extensive biodiversity preservation and numerous species and vegetation communities protected within the cats range (Hatten et al., 2005; Kelly, 2003; Sanderson et al., 2002). The reduction in historic range of some 50% during the 20th century through habitat loss and degradation combined with persecution (Hatten et al., 2005; Sanderson et al., 2002) has resulted in a Near Threatened Red Listing for the global jaguar population (Caso et al., 2010; International Union for Conservation of Nature, 2013).

The permeability of a landscape to an animals movement depends on structural characteristics of the landscape as well as the mobility of the individual. Extensive fieldwork in Belize, including camera trapping and telemetry, has demonstrated barriers to jaguar population continuity that can destabilise ranging behaviours (Foster et al., 2010a). Major transport infrastructure networks currently bisect the large tracts of protected forests that exist to the north and south of the country and which form a key link in the intercontinental Mesoamerican Biological Corridor (Rabinowitz and Zeller, 2010).

Landscape connectivity refers to the degree to which an animals interactions with its environment and conspecifics impede or facilitate its movement and acquisition of resources (Coulon et al., 2004; Janin et al., 2009; Rayfield et al., 2010; Taylor et al., 1993). For dispersing individuals, least-cost models have proved a useful tool for predicting the connectivity of a landscape and create a cost map of the landscape based on the assumption that animals take a route of least resistance when exploring novel environments (Pinto and Keitt, 2009). Here we adapt the least-cost modelling concept to movement costs based on general daily movements rather than specific dispersal movements, in order to facilitate integration into an agent-based simulation model. Application of this approach to a population of jaguars (*Panthera onca*) has allowed us to capture movement decisions based on a number of environmental and species-specific factors, such as food resources, habitat type, disturbance, water and mating opportunities, within a single parameter set. The only other published least-cost model for the jaguar estimates a permeability matrix for the species across its entire geographic range in Central and Southern America (Rabinowitz and Zeller, 2010). This biogeographic model addresses a need for planning at international scales, and for conservation of pan-continental corridors and functional links between populations and metapopulations.

Agent-based models (ABMs), in contrast, are able to capture the fine-scale effects of individual movements and the spatial distribution of individuals in driving dynamics within populations. These models take a bottom-up approach to predicting system-level properties as an emergent product of the interactions between agents that represent individuals (Grimm, 1999; Macal and North, 2005; Matthews et al., 2007; McLane et al., 2011; Railsback, 2001). The agents can learn and adapt their behaviour as they respond to other agents and changes in the environment (Matthews et al., 2007; Nonaka and Holme, 2007). The ABM approach has a major advantage over top-down approaches in enabling extensive exploration of the effects and implications of future landscape changes at the scale of a single population, including potential degradation or fragmentation of a landscape and mitigating conservation management strategies (Grimm et al., 2006; McLane et al., 2011).

This paper introduces a single-species ABM integrated with an adapted least-cost model, designed as a management tool to explore jaguar population dynamics under alternative scenarios of conservation management. The model demonstrated here aims to create a simulation that captures the complex behaviour and population dynamics of jaguars in a real-world setting, calibrated and validated with field data. Although others have used agent-based simulations of animal foraging and movement (e.g., Bernardes et al. 2011; Brooker et al. 1999; Nonaka and Holme 2007; Pitt et al. 2003; Tang and Bennett 2010; Topping et al. 2003), to our knowledge none has set their simulations in a least-cost context, or focused on large felids. The detailed nature of our model also complements and contrasts similar, but more simplified, approaches that focus only on dispersal movements or do not incorporate key features of our ABM approach: individual variation, adaptation, interactions and feedbacks (for example Imron et al. 2011; Kramer-Schadt et al. 2004; Revilla and Wiegand 2008; Revilla et al. 2004).

We aim to demonstrate the flexible nature of our detailed behavioural and movement model and present only the first stages of model demonstration and application. Our intention is to provide a platform from which a wide range of biological and ecological dynamics can be examined, particularly regarding the relationship between individual jaguar movement, population distribution and landscape and habitat structure. We set the agents in a region of central Belize, which contains the worlds first jaguar reserve: Cockscomb Basin Wildlife Sanctuary (CBWS). Fieldwork in this region has informed much of our understanding of jaguar ecology and population dynamics (e.g., Foster et al. 2010a,b; Harmsen et al. 2010a,b, 2009, 2010c,d; Rabinowitz 1986; Rabinowitz and Nottingham 1986) making it an ideal location for model calibration, validation and testing.

4.2 The model

The model used the object-oriented programming language Java (http://java.sun.com) within the Repast agent-based modelling toolkit (http://repast.sourceforge.net). All model code is available within figshare (Watkins et al., 2014). Model description below employs the protocol of ODD (Overview, Design concepts and Details: Grimm et al. 2006).

Purpose

The model simulated the population dynamics of jaguars in a heterogeneous landscape representing part of the CBWS in central Belize, with the purpose of creating stochastic agents that reflected the behaviour and life history of a population of jaguars in a real-world context, informed by a real landscape and validated with empirical field data. The detailed ABM design facilitates the exploration of the effect of local individual daily movements on a range of population-level behaviours and spatial and temporal distributions. The model aims to facilitate forecasting of likely jaguar distribution and abundance in scenarios that change the distribution and structure of habitats in the landscape.

State variables and scales

Model architecture comprised a grid of 412 × 568 square cells, each representing 1 ha and summing to a contiguous area of 2340 km^2. Satellite imagery of the region (Meerman and Sabido, 2001) informed all habitat data included in the model, as well as road presence/absence, and protection status of land. Agents, representing individual jaguars, each occupied a single cell within the grid map at any one time. Each agent had: a unique identifier; gender; identity of mother (if born during the simulation); current age; reproductive status; energy reserves; and location. The arrival of an agent in a cell caused the creation of a unique signalling marker at that location that identified the agent, its gender and its reproductive status. This marker represented the individual marking behaviours of wild jaguars, including scats and scrapes (e.g., Harmsen et al. 2010a). Multiple marker objects, from different agents, could exist in a single location and be detected by agents in neighbouring locations.

Additional environmental information available to agents included cell cost and food availability. Jaguars have a wide distribution in a range of habitat types from tropical and subtropical, semi-deciduous and pine forests to scrublands, wet grasslands, savannah and swamps (Cavalcanti and Gese, 2009; Foster et al., 2010a; Hatten et al., 2005; Silver et al., 2004; Weckel et al., 2006b). An adapted least-cost model, informed by expert opinion of authors BJH and RJF, generated the set of cost values for habitats included in the model landscape, where lower costs represented more suitable habitats. These represent parameters that decide the probability that an individual enters a neighbouring cell.

The combined total food stock assigned per grid-cell depended on the habitat type but not its cost (i.e., some high-cost habitats had higher food availability than some lower cost habitats, as described in Table 4.1). As the simulation progressed, the current food amount decreased in response to consumption by agents, and replenished with subsequent self-renewal of prey through production of new prey biomass. Table 4.1 details a reduction in prey resources by 30% attributed to forest grid-cells outside CBWS in recognition of an impact of unregulated hunting by humans (Foster et al., 2009).

Table 4.1: Environment costs and resource availability. Food values are given for inside and outside CBWS

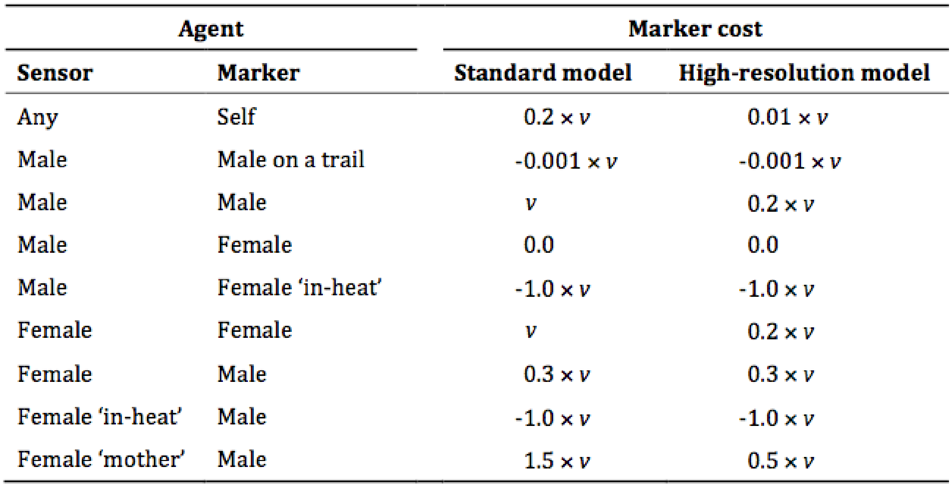
Habitat Type	**Cost**	**Food Availability**	
		Inside	**Outside**
Lowland moist broadleaved forest	1	10	7
Submontane moist broadleaved forest	1	10	7
Lowland wet broadleaved forest	1	9	6.3
Submontane wet broadleaved forest	1	9	6.3
Lowland pine forest	10	8	5.6
Shrubland	10	3	3
Wetland	10	1	1
Savannah	20	2	2
Water	20	0	0
Urban	50	1	1
Agricultural land	50	5	5
Mangrove	100	0	0
Coral	100	0	0
Seagrass	100	0	0
Sea	100	0	0
Tarmac roads	100	0	0
Non-tarmac roads for males	-1	0	0
Non-tarmac roads for females	1	0	0

Two model designs tested the effect of environmental resolution: the standard model that used 10 time-steps per day with each time-step equating to 2.4 hours; and a higher-resolution model that used 24 time-steps per day with each time-step equating to 1 hour. The higher-resolution model design required a small number of additional changes to agent-agent interactions to maintain population stability (described in Table 4.2). Simulations lasted 100 years of simulated time (i.e., 365,000 time-steps, or 876,000 in the high-resolution model).

Process overview and scheduling

The main sequence of events during a model run began with model construction and ended with the output of data files (SI: Fig. 4.5). Following initialisation, behavioural rules dictated decision-making for each agent in each time-step, which occurred one agent at a time in a randomised order. Reflecting natural population dynamics, agents moved,

Table 4.2: Costs of agent-agent interactions. Costs refer to the agent in the left column, given its sensing of another agents marker with current value v.



Agent		Marker cost	
Sensor	**Marker**	**Standard model**	**High-resolution model**
Any	Self	0.2 × *v*	0.01 × *v*
Male	Male on a trail	-0.001 × *v*	-0.001 × *v*
Male	Male	*v*	0.2 × *v*
Male	Female	0.0	0.0
Male	Female 'in-heat'	-1.0 × *v*	-1.0 × *v*
Female	Female	*v*	0.2 × *v*
Female	Male	0.3 × *v*	0.3 × *v*
Female 'in-heat'	Male	-1.0 × *v*	-1.0 × *v*
Female 'mother'	Male	1.5 × *v*	0.5 × *v*

consumed food, interacted, and followed natural cycles of oestrus (females only), birth, and mortality (Fig. 4.1). Presented in more detail in section 2.6, movement and decision-making occurred in response to consumption of resources and interactions between agents. Continuous updating of all state variables ensured feedback between agent-agent and agent-environment interactions, and subsequent processes within individual each time-step (such as agent movements, food consumption and reproduction).

Design concepts

Emergence. Instantaneous changes in individual home range size and shape occurred through deposition, degradation, upgrading and removal of marker objects that aimed to reflect the dynamic patterns observed in natural jaguar home ranges (Cavalcanti and Gese, 2009; Schaller and Crawshaw, 1980). The distribution of food resources changed over time following consumption and replenishment. The distance and movement of sub adults away from the mother depended on their respective locations at the time of separation and the distribution of other agents and their markers in the surrounding landscape.

Adaptation. Agents attempted to minimise movement costs by choosing least-cost pathways where possible. The probability of selecting a cell of lowest cost depended on food availability, current energy reserves and interactions with other agents (described in section 2.6).

Fitness. Per capita mortality risk and fecundity included implicit fitness evaluations. Movement costs influenced the choice of movement only, and not the mortality of the agent per se.

Sensing. All agents could access environmental data, costs and markers in their current

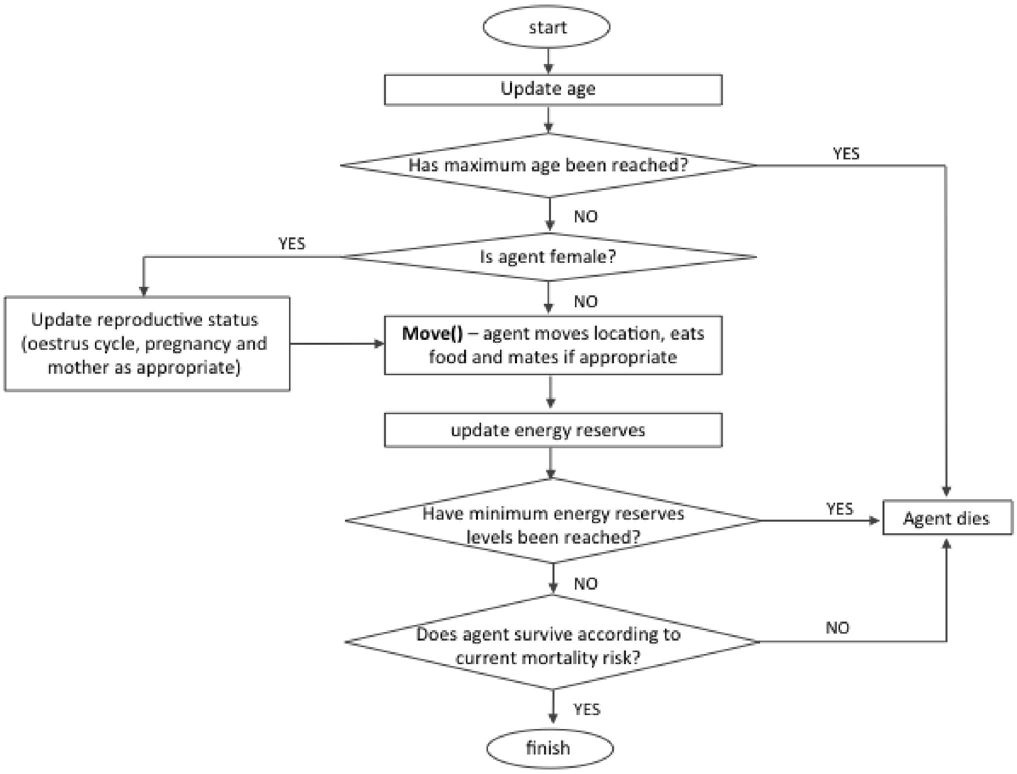


Figure 4.1: Flow diagram illustrating the operation of rules for each jaguar agent, iterated each time step

cell, and each of its four abutting cells, representing potential N-S or E-W displacements for the next time-step (disallowing diagonal movements which would involve a larger displacement per time-step). Agents had no information on the locations of camera traps or of protected areas.

Interaction. Agents interacted with each other by sensing markers or by sharing the same cell. The higher probability of selecting cells with no, or low value, marker cells minimised risk of the latter, except during mating when agents of the opposite sex became attracted to each other.

Stochasticity. Probability equations determined the likelihood of an agent moving and eating, the location of movement and the consumption of food and its regrowth, and are described in section 2.6. In addition, agents had a 1% chance of moving to a random cell instead of a selected cell. A random draw from a uniform distribution determined litter sizes of 1 to 4 cubs.

Observation. For model testing, the Graphical User Interface (GUI) facilitated inspection of individual agent and population-level behaviour, with specific observations taken on population size, home range size and the interaction of agents.

Initialisation

For each new run, the model cleared and reset all parameters, agents and environmental data. Runs began with a population of 150 agents in random locations within a 10 km^2 buffer zone surrounding the 47 camera traps. This allowed agents to establish home ranges in and around the area of sampling for validation purposes. Life history variables for each agent were drawn from a uniform distribution and included: gender, at ratio 1:1; current age, between 2 and the maximum lifespan of 15; and energy reserves, between 50 and 100. Females took one of three reproductive states: oestrus; gestating; or mother; with respective probabilities 0.1, 0.3 and 0.6, and a randomly chosen time interval for progression through the state (detailed in Table 4.3). Progression of life history variables began only after the first 3 years of a simulation run (10,950 time-steps), to give the initial population time to establish stable home ranges. A further 7 years of lower than standard mortality (described in Table 4.3) ensured a stable balance between the high mortality observed during these initial stages and the establishment of successful reproduction. The evaluation of each simulation run started at year 11.

Submodels

Moving

Movement decisions were two-fold: whether to move and where to move. Low food consumption generated a higher probability of agents moving location in the next time step in the form: $1\frac{(\frac{a}{2})}{b}$, where a is food consumption and b is maximum possible food consumption in cells with maximum food availability. In 99% of movements, when agents moved, they did so according to the stochastic probability equation of: H $(\frac{v}{w})$ + P $(\frac{v}{w})$ F $(\frac{w-v}{w})$, where the likelihood of movement into a cell depended on H, the habitat cost (representing a cumulative cost of habitat and road, if present and described in Table 4.1), P, the marker cost, F, current food availability, v, current agent energy reserves and w, maximum potential energy reserves. The total cost of moving to a cell therefore depended on its habitat type, the presence and intensity of markers, and food availability, all weighted by the current energy reserves of the agent. Low energy reserves raised the weighting on food-availability, while high energy reserves raised the weighting on habitat and marker costs.

Consumption and replenishment of food resources

The consumption of food was also two-fold: whether to eat and how much to eat. Lower energy reserves indicated a greater likelihood of consuming available resources, with all probabilities falling between 0.5 and 1.0 in the form: $1\frac{(\frac{a}{2})}{b}$, where a is the agents current energy reserves and b is the maximum possible energy reserves (set at 100). Following the decision to eat, food intake rate followed a Holling type II response, which depended on the amount N of available food, the capture rate a of prey (set at 0.9 units per time-step)

Table 4.3: Parameters and values of the jaguar agents in the model.

Parameter	**Value**	**Reference / Classification of uncertainty**
Time steps, per day	Standard model – 10 Higher resolution model - 24	Calibrated during model development to match average individual movement rates between model and best estimates from the field (Harmsen, 2006).
Moves per time step	1	As above.
Moves per time-step for a male attempting a mating	1-25, chosen randomly	Females space themselves according to food resources and males space themselves according to access to females, sometimes travelling extensive distances to the exclusion of consuming food and resting, in order to locate a reproductively active female (Ostfeld, 1985; Ims, 1987; BJH & RJF, unpublished data).
Probability of moving randomly to a new location	0.01	Additional stochastic process to capture movements and motivations outside of those included in the model. Agreed by experts BJH and RJF.
Maximum energy reserves	100	Arbitrary absolute value.
Energy decrease per time-step	Male: 1 Female: 0.7 Mother: 1.3	Arbitrary relative amounts based on energetics of jaguars (Foster, 2008) and assumption that larger males and females rearing young consume more resources than females, and calibrated via POM (pattern oriented modelling).
Maximum level of marker	100	Arbitrary absolute value.
Decrease in marker value per time-step	0.08	Arbitrary absolute value, calibrated via POM to generate realistic home range sizes (Rabinowitz & Nottingham, 1986; Schaller & Crawshaw, 1980; BJH & RJF, unpublished data).
Length of oestrus cycle	430 time-steps (43 days)	Wildt *et al.* (1979).
Length of pregnancy cycle	1000 time-steps (100 days)	Wildt *et al.* (1979).
Length of mother status	7300 time-steps (2 years)	Wildt *et al.* (1979).
Conception probability	0.9	Additional stochastic process to account for the probability that not all matings lead to successful pregnancies.
Cub survival rate	1st cub: 0.85 2nd cub: 0.85^2 3rd cub: 0.85^3 4th cub: 0.85^4	Based on ecology of pumas where smaller litter sizes equate to cubs with larger mass and greater survival probability (Jansen & Jenks, 2012). Absolute values calibrated via POM to allow realistic average litter sizes of around 2 (Foster, 2008) to emerge during model run.
Cub dispersal period	1460 time-steps (1 year)	BJH & RJF (unpublished data). Starts at age 2 when subadult leaves mother (Schaller & Crawshaw, 1980) and based on dispersal in similar species: leopards (Sunquist, 1983) and pumas (Sweanor *et al.*, 2000).
Mortality rate during initial setup period	Habitat cost of cell / 500,000	Calibrated via POM to stabilise population.
Mortality rate for an adult	Habitat cost of cell / 50,000	Calibrated via POM to stabilise population.
Mortality rate for sub-adults during cub dispersal period	(Habitat cost of cell)^2 / 50,000	Calibrated via POM to stabilise population and based on assumption that subadult mortality is higher than adult mortality in leopards (Nowell & Jackson, 1996; Foster, 2008).

and the handling time b (set at 0.05 units per time-step) in the form: $\frac{aN}{1+bN}$. A logistic regrowth of prey offset its depletion through consumption, described as the intrinsic growth rate per capita per time-step, and depending on r, set at $1 + 10^{-100}$, N, the current amount of food available in the cell (representing current prey density) and k, the maximum food capacity of the cell in the absence of offtake by predators in the form: $rN(\frac{K-N}{K})$. Agents experienced a reduction in energy reserves during every time-step unless they consumed prey (Table 4.3).

Interactions between agents Marker objects facilitated agent-agent interactions. Set at maximum with object creation, the value of these objects degraded until they became undetectable after 1250 time-steps, approximately 4 months (Table 4.1). The re-entry of an agent into a previously visited cell reset the marker object to maximum, or created a new marker object if none remained of the previous one. The calculation of cell cost for an agent partially depended on its agent-interaction preferences with respect to the gender and reproductive status of other agents or their markers in the cell (Table 4.1).

Reproduction and addition of cubs

All agents became reproductively active at 3 years old. Females followed the natural course of oestrus and reproduction, informed by Wildt et al. (1979) who reported a female captive jaguar exhibiting her first oestrus cycle at 29.5 months old, and thereafter having oestrus periods and cycles lasting respectively 12.9 and 42.6 days on average. Successful mating caused a change in female status to gestating', which progressed in due course to mother. Mother status triggered a higher depletion of energy reserves per time-step (Table 4.3), reflecting the additional food burden incurred by female jaguars while raising young. The creation and addition of up to 4 new cub agents at the current location of the female occurred upon termination of the mother status. Only those cubs that survived the 2-year raising period could attempt integration into the adult population (additional cub survival rates described in Table 4.3) and cubs died before joining the population if the energy reserves of the mother fell below a threshold value of 15 per cub (reserves of 60 sustained all four cubs; 45 sustained three, and so on). Sub-adults spent a discovery period of 1 year (3650 time-steps, or 8760 time-steps in the high-resolution model) exploring the landscape for a suitable home range, without impediment from their mothers markers.

Mating required a male and female agent (not mother-son) to occupy the same location while the female exhibited the in-heat phase of the oestrus cycle. Females in heat strongly attracted males, who maximised the mating opportunity by moving at a faster than normal pace (detailed in Table 4.3, BJH and RJF unpublished data) and choosing to travel in preference to consuming food (in accordance with field data).

Mortality

Each agent had its age-specific survivorship prescribed at creation, defining an increase in mortality risk with age that would result in a lifespan within the natural distribution of lifespans. The agent died at its pre-determined maximum age, if it had not previously died from age-independent causes.

Two age-independent mortality factors, habitat cost and low energy reserves, described the probability of an agent dying (Table 3). Habitats that risked human-induced mortality (e.g. poisoning, hunting, and vehicle collisions) carried higher costs. Newly added agents (subadults) experienced greater mortality (depending on habitat type) risk during the initial discovery period (Table 4.3).

4.3 Calibration and Validation

Known jaguar ecology informed model parameters (Table 4.3). Where no published data existed, authors BJH and RJF provided expert field knowledge from extensive studies of jaguars in and around the CBWS area (Foster, 2008; Foster et al., 2010a,b, 2009; Harmsen, 2006; Harmsen et al., 2010a,b, 2009, 2010c,d). A number of heuristic parameter settings existed (described in Table 4.3) and calibration of all parameters, outside those set by ecological bounds, occurred through pattern oriented modelling (POM) approaches (Grimm et al., 2005).

The first step in calibrating and validating model output comprised observation and visual inspection of the running model. We manually ran the model with a range of initial population sizes, from single agents to many hundreds, to analyse agent movements and interactions. Empirical estimates of population size (Foster, 2008; Harmsen et al., 2010d; Rabinowitz, 1986), home range size (Foster, 2008; Harmsen et al., 2010d; Rabinowitz, 1986), mortality rates and causes (Harmsen et al., 2010d), use of habitats (Foster, 2008; Foster et al., 2010a; Harmsen et al., 2010a,b,c,d) and individual interactions (Foster, 2008; Foster et al., 2010a; Harmsen et al., 2010a, 2009) facilitated the calibration of individual- and population-level behavioural outputs to within naturally-expected bounds. Further validation against camera-trap data collected by BJH and RJF provided comparison to empirical estimates of sex-specific movement rates, and home range sizes and configurations. The modelled landscape (Fig. 4.2) contained 47 camera traps within the eastern section of CBWS and to the east of the protected area boundary, which provided empirical field data over a period of several months (Foster, 2008; Foster et al., 2010a; Harmsen, 2006; Harmsen et al., 2010b). Model validation used camera trap objects placed in the same locations in the simulated landscape, and compared simulated to empirical capture data. Camera trapping in the field focused on trails to maximise capture probability, in four habitat types: agricultural land, lowland moist broadleaved forest, lowland pine forest, and shrubland (Fig. 4.2). Camera trap objects in the model recorded positive sightings of agents that entered the same location, noting their identity and gender. Data capture for validation occurred at three points during the simulation, chosen randomly between years 10-40, years 40-70 and years 70-100, and yielding a total of 300 samples.

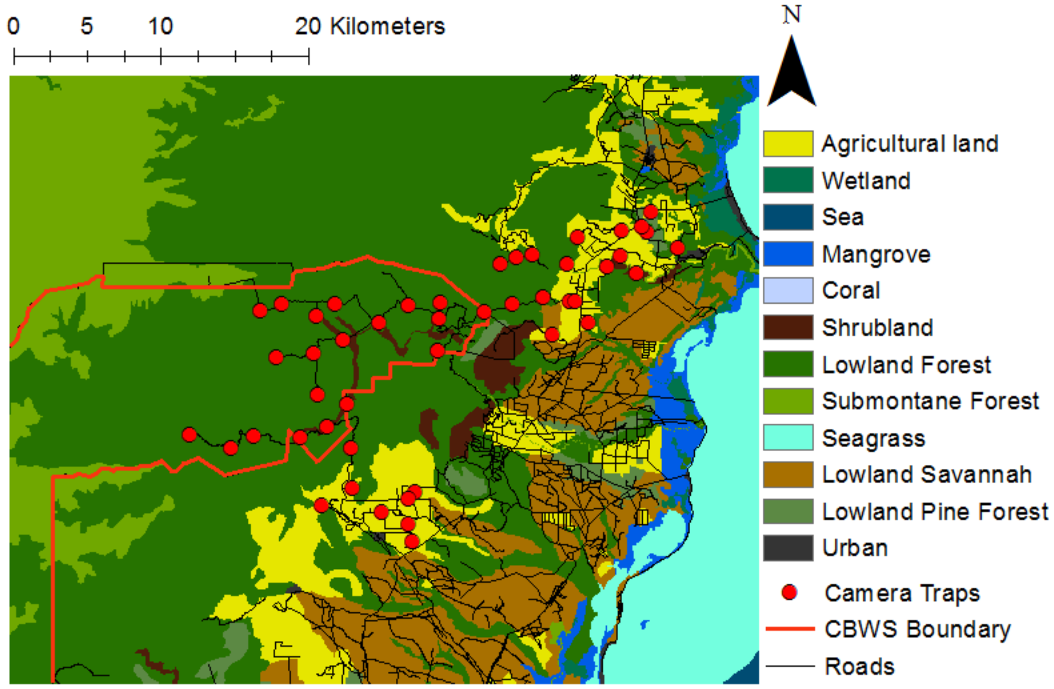


Figure 4.2: GIS map of the real landscape and camera-trap locations inside and outside the CBWS protected area, as used for the simulation.

4.4 Sensitivity Analysis

A sensitivity analysis of the model determined which biological parameters, or combination of parameters, had most impact on output variables. This analysis included three parameters critical to population dynamic processes: adult mortality, fecundity, and agent-agent interactions, and aimed to test for biological significance and not to test all combinations of all parameter values. A 3 × 3 Latin Square of the standard form generated test combinations of parameter values (supplementary information (SI): Table 4.5). This type of analysis quantified the importance and impact of each parameter on the outcome variables and the sensitivity of the model to these parameters.

4.5 Results

4.5.1 Population dynamics and habitat utilisation

Following an initially heavy decline in population size during the first 10 years of the simulations, model populations increased slowly and steadily to average 92 ± 28 (mean ± s.d.) agents (SI: Fig. 4.6), with sex ratio 0.48:0.52 (M:F) by the end of 100 years. This density falls within empirical estimates from the expected number of individuals within and outside CBWS of between 50 and 110 given estimates of 10 and 2 individuals per 100 km2 respectively (Foster et al., 2010a). Of the total 100 runs, 82 provided a relatively stable population size over the 100 years of the simulation, 3 decreased to zero, and 15 exhibited a slightly increasing trend, or a population size above a reasonable limit of 120 agents.

Abutting home ranges averaged 36.07 km^2 ± 3.99 km^2, as illustrated in Figure 4.3, and calculated by summing locations an individuals marker objects. Overall, average male and female home ranges fell within realistic bounds, at 13.22 km^2 ± 2.86 km^2 for females and 61.02 km^2 ± 6.07 km^2 for males, given estimates in the region of 10-40 km^2 for females (Rabinowitz, 1986) and 60-70 km^2, and up to 100 km^2 for males (RJF and BJH, unpublished data). However, the smaller home ranges sizes of female agents specifically inside CBWS fell below minimally expected bounds (SI: Table 4.6). Male agents achieved more realistic home range sizes, but the larger home ranges observed inside CBWS contrasts natural tendencies for larger male range to occur in the less resource-abundant areas outside of protected reserves (RJF and BJH, unpublished data). Home range sizes of male agents remained relatively stable over the course of the simulation, and home range size correlated negatively with population size for females (r = -0.59, d.f. = 9111, $p < 0.0001$), but positively for males (r = 0.30, d.f. = 9108, $p < 0.0001$), Fig. 4.3. The inhibition of female movement by neighbouring males reduces the probability of home range expansion for females with larger population sizes (particularly evident in the resource-rich environment inside CBWS), whereas the higher incidence of coming into contact with a female, under the same conditions, entices males to move further in search of additional mating opportunities.

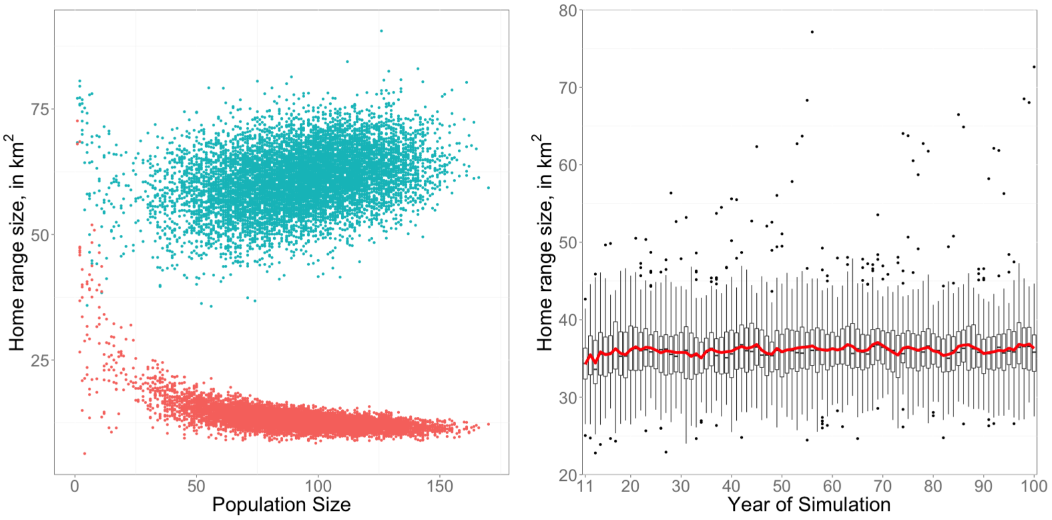


Figure 4.3: Home range size dynamics across all 100 simulations. (a) Population-size dependent sex differences, with males in blue and females in red; (b) relatively consistent dynamics over time. Boxplots and dots of interquartile ranges and outliers, and mean home range size in red.

The first 10 years of the simulation coincided with very high levels of adult mortality, with 75% of the population dead by year 11 (SI: Fig. 4.7). The random initial starting locations and short sensing range of agents (the adjoining 4 cells only) likely caused them to become trapped in unsuitable locations from which they could not successfully exit before suffering from an age-independent mortality. The design of the model, with a large initial population size, aimed to absorb this early high mortality event.

Age-dependent mortality accounted for 68% of total deaths, energy-related mortality for 10% and habitat-related for 23%. The unprotected area outside CBWS accounted for 67% of total deaths, 90% of energy-related and 100% of habitat-related mortality events. Habitat accounted for 34% of all agent deaths in unprotected areas, compared to 45% in empirical data (Foster, 2008).

Trial runs over 500 simulated years showed the populations retaining long-term stability in size (SI: Fig. 4.6). Despite more variable population sizes, they fell within the bounds of empirical knowledge at 99 ± 22 individuals. Although some runs displayed higher than expected population sizes, none maintained these high densities for longer than 10 years. Home ranges remained similar to those observed in the standard 100-year runs and stayed within realistic estimates with an average of 34.89 km^2 ± 5.59 km^2 (58.98 km^2 ± 9.29 km^2 for males and 13.24 km^2 ± 3.67 km^2 for females). Mortality events stabilised over time, levelling off from $\sim$ 200 years into the simulation (SI: Fig. 4.7).

In line with expectation for natural populations, the model exhibited a positive correlation between number of matings and population size ($r = 0.56$, d.f. = 9155, $p < 0.0001$). Amongst agents of reproductive age, 68% of males and 100% of females achieved at least one successful mating. Agents reproduced at age 5.2 ± 2.13 years on average with an average of 1.77 ± 0.48 cubs per litter surviving to 2 years of age, reflecting the natural average of around 2 cubs per litter (Foster, 2008).

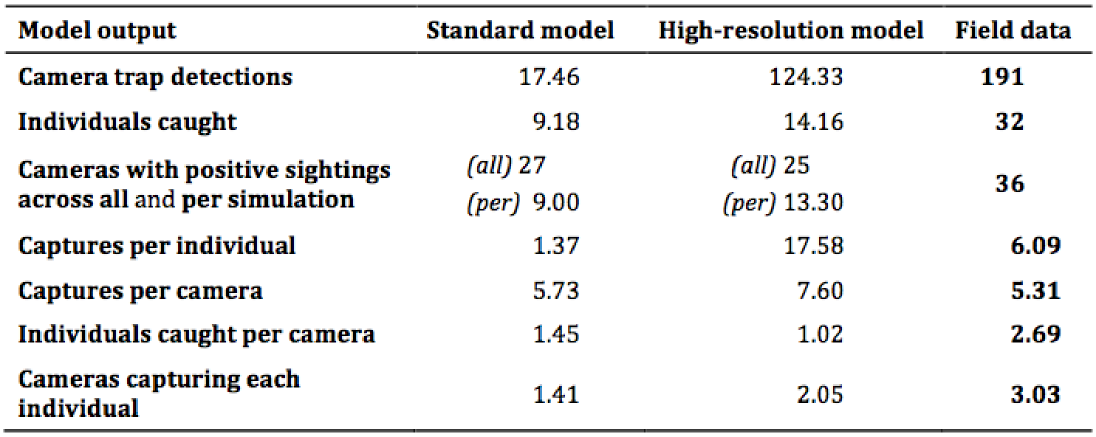
The area encompassed by CBWS comprised 30% of the total area of broadleaved forest found across the landscape, but accounted for 55% of total agent movement. Agents used habitat types inside CBWS in proportion to their aerial coverage ($\chi^2 = 7.76$, d.f. = 4, $p = 0.10$). Outside the protected area, however, agents preferentially selected favoured habitats, and avoided habitats with higher mortality risk or lower food availability ($\chi^2 = 453.82$, d.f. = 9, $p < 0.0001$). Agents showed a strong preference for the most suitable habitats (77% and 19% of total time spent in lowland and submontane forest respectively) and used a wider variety of habitats outside than inside CBWS (10 versus 6 habitat types), reflecting the presence of additional habitats and more fragmentation outside CBWS.

Inside CBWS, agents took advantage of the higher food resources available inside CBWS to maintain higher fitness, in terms of health (measured via energy reserves) and reproductive activity (SI: Table 4.6). Agents located outside CBWS had less frequent matings and produced fewer viable cubs, due to a lower availability of mates and food. Less free habitat for cubs and sub-adults accounted for the higher average age of agents inside protected areas (SI: Table 4.6).

4.5.2 Validation

Compared to numbers of individuals caught in field camera traps, fewer of the simulated camera traps recorded agents, and those that did, caught fewer agents and fewer detections of each agent (Table 4.4). Sightings of male agents in the model replicated field data insofar as they accounted for an average of 70% of positive observations, compared to 76% in the field: itself reflective of the extensive use of trails by males (Foster et al., 2010a; Kelly, 2003; Rabinowitz, 1986; Sollmann et al., 2011; Weckel et al., 2006a), and their avoidance by females, which may indicate alternative hunting strategies and avoidance of male harassment (Foster et al., 2010a).

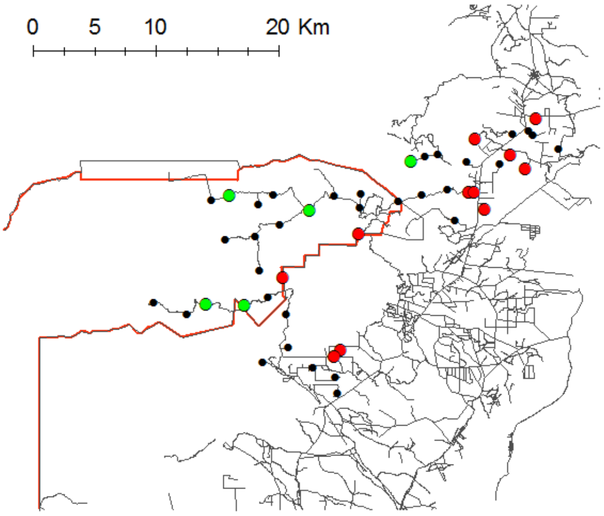
Table 4.4: Comparison of detection frequencies at camera traps in the standard model (10 time-steps per day) and the high-resolution model (24 time-steps per day) to empirical data from the field. Model values report means calculated across all 300 samples for validation, after removal of 5 outliers that each accounted for > 50 consecutive sightings of a single agent in a single camera trap.



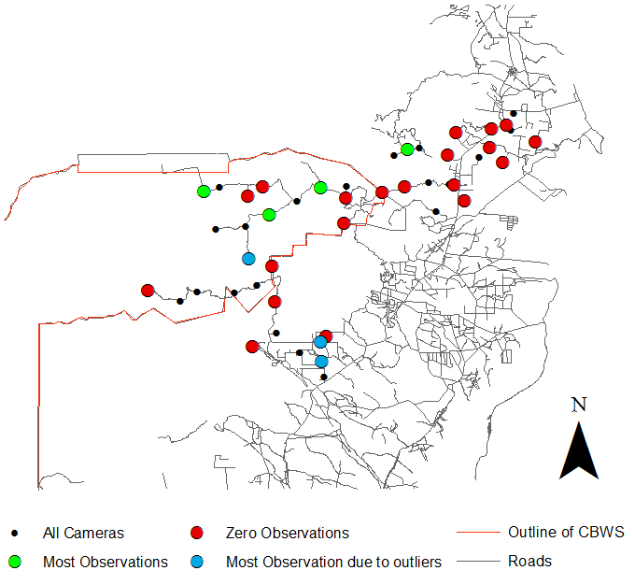
Model output	**Standard model**	**High-resolution model**	**Field data**
Camera trap detections	17.46	124.33	**191**
Individuals caught	9.18	14.16	**32**
Cameras with positive sightings across all and per simulation	*(all)* 27 *(per)* 9.00	*(all)* 25 *(per)* 13.30	**36**
Captures per individual	1.37	17.58	**6.09**
Captures per camera	5.73	7.60	**5.31**
Individuals caught per camera	1.45	1.02	**2.69**
Cameras capturing each individual	1.41	2.05	**3.03**

Figure 4.4 shows the spatial distribution of camera traps that recorded the most and the least observations. Of those that recorded no jaguars in the field (Fig. 4.4a), 73% occupied agricultural land and 27% lowland forest, whereas in simulations 50% occupied lowland forest, 45% agricultural land and 5% lowland pine forest (Fig. 4.4b). Overall, a 73% match between simulated and field camera traps with no jaguar detections suggested a similar avoidance of less suitable habitats. Their locations closer to developed areas, compared to those with the most detections, showed that simulated camera traps also reflected the avoidance of developed areas by wild jaguars (1.38 km and 2.23 km for model and field camera traps with no positive sightings versus 5.9 km and 6.87 km for model and field camera traps with the most sightings).

Of those camera traps with the most jaguar detections, CBWS housed all but one in both the field (Fig. 4.4a) and model data (Fig. 4.4b), and all occupied the most suitable habitat, of lowland forest. These camera traps did not match between the simulation and the field, although they occupied the same general part of the landscape. The spatial distribution of camera traps with positive jaguar detections reflected the adaptable nature of jaguars by confirming varied use of habitats and movement in areas both within and outside CBWS (Fig. 4.4b). Model agents also showed strong preference for undisturbed forest coupled with an avoidance of more fragmented and heterogeneous areas. However, a higher number of jaguar detections in the field, versus the model, reflect the more sophisticated social behaviours of wild jaguars in visiting trails more often to gather information on other jaguars via scent marks (Harmsen et al., 2010a).



(a) Field data



(b) Model data

Figure 4.4: Detection by camera traps. (a) Field data; (b) simulations. Dots show camera traps with zero observations (red); most observations (green); high observations caused by outliers (blue); other camera traps (black). Red line demarks the boundary of CBWS; other lines show roads.

High-resolution model

The high-resolution model increased the number of camera traps with positive detections, the number of detections per camera trap, and the total number of agents sighted, resulting in an increase in the distance travelled by each agent per day and a closer match to field data than found with the standard model, shown in Table 4.3. Ninety-four % of simulated camera trap detections constituted males, revealing a much higher proportion than the 76% found in empirical data. Reducing the attractiveness of trails to male agents did not solve this issue and caused a widespread population crash. Some small variations in model output variables therefore occurred. Outlying data points (> 300 consecutive sightings per agent in a single camera) occurred through agents becoming trapped on a trail surrounded by inhospitable habitat, i.e., habitat perceived as less suitable than the trail itself. These increased in frequency in these high-resolution model settings: 0.005% of agents compared to 0.0004% for the standard model.

4.5.3 Sensitivity Analysis

Rate of fecundity directly influenced the values of all response variables (SI: Table 4.7). The effect of fecundity on population dynamic variables depended on agent-agent interactions and its effect on home range size of males depended on mortality. Both positive and negative changes in agent-agent interactions caused a reduction in population size. Mortality alone did not affect any of the output variables.

4.6 Discussion

The simulation presented here demonstrates the first spatially explicit agent-based model of jaguar population dynamics in a real-world context. We have described a method for adapting a least-cost modelling approach to fit an agent-based simulation, and validated its application in a real ecological system. Simulated populations had behaviour consistent with key characteristics of the dynamics of a natural jaguar population inside and outside the CBWS region of Belize, notably in the frequencies of reproduction and mortality, and the home-range dynamics.

The stochastic nature of the model demonstrates the complexity of natural population dynamics in a closed system. In the absence of immigration or emigration, the model displays some variation in population stability largely due to the lack of exchange of individuals across the population boundary that may have served to alleviate biases in gender spatial distribution or stochastic adult mortality events.

The use of markers to represent visual and non-visual signals of recent agent activity appeared to capture the fluid ranging behaviour of wild jaguars, which do not exhibit the normally more territorial behaviour of other predatory cats (Cavalcanti and Gese, 2009; Schaller and Crawshaw, 1980). The large variation in size and overlap of simulated male home ranges agree with the findings of Harmsen et al. (2009) that wild jaguars in the prey-rich area of CBWS show unusual flexibility in home-range configurations. In contrast, female agents showed less variation, with home ranges more constrained by neighbouring agents (Fig. 3a), likely due to the avoidance of conspecifics by females during the rearing of young.

Protected areas provide refuge for wildlife in Belize from hunting pressures, logging and other potentially detrimental human activities. The higher food availability simulated inside CBWS, and attributed to its contiguous forest patches, reflected this effect and explained the greater use of forest patches by agents, also observed by jaguars in the wild (Foster et al., 2010a), and higher fitness of agents inside the protected area (SI: Table 4.6). Empirical data, however, suggest that unprotected areas outside CBWS require larger home ranges for individuals to support themselves on a lower abundance of prey species (Foster et al., 2009). The small home range sizes of female agents, well below those recorded in the wild (Rabinowitz, 1986) indicated insufficient linkage between resource availability and home range size and future model developments should investigate movement as a trade-off between resources availability and habitat cost.

Age-dependent mortality accounted for the highest proportion of mortality across all simulations. However, as the population established over time, the formation of stable home ranges in prime habitats forced the movement of agents into less suitable locations, which caused a rise in low-energy and habitat-related mortality (SI: Fig. 4.7). The combined decrease in age-dependent mortality and increase in age-independent mortality over time reflected the establishment of a stable population. The equilibration of mortality and reproduction allowed the population to overcome the relative high frequency of mortality events observed in young agents and reflective of naturally occurring trends (Foster, 2008): both those within the 2-year rearing period and those traversing the landscape in search of favourable habitat.

Rare and cryptic carnivores always pose exceptional problems for collecting empirical data on movement behaviour, and knowledge remains sparse on vital rates and movement parameters (Harmsen et al., 2010c; Sollmann et al., 2011). Modelled jaguar behaviour thus required input from expert opinion (Table 4.3). It nevertheless captured all the key input features of jaguar population dynamics and interaction behaviour at least qualitatively in a stable system.

The spatial distribution of jaguar sightings in camera traps in the field reflected the adaptable nature of jaguars, revealing the use of a variety of habitats both within and outside of the protected CBWS. Model data was able to capture this variability and simulated jaguars showed a similar distribution of movements across the landscape, with limited movement in the more disturbed areas outside of the protected reserve reflecting natural trends in the region (Fig. 4.4a). Lowland forest housed those camera traps exhibiting the most jaguar sightings, both in the model and in the field, but revealed no bias in movement in protected, compared to non-protected, forest patches. However, the validation of model output with field data revealed limitations in capturing fine-scale movement of agents and highlighted the problems of using a medium-resolution landscape map to analyse high-resolution behaviours, reflected, at least partially, by the low number of positive camera-trap detections in the model. Both the size of each cell in the landscape (10,000 m^2) and the length of each time-step (2.4 hours) may have resulted in single-agent detections in the model accounting for several detections of a single individual in the field data. Although the high-resolution model resolved some issues, differences remained in the extent and range of camera traps with positive detections. Our inability to fully capture the range and complexity of real jaguar behaviour, particularly socially oriented behaviours unrelated to reproduction and food consumption, emphasizes the complex nature of individual movements and interactions.

This study comprises the first steps at testing the validity of an integrated least-cost and detailed agent-based model, underpinned by real-world geographical information, to inform conservation planning and management. Future model development will focus on the application of the model as a conservation decision-support tool, allowing for multiple scenario-testing of the specific effects of habitat change on jaguar population persistence and resilience over time as well as individual and population-level spatial and temporal distribution. More generally, the model will also function to analyse how the movement of individuals responds to a trade-off between habitat cost and food availability.

4.6.1 Management Implications

The model was developed to meet a management need for modelling the effects of landscape structure on wild jaguar populations. The variability in model output revealed a strong dependence of population size and stability on the spatial distribution of agents in the modelled space. This emphasises the value of using tools that incorporate spatially dependent variables when investigating the implications of management strategies and conservation practices on population resilience and persistence. Analytic connectivity models cannot include these attributes and this study highlights the greater informational richness obtained from models of movement within heterogeneous population structures and landscapes.

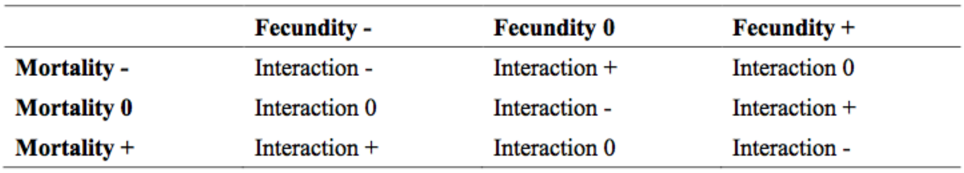
Assessments of the robustness and resilience of such models benefit greatly from precise empirical data with which to validate behavioural predictions at a range of scales. Future plans for this project include exploring population persistence in an area further north in Belize with more fragmentation and exposure to human disturbance. An improved model will depend crucially on better resolution of habitat data, and inclusion of the effects of human behaviour and disturbance.

4.6.2 Conclusions

The model achieved realistic population dynamics by integrating least-cost movements into an agent-based model. Validation against field data from the simulated area revealed limitations in the way we have captured the fine-scale movement of our agents. The model nevertheless remains useful when applied at the landscape scale and demonstrates how a spatial modelling approach that considers the impact of landscape properties on the individual can provide novel insight into large carnivore population dynamics, both spatially and temporally.

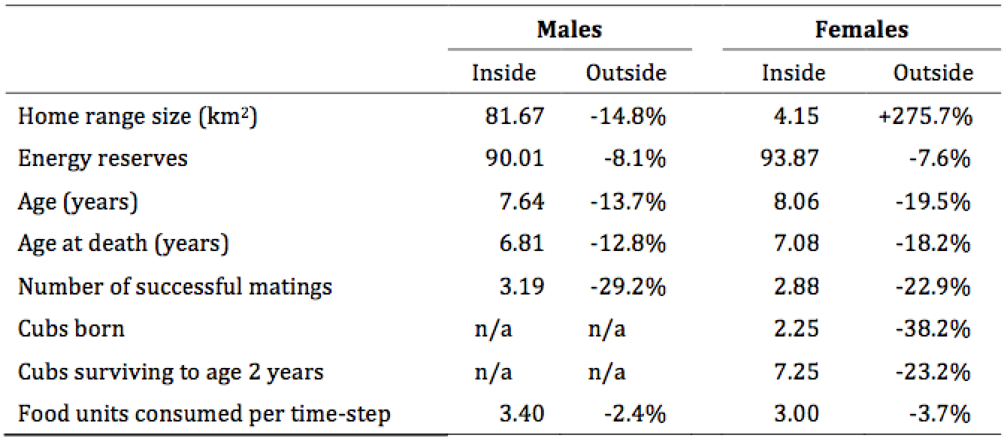
4.7 Supplementary Information. Additional parameters and population dynamics

Table 4.5: Sensitivity analysis used a Latin square of the standard form for three parameters. In the table below, - indicates a 20% reduction in the parameter; + indicates a 20% increase in the parameter; 0 indicates the original setting.



	Fecundity -	**Fecundity 0**	**Fecundity +**
Mortality -	Interaction -	Interaction +	Interaction 0
Mortality 0	Interaction 0	Interaction -	Interaction +
Mortality +	Interaction +	Interaction 0	Interaction -

Table 4.6: Mean statistics per agent inside and outside CBWS



	Males		**Females**	
	Inside	Outside	Inside	Outside
Home range size (km^2)	81.67	-14.8%	4.15	+275.7%
Energy reserves	90.01	-8.1%	93.87	-7.6%
Age (years)	7.64	-13.7%	8.06	-19.5%
Age at death (years)	6.81	-12.8%	7.08	-18.2%
Number of successful matings	3.19	-29.2%	2.88	-22.9%
Cubs born	n/a	n/a	2.25	-38.2%
Cubs surviving to age 2 years	n/a	n/a	7.25	-23.2%
Food units consumed per time-step	3.40	-2.4%	3.00	-3.7%

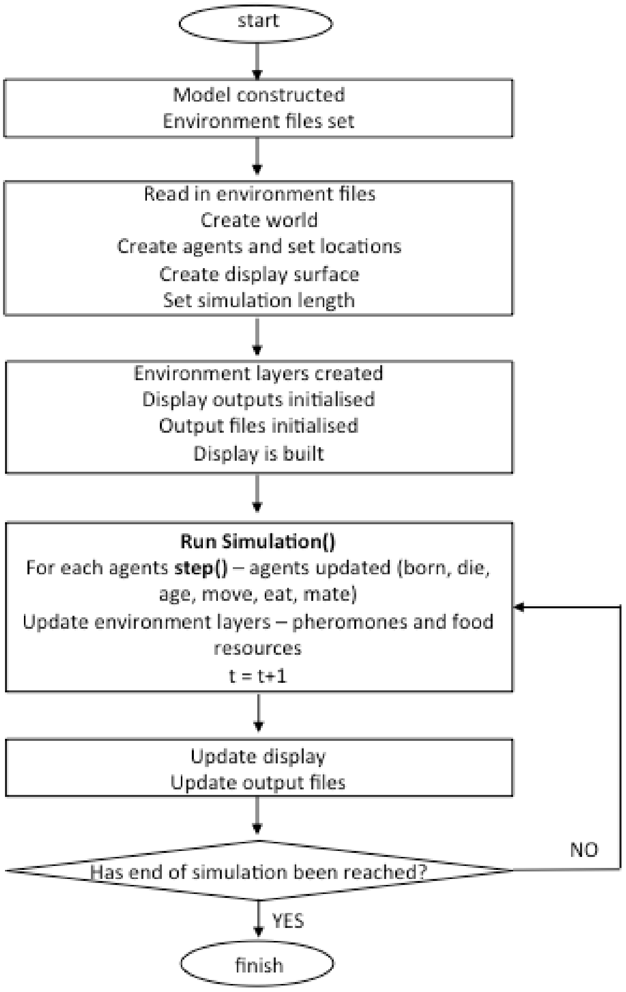


Figure 4.5: Flow diagram illustrating the operation of rules at each stage of the model run (individual jaguars are 'agents')

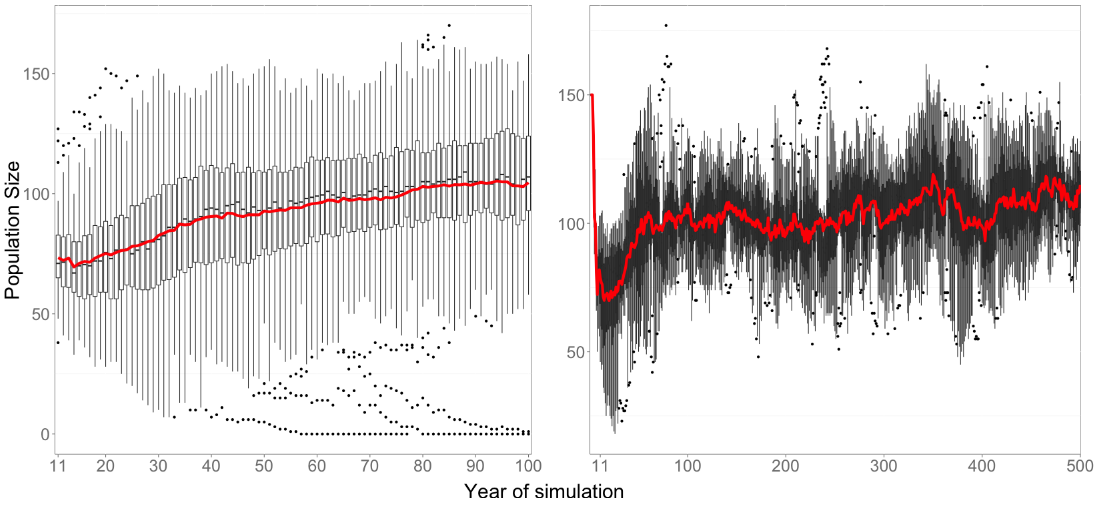


Figure 4.6: Population trend over time. (a) Standard 100-year simulations (100 runs); (b) long 500-year simulations (20 runs). Boxplots and dots show interquartile ranges and outliers, with mean population size in red.

Table 4.7: Sensitivity of the model to mortality, fecundity and agent-agent interactions, tested by general linear model with 6 and 38 d.f., and showing only those outcomes with a p value of < 0.05.

Model Response Variable	**Model Parameter**	***F***	***p***
Population size	Fecundity	23.96	<0.0001
	Interactions		0.0001
	Fecundity*interactions		<0.0001
Number of cubs	Fecundity	29.02	<0.0001
	Fecundity*interactions		0.0002
Number of matings	Fecundity	26.66	<0.0001
	Fecundity*interactions		0.0002
Home range size	Fecundity	12.03	<0.0001
	Fecundity*interactions		0.04
Home range size of males only	Fecundity	19.67	<0.0001
	Mortality*interactions		0.014
Home range size of females only	Fecundity	7.58	<0.0001

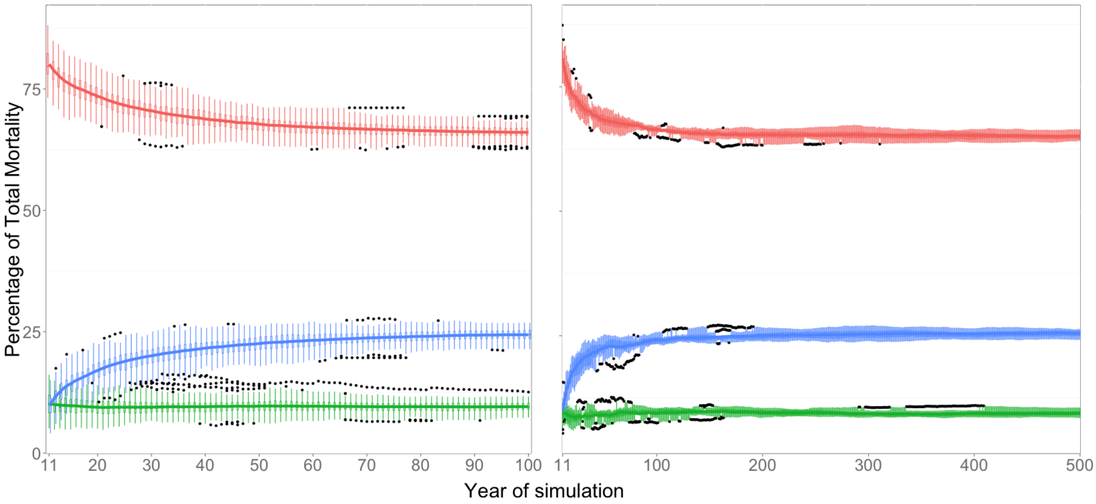


Figure 4.7: Percentage of mortality attributed to each of the three mortality types: age-dependent (red); low energy (blue); habitat (green). (a) Standard 100-year simulations; and (b) long 500-year simulations. Boxplots and dots show the interquartile ranges and outliers, with solid lines showing means.

Chapter 5

Conservation of the jaguar: modelling the effect of corridor design in response to landscape change

Abstract

The permeability of a landscape to an animals movement depends on structural characteristics of the landscape as well as the mobility of the individual. Agent-based models predict system-level properties of populations from stochastic simulation of fine-scale movements. Their potential value to conservation lies in the ability to consider the impact of individual variation in movement and decision-making on populations under future landscape changes. Here, a previously validated spatially explicit agent-based simulation of jaguars, *Panthera onca*, is applied to a heterogeneous wildlife corridor in central Belize; the first application of a detailed behavioural model of jaguars to direct conservation management. Under current landscape conditions and in the absence of immigration into the region, populations persisted for less than 40 years. Immigration increased the population size and extended persistence to at least 100 years. However, increased intra-specific competition in these simulations generated smaller home ranges and lower fecundity. Under conditions of high immigration, multiple scenario testing incorporating degradation and mitigating conservation corridors showed landscape structure strongly influencing the spatial distribution of individuals, facilitating increased movement through the most highly fragmented central zone of the landscape with the largest tracts of protected forests. However, increased movement into more heterogeneous areas increased population vulnerability to environmental degradation.

5.1 Introduction

Connectivity is considered a critical factor in ecology and conservation for determining species viability and persistence (Crooks et al., 2011; Kool et al., 2013; McRae et al., 2008; Moilanen, 2011; Pe'er et al., 2011; Rayfield et al., 2011; Stevens et al., 2006) and is defined as the 'degree to which the landscape facilitates or impedes movement among resource patches (Taylor et al., 1993). Corridors constitute a popular strategy for widespread conservation of biodiversity (Beier and Noss, 1998; Bennett, 2000; Haddad and Tewkesbury, 2005; Hilty et al., 2006; Petracca et al., 2014; Pouzols and Moilanen, 2014; Pullinger and Johnson, 2010) and may mitigate the adverse effects of habitat fragmentation (Ng et al., 2004; Petracca et al., 2014; Salek et al., 2009). They are defined as 'linear habitats embedded in a dissimilar matrix connecting two or more larger blocks of habitat' (Beier and Noss, 1998) and serve to increase physical connections between habitat patches by increasing biota movement and/or providing additional foraging or refuge space (Baguette et al., 2013; Saunders et al., 1991). Corridors may therefore exist as additional tracts of habitat or as conduits of movement, or both (Noordijk et al., 2011).

Connectivity can be separated into two distinct forms: *structural connectivity*: the physical relationship between habitat patches; and *functional connectivity*: an organisms' behavioural response to the landscape structure and matrix composition (Baguette et al., 2013; Stevens et al., 2006). Conservation calls for functional ecological networks that support viable metapopulations and will therefore require high quality habitat patches that are efficiently linked to allow individuals to transfer between these patches (Baguette et al., 2013). Species-specific ecology regarding social structure, diet, foraging patterns and home range size inform predictions of the minimum corridor area required for successful movement between patches (Lindenmayer and Nix, 1993). Habitats may be connected through either some combination of discrete patches or a continuous corridor that may serve as a movement route or also provide some of the resource requirements of the species in question (Pullinger and Johnson, 2010). Where relatively large distances between patches occur, species may require wider and better quality corridors to reduce potential edge effects, particularly where crossing requires multiple generations (Haddad and Tewkesbury, 2005).

However, the effectiveness of corridors per se is not clear when comparing across taxa and spatial scales (Gilbert-Norton et al., 2010) and may depend on the distance they traverse between habitat patches in relation to the dispersal dynamics and daily movement distances of the species in question (Bennett, 1990). There are also few scientifically-based guiding principles for the evaluation and design of connected habitat systems (Lindenmayer and Nix, 1993; Pouzols and Moilanen, 2014) and corridors can serve to increase the spread of catastrophic disturbances (wildfires for example) and invasive or exotic species, and could facilitate the movement of animals into areas where they suffer a greater mortality risk (Beier and Noss, 1998). The conservation value of corridors therefore only accrues when animals are able to successfully traverse these areas.

Common approaches to quantifying spatial connectivity include the derivation of landscape pattern indices (commonly used for describing *structural* connectivity), analytical measures of network connectivity, such as graph theory or least-cost paths, and individual-based simulations (McRae et al., 2008). Least-cost models have proved a useful tool for describing the species-specific *functional* connectivity of a landscape by identifying resistance values for each land cover type based on the facilitating or impeding impact on species movement (Cushman et al., 2013b; Stevenson-Holt et al., 2014). They work on the basis that dispersing organisms are more likely to use a route of least resistance when traversing their environment (Pinto and Keitt, 2009). However, whilst these least-cost resistance maps can be useful in conservation planning and provide the foundation for applied analyses of population connectivity, they often lack biological realism (Kanagaraj et al., 2013) and sufficient information cannot be gained to allow evaluation of the existence, strength/effectiveness and location of movement barriers and corridors (Cushman et al., 2013b; Kanagaraj et al., 2013).

Models that focus on processes at the level of the individual offer a complementary approach that is able to model finer scales of individual behaviours contributing to population dynamics. Agent-based models (ABMs) capture the fine-scale effects of individual movements and the spatial distribution of individuals in driving dynamics within populations. These models make bottom-up predictions of system-level properties as an emergent product of the interactions between agents that represent individuals (Grimm, 1999; Macal and North, 2005; Matthews et al., 2007; McLane et al., 2011; Railsback, 2001). The agents can learn and adapt their behaviour as they respond to other agents and changes in the environment (Matthews et al., 2007; Nonaka and Holme, 2007). The advantage of ABMs lie in their ability to explore real-world population-scale landscape changes including loss and degradation of habitats as well as mitigating conservation management strategies (Grimm et al., 2006; McLane et al., 2011).

We have presented and described an integrated least-cost and agent-based model of jaguar (*Panthera onca*) movement in chapter 4. Here we adopt a least-cost modelling concept that bases movement costs on general daily movements rather than specific dispersal movements, in order to facilitate integration into an agent-based simulation model. Application of this novel approach has allowed us to capture movement decisions based on a number of environmental and species-specific factors, such as food resources, water and mating opportunities, within a single parameter set. We now apply this validated model to real-world conservation management in a wildlife corridor. As the largest cat in the western hemisphere, the jaguar can reasonably form the basis for large-scale conservation. Their large home ranges, adaptability to a wide variety of environmental conditions and presence in any countries throughout Central and South America encourage landscape-scale approaches at conservation of the species that will likely lead to extensive biodiversity preservation and numerous species and vegetation communities protected within the cats range (Hatten et al., 2005; Kelly, 2003; Sanderson et al., 2002). The reduction in historic range of some 50% during the 20th century through habitat loss and degradation combined with persecution (Hatten et al., 2005; Sanderson et al., 2002) has resulted in a Near Threatened Red Listing for the global jaguar population (Caso et al., 2010; International Union for Conservation of Nature, 2013; Petracca et al., 2014).

In our simulations, we set jaguar agents in a region of central Belize that forms the Central Belize Corridor (CBC) constituting the culmination of a 3-year Darwin initiative project to identify, examine and present a case for a large mammal corridor in order to achieve positive impacts on biodiversity and sustainable use / equitable sharing of biodiversity benefits (Doncaster, 2012). This corridor secures the only remaining link at this latitude, for jaguars and other wildlife, of continuous natural habitats connecting North and South America, within the intercontinental Mesoamerican Biological Corridor (Rabinowitz and Zeller, 2010). Extensive field work including camera-trapping and telemetry has demonstrated barriers to population continuity caused by a major highway bisecting the CBC region, as well as human behaviours (including hunting and deliberate fires) that destabilise ranging behaviours (Foster et al., 2010a). Regional threats to the CBC area stem from land conversion to human habitation and agricultural encroachment (Petracca et al., 2014).

This study demonstrates the application of our model. Our goal was to facilitate the exploration of the synergistic effects of landscape structure and human disturbance to explore and understand how changes in landscape configuration affect the spatial distribution and long-term persistence of species. Others have demonstrated agent-based models of animal populations (e.g., Bernardes et al. 2011; Brooker et al. 1999; Nonaka and Holme 2007; Pitt et al. 2003; Tang and Bennett 2010; Topping et al. 2003) but they have not been used extensively to ask questions of direct conservation value. The role of individual behaviours, and the adaptability, interactions and feedbacks of the model presented here also set this work apart from other individual-based models of large felids (e.g., Ahearn et al. 2001; Imron et al. 2011; Kanagaraj et al. 2013), population viability analyses of jaguars (e.g. Zanin et al. 2014) and spatial models of jaguars (e.g., De Angelo et al. 2013; Zarco-Gonzalez et al. 2013). We wanted to better understand causal factors of changes in species distribution and population viability in heterogeneous landscapes and present our model as a potential tool for assessing the relative effectiveness of corridors in light of the relative importance and strength of effects of disturbance, or changes in land-use/human activities. We do not attempt to provide quantitative predictions of likely population size or persistence over time, but rather demonstrate how we can begin to better understand and explore the relative success of proposed conservation management strategies.

5.2 The model

The model used the object-oriented programming language Java (http://java.sun.com) within the Repast agent-based modelling toolkit (http://repast.sourceforge.net). Chapter

4 describes the model in detail, but this study sets agents in the real-world landscape of central Belize, as illustrated in Figure 5.2.

Purpose

The model simulated the population dynamics of jaguars in a heterogeneous human-dominated landscape representing part of central Belize, with the purpose of creating stochastic agents that reflected the behaviour and life history of jaguars in a real-world context, informed by a real landscape comprising the Central Belize Wildlife Corridor. The model set agents in contrasting landscape scenarios, comprising four alternative wildlife corridor designs together with four human-induced degradation factors that test for the effect of connectivity changes and habitat loss on the spatial distribution, individual movement and population-level resilience of a population of jaguars.

State variables and scales

Model architecture comprised a grid of 506 × 608 square cells, each representing 1 ha and summing to a contiguous area of 3076.48 km^2 (Fig. 5.1). Agents, representing individual jaguars, each occupied a single cell within the grid map at any one time. Each time-step equated to 2.4 hours, making 10 time-steps per day. Simulations lasted 100 years of simulated time (i.e., 365,000 time-steps).

Satellite imagery of the region from Meerman and Sabido (2001) (Fig. 5.1) informed all habitat data included in the model, as well as road presence/absence, and protection status of land. Additional information derived from GIS data included: cell cost, food availability, and the presence and level of behavioural markers. The adapted least-cost model used in chapter 4 generated the set of cost values for habitats included in the model landscape, where lower costs represented more suitable habitats, reflecting the wide use of habitats observed in the wild combined with a preference for lowland forest that offers high resource availability (Cavalcanti and Gese, 2009; Foster et al., 2010a; Hatten et al., 2005; Silver et al., 2004; Weckel et al., 2006b). This chapter also described food availability, its reduction outside protected areas, and its depletion and replenishment.

Process overview and scheduling

The model begins with construction and ends with output of data files. Agents execute processes at each time-step, one at a time in a randomised order. Agents make a number of decisions describing movement in response to least-cost choices, consumption of resources in response to energy reserves and conditional reproduction. Continuous updating of all state variables ensured feedback between agent-agent and agent-environment interactions, and subsequent processes within a time-step, such as agent movements, food consumption and reproduction. Chapter 4 describes these process in more detail, summarising model sequences, agent processes and decisions per time-step.

Design concepts

Chapter 4 describes design concepts in full, covering emergence, adaptation, fitness, sensing, interaction, stochasticity and observation.

Initialisation

For each new run, the model cleared and reset parameters, agents and environmental data. Runs began with a population of 150 agents in random locations within protected reserves. Agents created at the beginning of the simulation had random gender assignment, starting age drawn at random between 2 years and a maximum lifespan of 15 years, and energy reserves randomly assigned between 50 and 100. Females took one of three reproductive states: oestrus cycle, gestating, or mother, with respective probabilities 0.1, 0.3 and 0.6, and a randomly chosen time interval for progression through the state.

The model followed the same 10 year setup period, described in chapter 4, to give the initial population time to establish stable home ranges and a balance between the high mortality observed during initial stages and the establishment of successful reproduction. The evaluation of each simulation run started at year 11.

Input

The modelled landscape comprised a formally defined corridor area connecting established reserves to the north and south and which forms a critical transitory route for jaguar movement between these reserves, interpreted from satellite imagery of the real landscape (fig. 5.1). A major highway running east-to-west bisects the CBC and connects the two largest cities in Belize and the area is vulnerable to land conversion steming from human habitations and arable and pasture farmlands. Table 5.1 describes the proportional representation of habitats for inside and outside protected areas showing the dominance of lowland forest, savannah and agriculture in the region. In contrast to the previous model environment (see chapter 4), protected reserves offered a heterogeneous resource encompassing all 9 habitats and accounting for only 27% of lowland forest in the region. Habitat outside of the protected areas was assumed to be degraded and reflected conversion from wilderness to human uses including citrus fruits and arable crops. These areas comprised few resources to jaguars and offered reduced availability of resources to model agents (more details shown in figure 4.1 in chapter 4).

The use of multiple landscape scenarios captured changes in habitat structure and quality and described four likely human-induced events in the region (fig. 5.2): (1) Agricultural

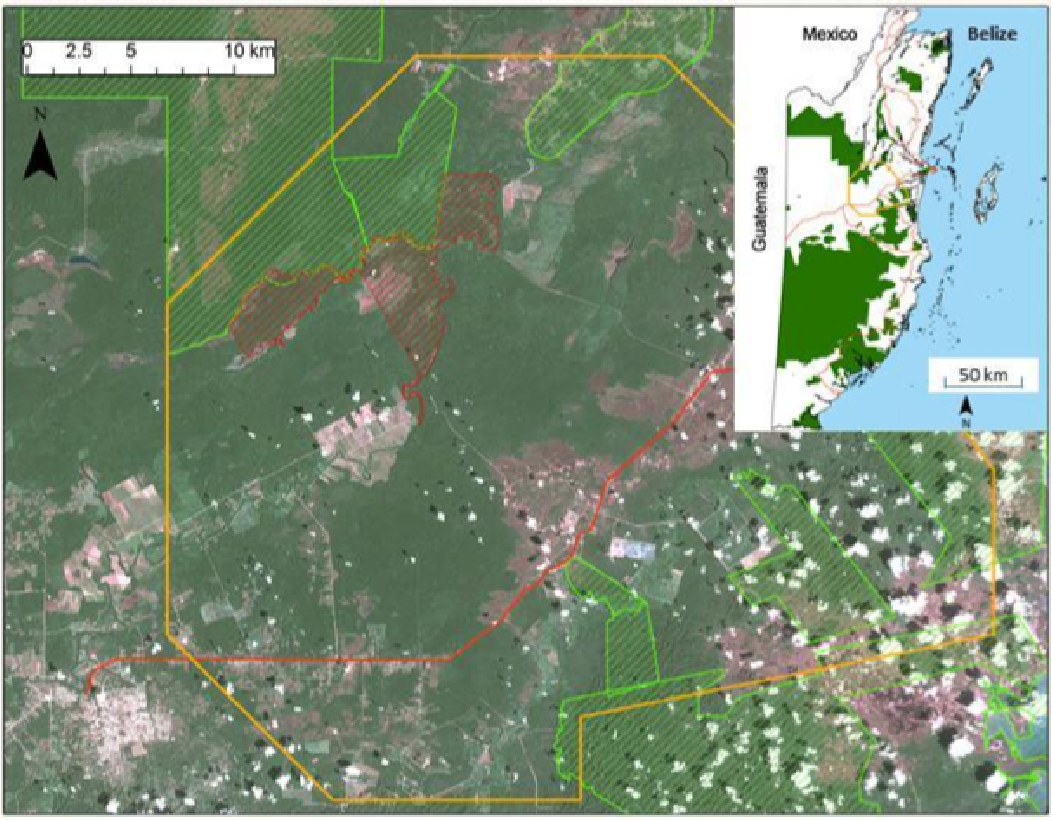


Figure 5.1: Habitat map of the formally defined Belize Wildlife Corridor (outline in yellow on satellite image and on inset map of Belize), showing protected reserves (green and red hatching), and the main highway bissecting the region (red). Inset shows protected areas (green) and highways (red). *Taken from Doncaster (2012).*

Table 5.1: Proportional representation of habitat types in the simulation environment. All values are shown as percentages. Italics show percentage representation in each of the two habitat classes: protected and non-protected areas.

Habitat Type	Total Landscape Cover, in %	Protected Areas Cover, in %		Outside Protected Areas, in %	
		Of total	*Of protected areas*	Of total	*Of non-protected areas*
Lowland forest	57.88	28.06	*69.76*	71.94	*45.58*
Shrubland	2.60	18.21	*2.14*	81.79	*2.73*
Lowland savannah	17.89	19.64	*15.84*	80.36	*18.47*
Agricultural land	13.40	3.23	*1.95*	96.77	*16.67*
Wetland	4.20	39.22	*7.44*	60.78	*3.28*
Lowland pine forest	0.19	33.10	*0.28*	66.90	*0.16*
Mangrove forest	0.97	24.26	*1.06*	75.74	*0.95*
Urban	2.11	4.56	*0.43*	95.44	*2.59*
Water	0.76	31.71	*1.09*	68.29	*0.67*

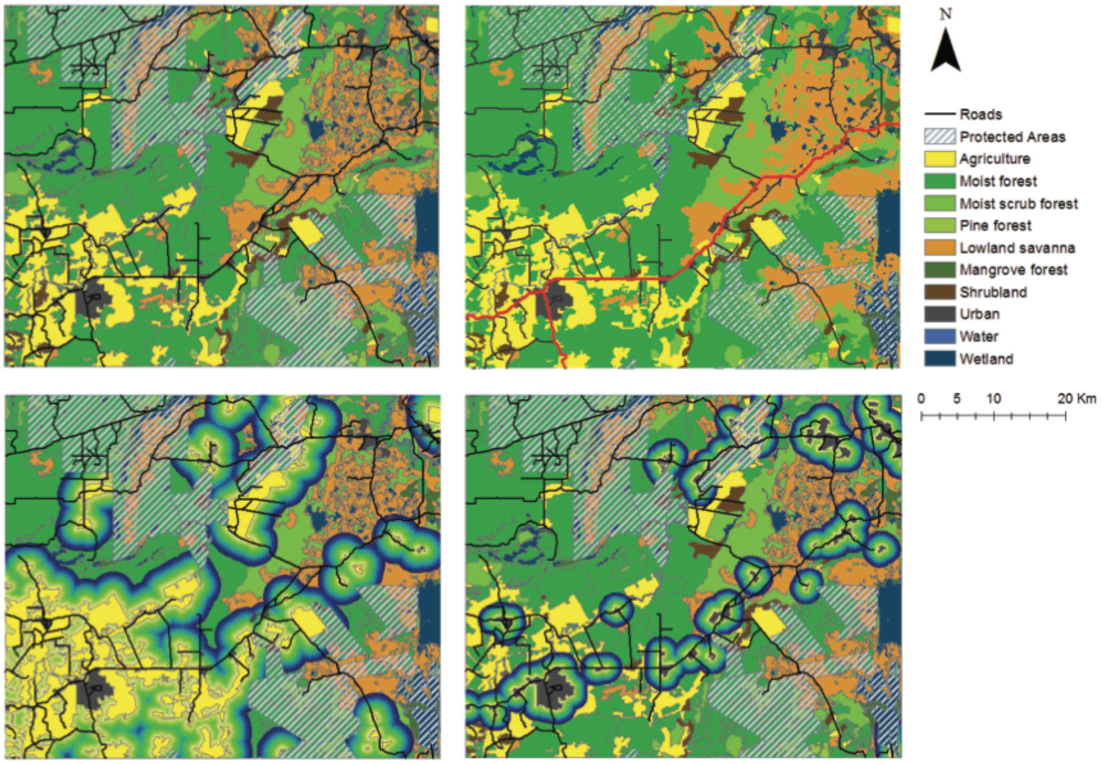


Figure 5.2: Habitat map of the landscape used in the model (top left) showing the location of the main highway bisecting the region (top right), buffer zones of existing agricultural (bottom left), and urban (bottom right) areas of up to a distance 3 km and 2 km respectively, moving from yellow to blue as distance increases.

expansion; (2) Urban development; (3) Intensification of road use; and (4) Degradation of forest quality. Landscape changes reflect the very real regional and global threats threats of land conversion (Petracca et al., 2014), as well as detrimental human activities such as game hunting and traffic collisions (Foster et al., 2010a). Implementation of landscape changes began at year 20 of the simulation and expanded by a buffer of 100 m around existing habitat patches. Expansion of disturbances occurred at three-yearly and five-yearly intervals respectively. Where agricultural land attempted to expand into urban areas or protected reserves, these habitats were excluded and remained intact across the landscape. The process of road intensification conferred an increased cost of movement and increased mortality risk to individual agents traversing the major highway bisecting the region. Degradation of food resources comprised reductions in food availability of 50% in lowland forest outside of protected reserves.

Four corridor designs offered alternative conservation management strategies to mitigate against population vulnerability to extinction and likely landscape degradation, and follow from earlier investigations of corridor design (chapter 3). Figure 5.3 shows these comprised the full corridor design proposed by the Jaguar Corridor Initiative, a reduced design consisting only of forest patches within the full design (corridor 1), a minimal design comprising the smallest linear patch of physically connected forest patches that linking protected areas (corridor 2), and a scattered pattern of disconnected forest patches comprising a larger network of protected reserves than corridor 2, but a smaller and potentially more likely design than corridor 1 (corridor 3). Designs 1 - 3 reflect logistical difficulties of protecting non-forest patchs that are already man-managed in various ways under private ownership (Doncaster, 2012).

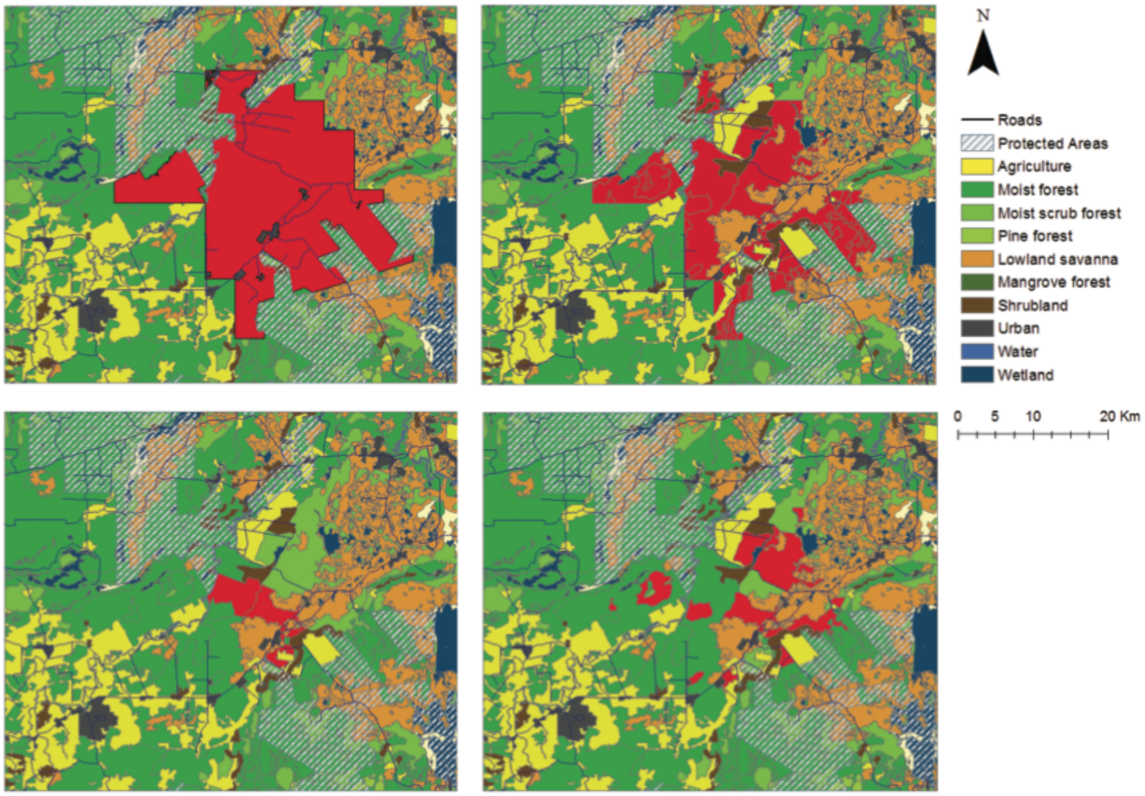


Figure 5.3: Habitat maps of the landscape used in the model, showing each of the four proposed conservation corridor designs, in red: full corridor (full: top left); only forested areas within the full corridor design (1: top right); a small narrow forest corridor (2: bottom left); and small patches of forest habitats (3: bottom right).

Submodels

See chapter 4 for movement, consumption of resources, agent-agent interactions and mortality.

5.3 Results

A stable, closed population could not currently be supported in the corridor region modelled here. Starting population sizes of between 150 and 600 all demonstrated a declining population that experienced high mortality and low reproduction, leading to extinction by year 30.36 ± 5.61 on average. Previous work has shown successful simulation of a closed population in the pristine protected setting of CBWS (chapter 4), revealing the less favourable heterogeneous conditions of the Belize Wildlife Corridor region that includes relatively large proportions of agricultural land, savannah and urban areas that offer more limited resources. Immigration of agents into the region (specifically into protected areas that existed across the entire landscape), mimicking the natural movement and dispersal of individuals from thriving populations located in established protected forest regions to the north and south of the area, increased both the size and persistence of the population. The introduction of agents, in abundances ranging from 2 to 12 per year (introduced at regular intervals), all provided population persistence to year 100 of the simulation (Fig. 5.4) that, despite initial high mortality, remained stable through years 30 - 100. As would be expected, higher immigration rates generated larger population sizes, but sustained populations over 4 times the size of the immigration rate (Fig. 5.4). Larger populations corresponded to smaller home range sizes (r = -0.31, d.f. = 4716, $p < 0.0001$), reflecting the increased competition for space as well as the regular presence of newly introduced agents without established home ranges. Figure 5.4 illustrates the variation in home range size through time across all simulations, showing larger home ranges in simulations without any immigration (red line), particularly through years 20-40 when very low population levels corresponded to reduced competition and interaction between agents.

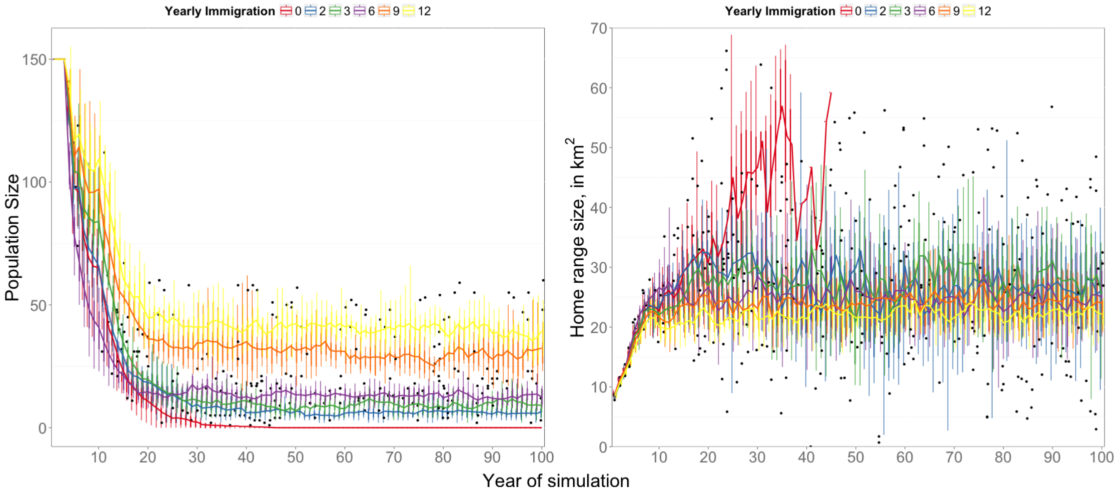


Figure 5.4: Population trend over time, for simulations with all rates of immigration.

The first 30 years of the simulations coincided with very high levels of adult mortality across all simulations, with an average of 83% of the population dead by year 11. Following the initial 10-year setup period, age-dependent mortality accounted for the largest proportion of deaths in all simulations, with observed proportions largest in simulations with less immigration (65% versus 54% with 12 agents introduced per year). Habitat-related mortality increased in simulations with higher rates of immigration (increasing from 24% in the absence of immigration to 35% with 12 agents introduced per year) demonstrating the increased competition for the most suitable habitats. Protected areas accounted for 54% of total deaths on average, increasing in simulations with higher rates of immigration and reflecting the dominant use of these areas by agents.

Despite their greater size and longevity through time, populations in simulations with higher rates of immigration exhibited lower lifespans through years 11-100 (5.80 ± 2.45 years compared to 6.36 ± 3.16 years for no immigration) and lower average age of mortality (4.94 ± 2.97 years compared to 6.61 ± 3.17 years for no immigration), described in more detail in Appendix A. In contrast these populations also showed increased reproductive activity (40% compared to 37% for no immigration) and more cubs per female (0.89 compared to 0.75 for no immigration), although this did not remain true for viable cubs reaching 2 years of age, where numbers remained similar across all simulations. Despite these differences and assuming fitness is a lifetime output of viable offpsring, population fitness does not change with immigration. In the absence of immigration, agents took advantage of the lower levels of intra-specific competition to maintain larger home ranges (36.11 ± 12.14 km^2 compared to 22.08 ± 11.24 km^2 for immigration rate of 12) and lower habitat-related mortality (24% compared to 36% for immigration rate of 12).

Agents preferentially selected habitats, showing strong preference for the most suitable habitats and avoiding those of higher mortality risk or lower food availability, both within and outside of protected areas (inside protected reserves: χ^2 = 35.48, d.f. = 8, $p < 0.0001$; outside protected reserves: χ^2 = 71.27, d.f. = 8, $p < 0.0001$). Lowland broad-leaved forest dominated the region, comprising 58% of the total modelled landscape, but accounted for 96% ± 0.002 on average of habitat use by all agents across all levels of immigration. The majority of agent activity occurred inside protected areas (65.74%) across all rates of immigrations, which reflects the higher food resources found in these areas.

5.3.1 Alternative Conservation Corridor Designs

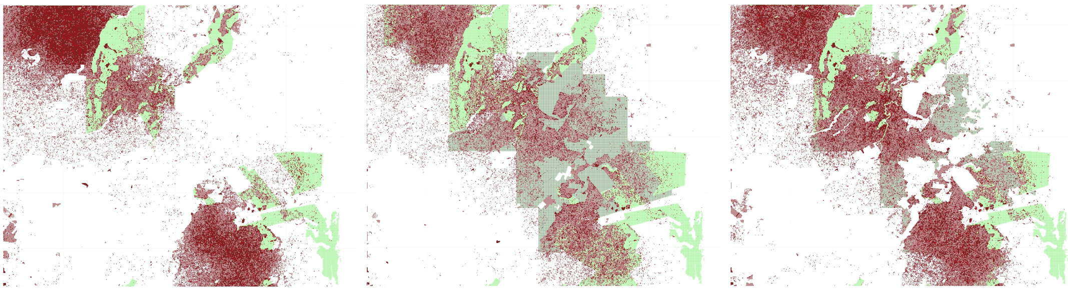
All simulations of experimentally modified landscape used an immigration rate of 12 agents per year. Corridor 1 sustained the largest population size through years 11-100 with an average of 55.49 ± 10.27 and allowing agents to generate the largest home range sizes, which averaged 26.75 ± 3.17 km^2 for males and 20.81 ± 3.08 km^2 for females: both at the lower end of naturally expected bounds for the region. Agents utilised the larger tracts of protected forest reserves in these simulations to maintain the highest fitness, in terms of longer lifespans, higher average age of mortality, most cubs per female and equal highest number of viable cubs per female, despite the lower average energy reserves per agent (Table 5.2).

Table 5.2: Population dynamics and life history with different conservation corridor designs.

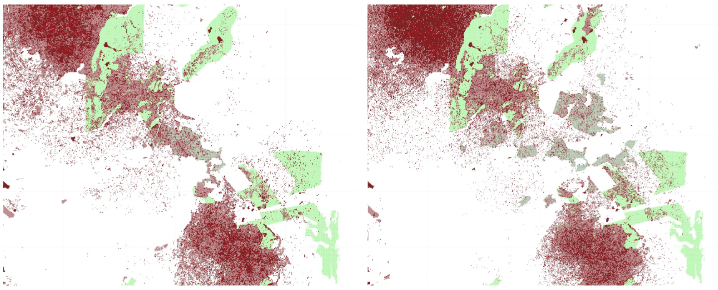
	Corridor Design				
	None	**Full**	**1**	**2**	**3**
Population Size, per year	43.62 ± 12.37	39.82	55.49	47.69	45.03
Home range size, male (km^2)	24.56 ± 4.04	25.92	26.75	25.38	24.96
Home range size, female (km^2)	19.79 ± 3.87	20.80	20.81	20.57	20.10
Energy reserves	92.31 ± 20.12	93.03	90.85	92.75	92.25
Age, years	4.15 ± 2.31	4.53	5.72	5.38	4.70
Age of mortality, years	4.74 ± 2.64	4.43	5.15	4.99	4.72
Successfully mated, %	40.23	34.66	39.80	41.86	39.08
Cubs, per female	1.78 ± 2.52	1.54	1.96	1.93	1.86
Cubs surviving to 2 years old, per female	0.73 ± 1.32	0.64	0.77	0.77	0.76
Age-dependent mortality, %	26.75	22.02	22.26	26.08	26.19
Energy-related mortality, %	3.59	2.79	3.80	2.96	3.25
Habitat-related mortality, %	70.03	75.19	73.95	70.57	70.95
Mortality inside protected reserves, %	33.49	53.46	40.24	30.59	35.44

The lowest population sizes occurred in simulations implementing the full proposed corridor design, reflecting the increased amount of suitable habitat and wider distribution of individuals across the landscape, which led to reduced interaction between agent and less successful reproduction. Corridor designs 2 and 3 sustained lower average population sizes than in corridor 1, but higher than with the full proposed corridor design or with no additional protected areas. Table 5.2 shows that despite similar population sizes, home range sizes, number of viable cubs per female and energy reserves per agent, populations in simulations incorporating corridor design 3 exhibited shorter lifespans and higher mortality within protected reserves than for simulations incorporating corridor design 2. Despite the largest tracts of protected areas in the full proposed corridor design, populations in these simulations exhibited the least healthy agents in terms of lower lifespan, lower age of mortality and relatively high proportion of habitat-related deaths, and fecundity — fewer viable cubs per females and smaller proportion of reproductively active agents. This reflects the heterogeneous nature of protected areas in these landscapes where only 65% comprised lowland broadleaved forest.

In the absence of additional landscape degradation, corridor 1 promoted the widest distribution of locations used by agents within the central zone of the landscape,



(a) No Corridor (b) Full Corridor (c) Corridor 1 - Wide



(d) Corridor 2 - Narrow (e) Corridor 3 - Patches

Figure 5.5: Distribution and density of individuals in landscapes with each of the four conservation corridor designs. All simulations with immigration rate of 12 agents per year. Red indicates positive agent movement, darker areas reveal higher densities of movements. Light green patches represent existing protected reserves, dark green patches represent proposed protected areas.

indicative of the greater mobility in these landscapes (Figure 5.5). Despite the smaller absolute amount of protected reserves in corridor design 2 as compared to design 3, the physical connectedness of protected forests promoted a higher density of movements through the additional centrally-located corridor area than through the same area in design 3, suggesting greater connectivity of populations and movement of agents between already established reserves in the north and south with design 2. Both corridor designs 2 and 3 also showed increased use of forest patches to the south-west of the conservation corridor, despite their non-protected status.

5.3.2 Impact of degradation on corridor design

The greatest vulnerability to environmental degradation occurred in landscapes incorporating corridor design 1, where reduced population size occurred under all four environmental conditions (Fig. 5.6). The large tracts of protected forest running through the central heterogeneous zone of the landscape increased the amount of edge habitats and brought agents into closer contact with human activities. The full proposed corridor provided protected non-forest zones around much of the central located forest patches, which buffered simulated populations from much of the introduced landscape degradation. Despite slightly lower population sizes and some variation, these remained relatively stable regardless of environmental disturbance. Urban development affected populations in landscapes with corridor design 2 to a less extent than other environmental factors, but populations showed increased vulnerability under all levels of disturbance compared to those in corridor design 3. Despite lower population sizes in the absence of any landscape degradation, the scattered distribution of protected reserves supported a greater abundance of agents than for any other corridor design in conditions of urban development, road intensification, and agricultural expansion.

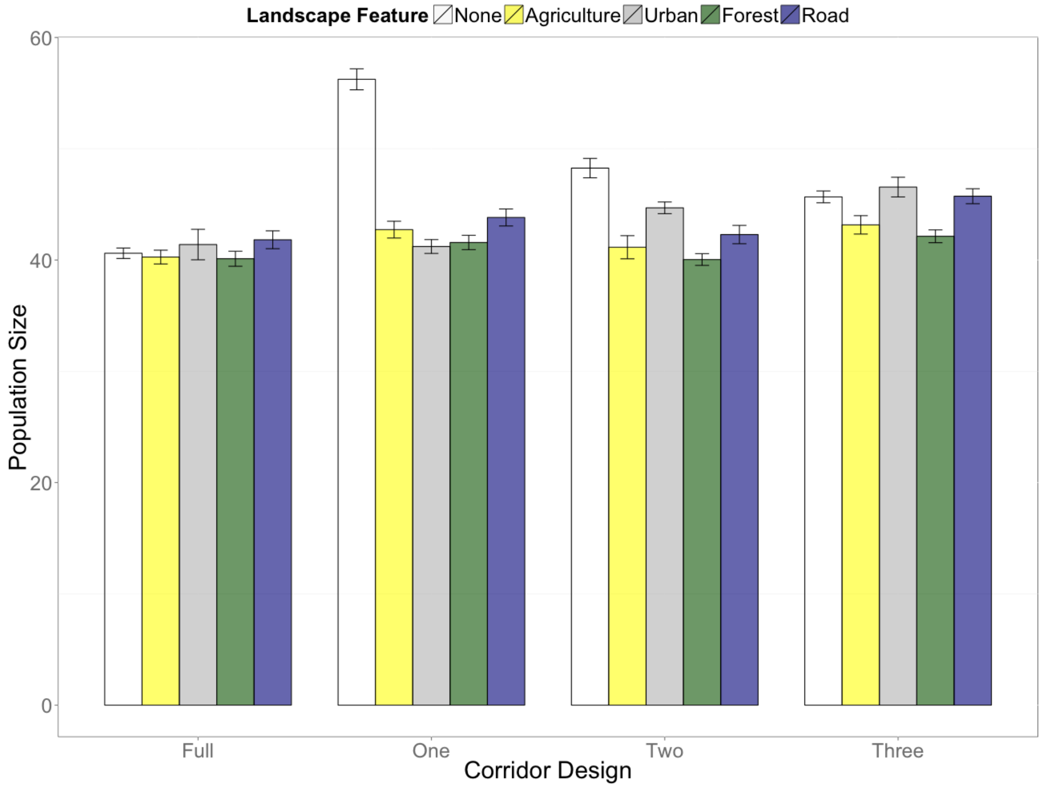
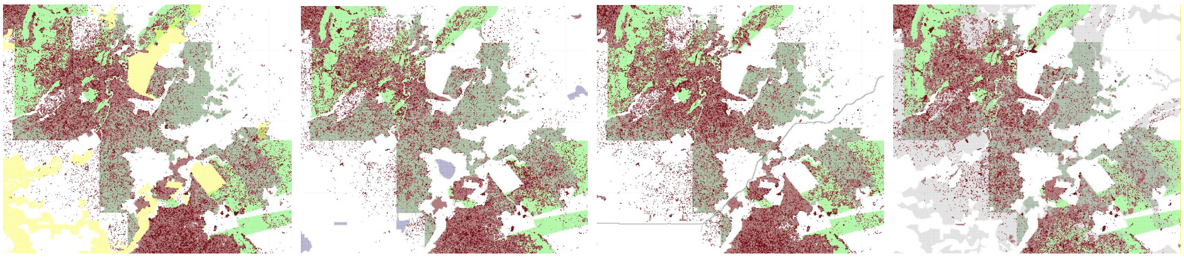


Figure 5.6: Summary of environmental disturbance effects on population abundance in simulations with each of the four proposed corridor designs. Bars show mean abundance ± s.e.

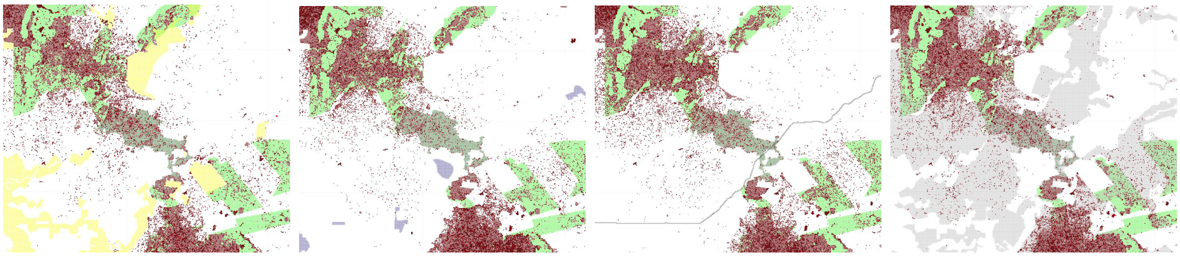
Population size reduced in all simulations with increased forest disturbance, regardless of corridor design (Fig. 5.6), reflecting the lower food available in these landscapes. The scattered nature of both protected reserves in corridor design 3, and urban centres reduced contact between simulated populations and human activities in these scenarios, and mitigated the negative effects of urban development on populations - the only conservation design to facilitate an increase in abundance under these conditions, although smaller mitigating effects also occurred with the small narrow strip of protected reserves generated by corridor design 2.

The large tracts of protected reserves in the full proposed corridor design (Fig. 5.7) minimised the effects of environmental degradation on simulated populations and enabled agents to continue moving through the central zone of the landscape under all

(a) Full Corridor



(b) Corridor 1 - Wide



(c) Corridor 2 - Narrow

(d) Corridor 3 - Patches

Figure 5.7: Population distribution (red, where darker red indicates a higher density of movement) in each of the four corridor designs under each of the four environmental degradation conditions: agricultural expansion (left-hand column) showing existing agricultural areas in yellow; urban expansion (second column from the left) showing existing urban areas in blue; road use intensification (second column from the right) showing the main highway in black; and increased forest disturbance (right hand column) showing existing forest patches in grey. Light green patches show existing protected reserves, dark green patches show proposed protected areas.

environmental conditions, despite the more fragmented movement densities exhibited under urban development and road intensification. Environmental disturbance reduced movement through the central zone of the map in landscapes with corridor design 1 under environmental disturbance (compare Fig. 5.7 to Fig. 5.5), reflecting increased mortality of agents outside protected reserves and reduced interaction between populations separated by unprotected forests. Of the four environmental factors, forest disturbance most strongly affected population connectivity under corridor design 1, with reduced and more fragmented movement particularly in the southern portion of the landscape, suggesting more limited movement between established reserves in the north and south of the landscapes in this scenario.

Although environmental disturbance reduced movement through corridor design 2 (Fig. 5.7), populations remained most connected under agricultural expansion. This reflected the reduced suitability of much of the landscape and the ‘funnelling’ of agents through centrally located forests. Despite the scattered distribution of movements in landscapes with corridor design 3, the larger population sizes supported in urban development scenarios allowed agents to maintain a high density of activity within centrally-located protected reserves in this scenario (Fig. 5.7).

5.4 Discussion

The simulation presented here demonstrates for the first time the application of a spatially explicit agent-based model of jaguar population dynamics to a real-world conservation problem. The testing of multiple scenarios has demonstrated the capacity of this model to help us understand and explore the influence of landscape structure on population dynamics both in terms of responses to environmental perturbation and likely outcomes of various conservation management strategies.

Long-term population survival under current conditions was hindered by the lack of sufficiently distributed food resources required to facilitate a large interactive group of agents able to successfully reproduce. The location of protected reserves to the north and south of the region, and the mixed-use area in the centre of the landscape forced individuals to split into two discrete populations that rarely interacted. Given the range of initial populations sizes and starting locations of agents, the probability of a closed population persisting for long in the real landscape is sufficiently low to suggest that management of the real corridor must ensure a free flow of individuals to and from protected forest blocks.

In spite of the long-term persistence of simulated populations incorporating immigration, populations still exhibited very low rates of successful reproduction. The transient nature of these populations demonstrates the role of the region as a sink, facilitating the recruitment and survival of individuals from source populations to the north and south, but demonstrating poor reproduction (Delibes et al., 2001). The high immigration rates required to generate long-term population persistence also demonstrates the negative impact of mixed use, heterogeneous landscapes on top-level predators, particularly when compared to the stable population demonstrated in the pristine forest conditions modelled in chapter 4.

The knock-on effects of heterogeneous areas acting as sinks, leads to protected, good quality patches of habitat supporting relative high densities of individuals, as has already been observed in the jaguar (Foster et al., 2010a; Harmsen et al., 2009) and in other large felids (Kanagaraj et al., 2013). The more insular these refuges become, and the increasing disturbance from human activity in areas outside these protected areas is likely to lead to greater vulnerability of these populations to inbreeding and other negative effects of population isolation (Kanagaraj et al., 2013). Connectivity between these protected areas is therefore crucial for effective and sustainable long-term conservation management. The Darwin Initiative-funded Belize large-mammal corridor project, has recently had success in this area, resulting in the designation of an additional 7,000 acre reserve adjoining existing protected reserves to the north and beginning to develop the protected network south into the CBC region (Doncaster, 2012).

The advantage of using corridors to physically connect habitat patches has been demonstrated here, and lies in directly linking previously isolated patches into larger habitat systems (Bennett, 1990; Haddad and Tewkesbury, 2005; Noordijk et al., 2011; Petracca et al., 2014). Corridor 1 (wide design) represented the management design with the highest level of connectivity between habitat patches (not including the full design) and hence the conservation management strategy that most effectively linked established populations in the north and south of the region. The increased movement in these additional protected corridor areas suggests that connecting corridors are more effective than isolated habitat patches (Gilbert-Norton et al., 2010). However, despite the lower fitness of agents in landscapes with corridor design 3 (patches), the reduced vulnerability of populations in these landscapes to disturbance suggests that different designs may bring different advantages (particularly where large protected areas that physically connect reserves is not possible): physically connected narrow strips (design 2) facilitated a fitter and better connected population in the absence of closely located environmental disturbances; but, discrete and separate patches (design 3) reduced vulnerability to disturbance and may facilitate increased connectivity under certain environmental conditions. Despite the increased vulnerability of jaguar populations, the higher population sizes in these simulations allowed this connectivity to be maintained under environmental disturbance scenarios. Corridor 1 therefore comprised the best conservation management strategy of those tested.

However, corridor design 1 demonstrates the potential problems of protecting corridors that promote movement into heterogeneous, mixed use landscapes - promoting movement between more established populations serves to bring individuals into closer direct contact with disturbance events where they suffer higher mortality, corroborating previous results analysing the effects of corridors on population abundance and movement (Astrom and Part, 2013). Given the potential negative effects of corridors in heterogeneous environments, it might be argued that a better conservation strategy in landscapes with a matrix of lower permeability would be to focus on supporting viable and stable populations *where they already exist* and then relying on the natural probability that even a very small number of successful dispersal movements between populations may be enough to maintain genetic continuity (Gilbert-Norton et al., 2010). However, this strategy may reduce the ability of recolonisation and may increase the vulnerability of locally isolated sub-populations that rely on a more steady influx of individuals (Astrom and Part, 2013). However, should it require protected physical connections to ensure sufficient functional connectivity (and hence genetic flow) between sub-populations, it is also worth considering the additional paradox generated by successful use of more fragmented human-influenced landscapes: the severely negative impacts caused by an increased risk of jaguars coming into contact with humans in these more human-dominated sections of the landscape coupled with the benefit to jaguar conservation of an effective and functional conservation corridor (Foster et al., 2010a). Can the meta-population benefits of genetic and demographic connectivity outweigh the increased mortality of individuals using the corridor area? - i.e. can the (assumed) healthier and larger meta-population absorb these potentially higher rates of mortality and still demonstrate increased viability? Further exploration is needed to tease apart these interesting factors.

Future Development

Despite the recognition of the role corridors can play in maintaining and increasing connectivity, rigorous approaches for building corridors, as an integrated part of spatial conservation strategies, are currently limited and are made more problematic given the diverse spatial scales and resolutions at which corridors may function (Pouzols and Moilanen, 2014). The relationship between jaguar population distribution, peristence probability and landscape configuration is also complex Zanin et al. (2014) and we have demonstrated the large impact that corridor design, as a fundamental property of landscape connectivity, can have on these processes. But how could we better measure the success, or effectiveness, of our potential corridor designs? The crux of this issues depends whether we are designing corridors to maximise population size, to minimise regional extinction threats, or potentially to hope to do both (Pouzols and Moilanen, 2014).

The former suggests we could measure population size directly as a measure of success, with reproductive capabilities (number of young per litter, litters per female, % of adults reproducing) and sub-adult mortality as secondary indicators of success. The latter suggests a more complicated approach. Here, we could consider using heritable markers, differentiated between source population to the north and south, and then compare the abundance and length of time taken for markers from northern source populations to appear in southern populations (and vice versa). This would give some indication of the genetic link between these relatively isolated sub-populations. By then combining these marker methods with more traditional landscape metrics that provide some quantitative analysis of structural connectivity (e.g. Mas et al. 2010; Turner 2005), we could also begin to better explore the relationship between structural and functional connectivity on a species-specific basis.

The instability of closed simulated populations reflects a limitation of any simulation modelling applied at the landscape scale. Where does the landscape end? What are the boundaries and why have they been chosen? For discrete closed natural populations these factors may not limit the effectiveness of the modelling technique. However, closed populations are unlikely in reality and movement of individuals between subpopulations must be incorporated to effectively capture population dynamics in the region.

5.4.1 Management Implications

Development of this simulation met a management need for modelling the effects of landscape structure on wild jaguar populations. The variability in population size and spatial distribution of agents revealed a strong dependence on the rate of immigration and the structural characteristics of the landscape. This emphasised the value of using tools that incorporate spatially dependent variables when investigating the implications of management strategies and conservation practices on population resilience and persistence.

Assessments of the robustness and resilience of simulated populations show that the landscape region modelled here cannot support a stable population under current conditions. Immigration from thriving populations in protected reserves to the north and south is necessary to facilitate long-term population persistence. The heterogeneous structure of the landscape presents obstacles to movement for simulated agents, restricting the majority of agent activity to within protected reserves or to forests and other land bordering the reserve boundaries. Conservation corridors facilitated the increased spatial distribution of agents, particularly within newly protected reserves in the centre of the landscape, maximised where reserves were physically connected. However, increased density and distribution of agents within more heterogeneous regions of the landscape increased the likelihood of conflict between animal populations and human activity. Where possible, conservation management strategies should therefore focus on protecting physically connected forest patches that allow agents to move between existing protected reserves in the north and south, but that are buffered from environmental disturbances.

5.4.2 Conclusions

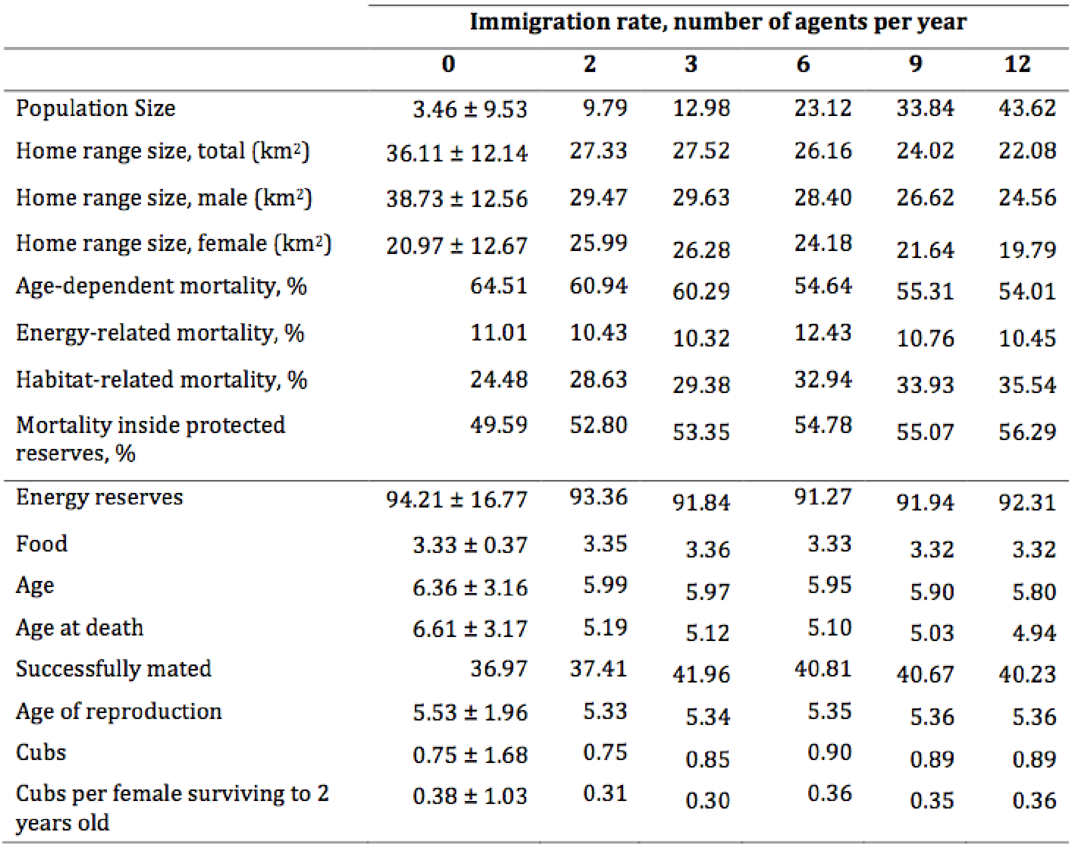
The model provided significant insight into the influence of landscape structure and quality on population persistence and distribution through time and space. Increased connectivity of habitat patches, through physically connected reserves maximised both population size and fitness, and movement between protected reserves across the landscape. However, increased spatial distribution into these more heterogeneous areas increased population vulnerability to environmental degradation.

Despite having validated the model in the more pristine habitat of Cockscomb (Chaper 4), the contrasting heterogeneous structure of the landscape modelled here suggest this study would benefit from greater ground-truthing and validation of agent movement with empirical data from the same location in the field. Despite this, and the limitations of the model described in chapter 4, the model prototype developed here serves as a useful tool to test hypotheses about jaguar resilience in heterogeneous landscapes. This study demonstrates use of this tool for investigating how connections between metapopulations can be established, maintained and enhanced but also how landscape structural changes, caused by human development and disturbance, can affect both connectivity and persistence of animal populations.

5.5 Appendix A. Population and life history output

Table 5.3 shows the breakdown of population and life history values for simulations in landscapes under different rates of agent immigration.

Table 5.3: Population dynamics and life history under different rates of immigration. % figures compare to same value with no immigration and not shown if less then 1% difference.



	Immigration rate, number of agents per year					
	0	**2**	**3**	**6**	**9**	**12**
Population Size	3.46 ± 9.53	9.79	12.98	23.12	33.84	43.62
Home range size, total (km^2)	36.11 ± 12.14	27.33	27.52	26.16	24.02	22.08
Home range size, male (km^2)	38.73 ± 12.56	29.47	29.63	28.40	26.62	24.56
Home range size, female (km^2)	20.97 ± 12.67	25.99	26.28	24.18	21.64	19.79
Age-dependent mortality, %	64.51	60.94	60.29	54.64	55.31	54.01
Energy-related mortality, %	11.01	10.43	10.32	12.43	10.76	10.45
Habitat-related mortality, %	24.48	28.63	29.38	32.94	33.93	35.54
Mortality inside protected reserves, %	49.59	52.80	53.35	54.78	55.07	56.29
Energy reserves	94.21 ± 16.77	93.36	91.84	91.27	91.94	92.31
Food	3.33 ± 0.37	3.35	3.36	3.33	3.32	3.32
Age	6.36 ± 3.16	5.99	5.97	5.95	5.90	5.80
Age at death	6.61 ± 3.17	5.19	5.12	5.10	5.03	4.94
Successfully mated	36.97	37.41	41.96	40.81	40.67	40.23
Age of reproduction	5.53 ± 1.96	5.33	5.34	5.35	5.36	5.36
Cubs	0.75 ± 1.68	0.75	0.85	0.90	0.89	0.89
Cubs per female surviving to 2 years old	0.38 ± 1.03	0.31	0.30	0.36	0.35	0.36

Chapter 6

The future of ABMs as a tool for conservation

6.1 Summary and overview

This is the first study to develop an integrated least-cost and agent-based model for the purposes of direct application to real-world conservation problems. From the direct analogy of ABMs to complex systems, I hope to have improved our understanding of the role of CAS theory in helping us better model and explore the relationship between structural and functional connectivity and population resilience and persistence over time. In doing so, I have demonstrated the development and application of a model that is more than a simple measurement of connectivity. It necessarily comprises a detailed representation of important individual and spatial population characteristics that facilitate addressing a variety of conservation-orientated questions.

Chapter 2 demonstrates the capacity for connectivity measures to set the foundation for applied population analyses and the increased exploratory power and understanding that can be gained by integrating landscape metrics with individual-based modelling methodologies. Here, I have been able to isolate dispersal behaviour from that of daily home-ranging movement, whilst also teasing apart the effects of fragmentation per se, from those of habitat loss, critical in guiding wildlife management strategies (Zanin et al., 2014).

Long-term experimental field studies with large-bodied, long-lived species are impractical and there is a need for methodology that allows for multiple scenario testing to generate more informed and resilient conservation policies (McLane et al., 2011). Exploration through computer simulation provides a necessary alternative to empirical data collection for long-term and/or large-scale studies (Grimm, 1999) and I have shown in this thesis that an integrated model can facilitate multiple scenario testing in both abstract (chapters 2 and 3) and real-world (chapter 5) landscapes.

The models demonstrated in this thesis distil field data and expert knowledge into behavioural models based on least-cost movement assumptions. An adaptation of traditional least-cost modelling used costs based on general daily movements rather than one-off dispersal movements. By combining metapopulation ecology with connectivity measures, chapters 4 and 5 demonstrate the capacity of this model design to capture and describe the interactions and movement of individuals within a metapopulation that fall within realistic bounds, despite the lack of explicit individual dispersal mechanisms of agents. This has established the importance of daily movements and individual behaviours when considering conservation strategies, particularly on long-ranging, long-lived species.

Detailed population demographic data includes lifespan, litter size, reproductive dynamics and mortality, all of which can and have been obtained directly from field data or expert knowledge, or calibrated with model outcomes via the pattern-oriented modelling (POM) approach (Grimm et al., 2005). This process represents the compromise between ecological realism and model complexity, simplifying model processes and agent decision-making where possible, but still demonstrating the capacity to capture realistic patterns of natural populations.

The aim of this final chapter is to draw together the main findings of the thesis, and to consider the future role of an integrated modelling approach in ecology and conservation management. I address the implications of this work to the wider research community as well as to conservation planning, highlight limitations in the modelling approach and outline areas where this research could be developed further.

6.2 Connectivity

The integration of some form of population modelling methodology with landscape metrics is not new to the world of ecology (e.g. Landguth et al. (2012); Stevens et al. (2006); Zanin et al. (2014)). However, chapter 4 introduces the first detailed behavioural ABM integrated with a quantitative representation of connectivity of a large-bodied felid. This thesis demonstrates the capacity for such a model design to effectively capture natural processes of wild jaguar populations that enable model output to exhibit individual and population-level behaviours that fell within empirical estimates of natural populations. The successful integration of real-world geographical information into the detailed behavioural ABM has also demonstrated the ability to use the outcome of simpler, abstract, modelling methodologies (such as that presented in chapter 3) to inform and develop more biologically-realistic models that can be successfully applied to real-world scenarios. Output from these more realistic models can also reasonably guide future field work and help direct data collection by field ecologists (McLane et al., 2011).

The clear response of simulated populations to landscape structure and human activities demonstrates the critical role that spatially-explicit aspects of the model play in enabling us to better understand population-level connectivity and responses to environmental change. The inclusion of individual-level movement and behaviour and the interactions between individuals and the environments, and the role this plays in driving population size and distribution across the landscape has been demonstrated in chapter 5. The reduced ability of model populations in the heterogeneous CBC region to successfully reproduce, despite large tracts of suitable habitat (compared to populations in the CBWS region modelled in chapter 4), implies we need a better understanding of the ways in which real jaguars interact, through the use of physical cues such as scats and scrape marking (Harmsen et al., 2010a), to enable more informed and robust predictions of likely population persistence and responses to future environmental change.

6.3 Conservation corridors

A review of existing and recent approaches to corridor building methodologies (Pouzols and Moilanen, 2014) finds that most approaches have centred on those connectivity measures discussed in chapter 1: least-cost path, circuit theory and graph theory. Challenges exist in designing effective corridors that include building corridors in irregular networks, in landscapes with diverse morphology, in determining effective corridor width and accounting for multiple species with diverse requirements and spatial scales (Pouzols and Moilanen, 2014). As discussed in chapter 5, static connectivity and landscape metrics also cannot help us explore the effect of landscape change and environmental disturbance on the functionality of potential corridors in preserving and maintaining viable populations and functional links between sub-populations(Kanagaraj et al., 2013).

By using my integrated agent-based and least-cost model I have shown that movement between habitat patches may be maximised with a larger number of narrower, physically connected corridors, rather than a single large connection or a number of discrete ‘stepping stone’ patches (chapter 3). This shows the advantage of using corridors to physically connect habitat patches and directly link previously isolated patches (Bennett, 1990; Haddad and Tewkesbury, 2005; Noordijk et al., 2011; Petracca et al., 2014). The observed difference in movement rates between populations under scenarios with varying corridor widths suggests that contrary to some recent studies (e.g. Haddad and Tewkesbury (2005); Salek et al. (2009)) corridors may serve either as conduits of movement, or as additional areas of refuge, but perhaps not as both.

Given the simplified nature of the agents in chapter 3, how might we expect that more complex and biological realistic individuals, in populations with more realistic behaviours, interactions and life histories to behave in similarly constructed landscapes? Corroborating the results presented here, previous simulation work in this area has demonstrated the importance of corridor width for determining the probability of individuals transitioning the corridor (Tischendorf and Wissel, 1997). Empirical work suggests a similar trend in behaviour in real-world populations where additional refuge, either as breeding, feeding, resting habitat, is sought in wider corridors that subsequently restrict the movement of other individuals ’through’ the corridor (Andreassen et al., 1996; La Polla and Barrett, 1993). However, simulation work on large carnivores, based in real landscapes, suggests that narrow corridors may actually reduce the likelihood of individuals moving between patches given the reduced probability of finding the entrance to the corridor (Kanagaraj et al., 2013).

The picture becomes more complicated when the quality of the corridor habitat and matrix are included (Astrom and Part, 2013; La Polla and Barrett, 1993; Ruefenacht and Knight, 1995) and where simulations based on observed natural behaviours at habitat boundaries show corridors may inhibit dispersal movement in some species where edge effects can strongly affect the choice of movement direction (Baur and Baur, 1992). The latter species-specific dynamics may be determined by the perceptual range of the species and/or its place on the specialist to generalist spectrum (Sozio and Mortelliti, 2013), adding support to the argument that corridor design and hence conservation management strategies require species-specific action (Gilbert-Norton et al., 2010; Lindenmayer and Nix, 1993; Pouzols and Moilanen, 2014; Rudnik et al., 2012). Furthermore, it has been suggested that simplified computational approaches are unable to effectively capture complex interactions of species-specific behavioural responses with matrix quality and inter-patch connectivity, leading to failures in the management of real-world conservation issues (Kanagaraj et al., 2013).

Understanding how jaguars utilise their environment is essential for predicting their long-term survival in what is an increasingly human-dominated landscape but there is little information on how jaguars may favour either wilderness or human-influenced landscapes (Foster et al., 2010a). The simplified nature of agent movements and simulation landscape characteristics presented in chapter 3 seem unable to fully capture and describe the relationship between population distribution and landscape pattern. However, to my knowledge, chapter 3 is novel in its efforts to merge ABM methodologies with comparisons of corridor design effectiveness for a large-bodied species (Kanagaraj et al. (2013) assessed the functionality of corridors, but did not compare corridor designs). Despite its limited scope, simplistic agent behaviours and abstract setting, this study comprises an analysis of fragmentation per se on population connectivity, independent of habitat loss, and shows that corridor design, or structural connectivity, can be critical in defining connections between locally isolated sub-populations. More recent empirical work on jaguar population connectivity has revealed the detrimental effects of fragmentation per se to be much stronger than habitat loss on jaguar population persistence (Zanin et al., 2014).

Chapter 5 constitutes a first test at developing more appropriate and suitable methodologies for real-world spatial conservation planning and despite its relatively ‘clunky’ description of temporal and spatial landscape changes, it more realistically represents agents and their environment. However, rather than attempting to ‘predict’ and provide quantitative forecasts of population persistence or distribution, as has been called for in the recent call for predictive systems ecology (e.g. Evans et al. (2013); Grimm and Railsback (2011)), I submit that this chapter instead presents a useful insight into how a jaguar population may be affected under future environmental scenarios. The ecologically complex relationship between landscape configuration (amount and connectivity) and population structure and persistence is clearly demonstrated and serves to remind us that design and interpretation of the benefits and adverse effects of potential conservation management strategies remains a serious challenge.

6.4 Computational simulation

The value of computational experimental work lies in its ability to explore systems in a way not possible with empirical field work. Combining individual-based simulation modelling with a geographically-based connectivity measure potentially presents the best of both worlds - a species-specific quantitative representation of the *structural* connectivity of a landscape, along with biological relevant computational agents that facilitate analysis of the associated *functional* connectivity for that species.

A review of current modelling approaches has been described in chapter 1. Generating a map of the connectivity of a landscape is an important step in exploring and understanding how a species may view a landscape but may be most helpful in understanding connectivity at a single point in time. Models that attempt to capture the way in which a species interacts with the environment can overcome the limits of landscape connectivity indices and least-cost path analysis (Kanagaraj et al., 2013) and help to advance our understanding of species responses to landscape configuration, habitat loss and fragmentation. However, it is not my intention for the approach described in this thesis to take the place of these less complex quantifications of structural connectivity but rather to complement the suite of methodologies available. Likewise with more traditional empirical work. In fact, recent studies like that of Petracca et al. (2014) necessarily complement alternative computational methodologies that exist, including both connectivity and corridor-mapping (e.g. Rabinowitz and Zeller (2010)) as well as more complex individual-based models (e.g. Kanagaraj et al. (2013); Palmer et al. (2011); Pe'er et al. (2011)). Computational simulations will never be able to truly capture the complexity of animal decision-making in complex and dynamic environments and empirical field work comprises an important ground-truthing function, particularly when dealing with species that lack detailed empirical datasets that can be used in validating model outputs.

I have discussed in this thesis that connectivity describes the permeability of, or degree to which a species can move around, a landscape. Connectivity studies therefore mostly focus on dispersal as the most important trait in population biology and ecology (Coulon et al., 2004) and which defines the functional connectivity of a landscape (e.g. Baguette et al. (2013); Kanagaraj et al. (2013); Palmer et al. (2011)). However, home ranging daily behaviour is an important component part of functional connectivity and focusing only on dispersal may overlook important effects of functional connectivity on meta-population dynamics (Pe'er et al., 2011). My approach stresses the important of these daily home-ranging behaviours and uses them as a mechanism for qualifying the interactions between individuals and between individuals and the environment. The explicit representation of daily behaviours together with individual-level variations in movement and decision-making and immediate interactive feedbacks set the work in this thesis apart from other connectivity models. Inherent problems of validating dispersal models with empirical data (Kanagaraj et al., 2013) is overcome to some extent with this approach given the relative greater availability of daily movement information with which to use in validating model outputs (demonstrated in chapter 4).

The ability to tease apart important population processes that are fundamental component parts of connectivity make the model presented by Pe'er et al. (2011) particularly powerful. However, the focus remains on a single aspect of population biology and ecology, in this case: functional connectivity per se (however future developments may facilitate a wider analysis). The model I have presented in this thesis will complement this newly emerging methodology by increasing the exploratory power for both functional connectivity and well as *potential future* functional connectivity (and hence population persistence) by delivering a tool for practical conservation-based landscape management. The role of ABMs as exploratory tools provides the opportunity to investigate possible future scenarios that then lead to greater understanding of the system under investigation (McLane et al., 2011). The explicit inclusion of temporally-and spatially-explicit behaviour and responses of individuals over long-time periods, in dynamically changing landscapes, allows exploration of factors that may be important in driving and shaping potential future population-level distributions and landscape-scale connectivity of populations.

6.5 Limitations

Chapter 4 demonstrates the heuristic nature of many model assumptions and the wealth and breadth of empirical data required to inform model parameters: movement path data, demographical data and expert knowledge of species ecology. For elusive and under-studied species such as the jaguar, absence of specific data on key population processes including dispersal and social behaviours, make calibration of model parameters particularly challenging. In these circumstances, validation and calibration must largely occur through POM approaches, that may mask the interactive effect of model parameters and reduce our ability to identify cause and effect mechanisms. Assessments of the robustness and resilience of ABMs, particularly where used as management tools, would benefit greatly from precise empirical data with which to validate behavioural predictions at a range of scales.

In most ecosystems humans arguably constitute the most important keystone species (Musiani et al., 2010). Explicit representation of humans, particular in heterogeneous landscapes such as the CBC (chapter 5), would allow for better clarity and resolution of behaviours that may be important at both the local and landscape scale. The importance of human decisions and subsequent actions, and their feedback is beginning to be recognised in modelling of natural systems (An, 2012). For predatory species such as the jaguar, hunting by local communities can represent a significant source of mortality, directly through trapping, shooting and poisoning of individuals, and indirectly through depletion of prey resources (Foster et al., 2010a). Incorporating a more detailed level of human behaviour, beyond that captured by the multiple landscape scenarios demonstrated in chapter 5, would allow for a more realistic representation of human activities and events that may better capture likely future landscape changes. ABMs are well suited to account for the learning, adapting and feedbacks inherent to human decision-making (An, 2012) making the models presented in this thesis well placed to deal with these future developments.

Chapter 5 demonstrated one of the problems of simulation modelling. Here, the fixed landscape boundaries and closed nature of simulated populations strongly impacted model output, leading to sometimes unrealistic and catastrophic population crashes given small changes to some model parameter settings. As a management tool for conservation, such dynamics increase our understanding of the connections between natural sub-populations and allow us to draw conclusions regarding the ecological status of particular regions. However, the acceptance of the disadvantages and limitations of simulation modelling, as well as a better integration of key metapopulation processes (dispersal, immigration ad emigration for example), would allow for better representation of population-level behaviours in any given setting.

Despite the model validation described in chapter 4, difficulties still occurred in interpreting cause and effect mechanisms within the simulation. Rigorous tests of changes in a number of model parameters during model development often caused unpredictable population crashes that could not be explained in detail. Minimising the complexity of movement behaviour was possible through the adapted least-cost model approach, but the model would benefit from further work in reducing the complexity of parameter interactions and in making a clearer link between causal factors. The inherent flexibility of agent-based simulations, given the wide range of available software packages and programming languages, provides much scope to develop models further to address these issues.

6.6 Future developments

The insightful approach to conservation-based scenario-planning shown in chapter 5 has identified a number of areas that could motivate future work, particularly focused on better understanding daily movements and social behaviours of jaguars, as well as better mapping of site-specific extents (temporal and spatial) of detrimental human-induced events. The integration of real-world geographical information into an individual-based model is not new in ecology (e.g. Cushman et al. (2013b); Kanagaraj et al. (2013); Landguth et al. (2012); Pinto et al. (2012)). Chapters 4 and 5 show that incorporating real-world landscape data into the integrated model design provided a direct link between model output and natural phenomenon, and facilitated the direct application of model findings to conservation planning and management in the experimental region. However, shortcomings in capturing the more complex and fine-scale social behaviour of jaguars identified in chapter 4 demonstrate the potential problems of not incorporating comparable resolution of agent behaviours and geographical data. An increase in the resolution of habitat maps that underpin simulation environments will likely lead to greater clarity of individual movements and greater confidence in model output, but must be weighed against losses through the additional time and computer resources required to run such high resolution simulations.

The heuristic nature of many model parameters (discussed in chapter 4) highlights areas of uncertainty that could be better supported with expert knowledge and data collection efforts should be coordinated with model development where possible (Altaweel et al., 2010). Figure 6.1 describes a best practice guide to integrating modelling with data collection that places fieldwork and information-gathering at the heart of model development.

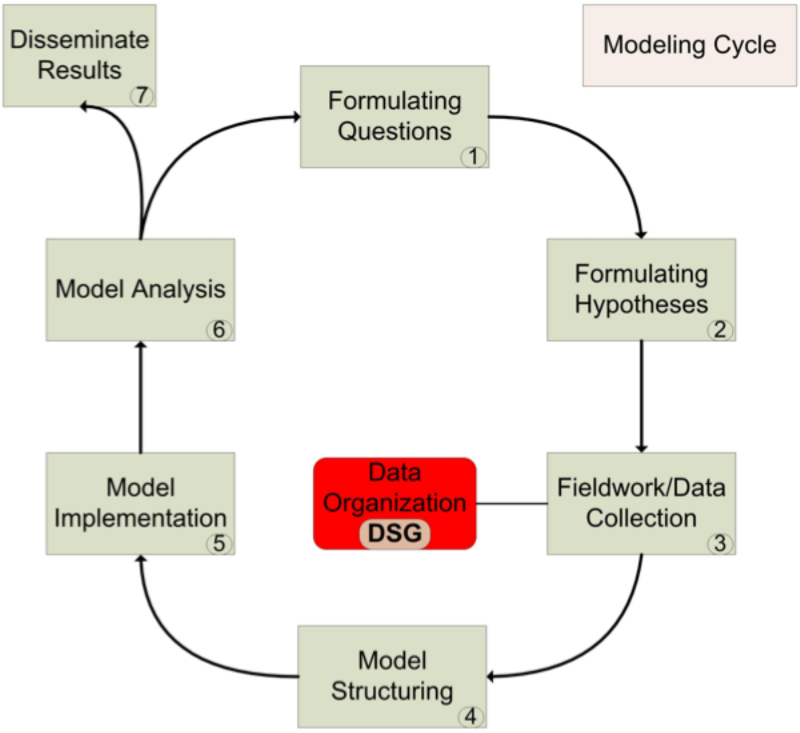


Figure 6.1: Schema showing a best practice modelling cycle integrating data collection with model development. Taken from Altaweel et al. (2010), red box indicates specific actions related to an approach of organising data called Delineate, Structure and Gather (DSG).

Adaptation of the model to a web-based interactive management tool comprises the logical next step in model development and would serve to better integrate the model into real-world conservation planning. The computer programming expertise required to run, adjust and interpret the model currently makes it of low use to field researchers or conservation ecologists who have minimal computer literacy. Development of a much simpler web-based tool with a simple user graphical interface would allow users to explore alternative corridor configurations or types of degradation other than those explored in chapter 5. This would extend the model design to direct conservation action now and in the future.

Adaptations of the model to represent alternative species with similar life history traits and sociality are expected to be fairly straight-forward given sufficient expert knowledge and empirical data from which to derive parameter settings and validate model output. The inclusion of species with a higher level of sociality, particularly those with complicated hierarchical structures and fluid group structures will be more complicated but can largely be based on existing models of wolves (Musiani et al., 2010) or gorillas (Robbins and Robbins, 2004).

Examples of IBMs that incorporate trophic interactions exist (for example, Musiani et al. (2010)), but most do so with only a single cognitive agent. To my knowledge, there currently exist no IBMs (or therefore ABMs) that account for multiple interacting species each with detailed behavioural individual decision-making. This comprises the most difficult next developmental step for the model presented in chapters 4 and 5 and could include the addition of human agents, or explicit representations of one or more prey species. This would allow for more informative interaction dynamics specific to conservation of the jaguar in resource limited and heterogeneous regions such as the CBC modelled in chapter 5. The use of marker objects to facilitate individual interactions has been demonstrated successfully in these chapters and should serve in future models to function as both intra- and inter-specific interaction parameters. However, the key limiting factor in developing robust models of this nature lie in the collection and use of sufficient empirical data from which information on inter-specific interactions can be obtained for the purposes of both calibration and validation. It is likely that there are only few instances where such detailed knowledge of a range of species ecology, together with their interaction dynamics, from a single system exist. In spite of this, the flexible and versatile nature of ABMs provides an inherent capacity for these models to integrate various types of agents and actions and to be designed as simply or as detailed as desired.

6.7 Final conclusions

Development of progressively more complicated model designs throughout this thesis has demonstrated the multi-disciplinary nature of agent-based modelling and I have had to develop substantial computer programming knowledge to successfully model and combine ecological, geographical and computational information. I believe that this may impede the rapid uptake of these models within fields that sit outside of those more traditionally linked with computer programming and simulation. However, I consider that CAS has an integral place in future research of this kind and that this more holistic approach to conservation management can shed new insight into how and why individuals and populations are affected by environmental variables.

The full potential of ABMs has yet to be fulfilled and they represent an advanced architecture that can capture a complicated animal movements and behaviour in complex environments. I have demonstrated the successful development of an ABM designed for real-world conservation management, and shown that improvements in model design and resolution of both empirical data for validation purposes, and geographical datasets for environmental conditions, are both necessary and possible.

ABMs can be useful to scientists, land managers, governments, conservation organisations and even the public and local communities in providing a conceptual and visual framework to simulate animal movements and environmental systems, at various scales and under a range of environmental conditions and scenarios. Integration with changing landscapes that represent human activities and environmental events reflect feedbacks between natural and human systems and can help identify appropriate conservation management strategies. I believe this multi-disciplinary approach comprises the most complete and promising approach to ecological modelling for conservation management.

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