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Applications and limitations of spatially-explicit mechanistic models for animal conservation

by

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ABSTRACT

BIOLOGICAL SCIENCES, FACULTY OF NATURAL AND ENVIRONMENTAL SCIENCES,
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APPLICATIONS AND LIMITATIONS OF SPATIALLY-EXPLICIT MECHANISTIC MODELS

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We live in a world of human-induced rapid environmental change, where the frequency of extinctions and resulting loss in biodiversity has reached levels associated with a mass extinction event. At the same time, technological developments in computing have facilitated the growth of highly complex, mechanistic models across all scientific fields. The challenge for conservation biologists is then to develop models that can predict how organisms respond to conservation measures and increasing anthropogenic pressures. Here I explore the potential and limitations for conservation applications of spatially-explicit mechanistic models of habitat selection, by developing a simulation applicable to large felids. I demonstrate that initial choice of resolution may bias the parameterisation process of spatially-explicit models, when applied to spatially-explicit empirical data. I use mechanistic models to address two current problems in conservation biology: (a) efficient calculation of movement metrics from telemetry data, tested with a virtual ecology approach; and (b) accounting for interacting influences on populations, quantified with a model that controls for confounding variables. I identify the major caveats to accurately predicting the complex behaviour of large-bodied animals. The spatially-explicit mechanistic models developed here, and applied to real-world problems, demonstrate the potential of these types of simulation for confronting otherwise impossible questions in diverse areas of conservation biology.

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Academic Thesis: Declaration Of Authorship

I, Alice Ball, declare that this thesis and the work presented in it are my own and has been generated by me as the result of my own original research.

‘Applications and limitations of spatially-explicit mechanistic models for animal conservation’

I confirm that:

1. This work was done wholly or mainly while in candidature for a research degree at this University;
2. Where any part of this thesis has previously been submitted for a degree or any other qualification at this University or any other institution, this has been clearly stated;
3. Where I have consulted the published work of others, this is always clearly attributed;
4. Where I have quoted from the work of others, the source is always given. With the exception of such quotations, this thesis is entirely my own work;
5. I have acknowledged all main sources of help;
6. Where the thesis is based on work done by myself jointly with others, I have made clear exactly what was done by others and what I shave contributed myself;
7. None of this work has been published before submission.

Signed:

Date:

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Abbreviations and Definitions

ABC	Approximate Bayesian Computation
ABM	Agent-Based Model
AIC	Akaike's Information Criterion
ASCII	American Standard Code for Information Interchange
CBWS	Cockscomb Basin Wildlife Sanctuary
GIS	Geographic Information Systems
GPS	Global Positioning System
HIREC	Human-Induced Rapid Environmental Change
IBM	Individual-Based Model
LHS	Latin Hypercube Sampling
MCP	Minimum Convex Polygon
SMS	Stochastic Movement Simulator

Agent. A modelled entity, whose behaviour is determined by a set of distinct rules.

Bushmeat. Synonym for 'wildmeat'. Meat for eventual consumption that humans obtain from the wild, as opposed to meat from agriculture. This word is more commonly utilised when referring to wildmeat consumption in Africa.

Corridor. A patch or number of patches of 'habitat' that facilitate movement of organisms through 'matrix'. Can be natural or man-made.

Deforestation. The act of removal of forest, either by natural or man-made means.

Depredation. The act of a predator attacking prey.

Home range. An area that an animal, or group of animals, regularly inhabits.

Wildmeat. Synonym for 'bushmeat', used when referring to areas outside of Africa.

Chapter 1.

Introduction

Chapter 1. Introduction

The aim of this chapter is to provide the reader with the necessary background knowledge to understand the methodologies used in this thesis, and to place it in the wider context of conservation issues currently being tackled with modelling approaches. Section 2.1 summarises the use of agent-based models in ecology. Section 2.2 then discusses the optimisation and parameterisation of agent-based models, and addresses potential issues with the development of highly mechanistic, spatially-explicit models. Section 2.3 provides an overview of the use of mechanistic models for studies in virtual ecology, and then goes on to describe an issue that agent-based models can address with a virtual-ecology approach: the calculation of metrics from telemetry data. Finally, section 2.4 details the rise of human-induced rapid environmental change, and highlights the role of agent-based models in conservation. The chapter concludes by defining the overall aims of the thesis to address specific aspects of these themes in the context of current knowledge gaps.

1.1 Agent-based modelling in ecology

Population models aid researchers in understanding how ecological systems react and adapt to Human-Induced Rapid Environmental Change (HIREC; Evans et al., 2013a; Sih et al., 2016). Such models complement empirical data by highlighting data gaps, generating hypotheses, and predicting alternative futures (Soetaert and Herman, 2008).

1.1.1 What is a model?

Ecological systems are often difficult to control and replicate due to both their innate stochasticity (Hillborn and Mangel, 1997) and large spatial-temporal scales (Hilborn and Mangel, 1997). Connectivity studies, which often study movement corridors for large mammalian species, are normally concerned with the large-scale movements of threatened species that we know little about. Moreover, ethics may limit studies on species threatened with extinction, or on human interactions with ecosystems. As a result of these issues, it may not be feasible to answer the questions we have on ecology using solely empirical studies. Researchers in this field can use models in order to identify hypotheses that can then be tested with empirical methods (Soetaert and Herman, 2008). By calibrating and comparing such models against data, we can discover which of these models best represents reality, referred to as being the ‘best fit’, and which is therefore most likely to provide an accurate representation with which to address the research question. However, it is important to note that, due to their abstract nature, models will always differ from reality in some way (Soetaert and Herman, 2008).

Recent developments in mechanistic, process-based models have incorporated a high level of complexity (Singer et al., 2016; Synes et al., 2016), reflecting a change in mindset from the more simplistic models that were previously favoured (Evans et al., 2014). Evans et al. (2013b) have argued that simpler models often have less predictive power than complex models, and that over-simplified models risk incorrect predictions by ignoring key ecological processes. In comparison, mechanistic models aim for as much of a realistic depiction of individual choices and interactions as possible (Singer et al., 2016). The growing prominence of these more complex models in the literature was termed "next-generation modelling" by Grimm and Berger (2016), who identified their essential elements as structural realism, emergence, and predictions.

1.1.2 Complexity theory

Complex systems are those that exhibit emergent behaviour at the system level as a result of local-level interactions between individual elements (Marques and Pain, 2000; Jacobsen, 2001). Examples of emergent behaviour include bird flocking formations, the collective behaviour of ant colonies, and the global behaviour of markets (Resnick, 1994). Such complex systems are viewed as being more than "the sum of their parts" (Grimm et al., 2005), and one can rarely predict how their emergent, sometimes unintuitive, behaviour arises from their simple components, with such macro-level behaviour often being the result of positive feedback mechanisms, randomness, and critical thresholds (Resnick, 1994). Indeed, as the system is a product of both components and interactions, and as these are dynamic and changing through time, it is difficult – if not impossible – to reduce them to a set of simple analytical equations (Grimm et al., 2005). It has also been suggested that the emergent behaviour of complex systems is the opposite of chaos, as macro-level order emerges from disorder at the local-level (Farmer and Packard, 1986).

Another important characteristic of complex systems is that they are self-organised. In bird flocks, for example, there is no central "leader" that organizes the flock, in the same way that there is no lead ant who administrates the complex bridge-building of foraging workers.

Instead, the flock and the bridges created by these animals are macro-level dynamics that occur without deliberate management, and without a driving environmental “seed” (Todd, 1994; Marques and Pain, 2000). This lack of a central organisational force is why such systems are often described as being “decentralised” (Resnick, 1994).

1.1.3 Agent-based models

Agent-based models (ABMs), also called individual-based models (IBMs; DeAngelis and Grimm, 2014), are mechanistic models that represent a population of individuals as a set of agents, allowing system-level behaviour to emerge from individual variability, adaptation, and local-level interactions with other agents (Bonabeau et al., 2003; Grimm et al., 2006). These properties are significant for the behaviour of real-world systems, but are usually overlooked in analytical studies that assume all individuals are identical and do not change (Grimm et al., 2006).

Another feature of ABMs that is particularly pertinent to ecological simulation is that they can represent complicated life cycles. In contrast, analytical models tend to assume a very simplified life cycle, which has severe implications for the model’s ability to correctly simulate the study population (Uchmanski and Grimm, 1996).

ABMs are appropriate for investigating decentralised complex systems, such as those encountered in ecology. By modelling individual-level rules rather than attempting to impose the system-level behaviour as a central controller, the system-level behaviour that results from the decisions and interactions of individual agents constitutes an emergent phenomenon. The inherent flexibility of ABMs allows users to investigate any system where individual-level rules are thought to result in system-level behaviour, with their mechanistic focus allowing predictions about how systems will react to change (Evans et al., 2013a; Stillman et al., 2015; Singer et al., 2016). Hence, ABMs incorporate all three essential elements of next-generation modelling.

Due to the above, ABMs have been adopted by a myriad of academic disciplines, and have become particularly commonplace in the field of ecology (Grimm et al., 2005). Ecology-based ABMs have been used to explore a wide range of topics, such as flocking behaviour (Reynolds, 1978), re-introduction of species (Gusset et al., 2009; Kramer-Schadt et al., 2004; Bar-David et al., 2008), dispersal (Palmer et al., 2011; Graf et al., 2007; Gustafson and Gardener, 1996; Gardner and Gustafson, 2004; Imong et al., 2014), foraging (Sibly et al., 2013; Turner et al., 1993), identification of animal corridors (Dickson et al., 2005; Watkins et al., 2015; Pe'er et al., 2005; Nabe-Nielsen et al., 2010; Kanagaraj et al., 2013), and ecological risk assessments for various species (Matsinos et al., 1994; Wiegand et al., 1998).

As the use of ABMs in ecology has increased, researchers have developed a number of specific methods and toolsets for developing them, such as "evaludation" (Augusiak et al., 2014) and TRACE (Grimm et al., 2014). One notable example is the Overview, Design Concepts, and Development (ODD) procedure presented by Grimm et al., (2006). This is a formalised and structured description of ABMs that aims to provide a standard practice framework in which to design and develop models. The method of pattern-oriented modelling has also been put forward as a way of aiding in model design and calibration when creating models based on real-world patterns (Grimm et al., 2005; Grimm and Railsback, 2012). In a similar vein, Van der Vaart et al. (2015) used Approximate Bayesian Computation (ABC; Hartig et al., 2012) in order to aid the parameterisation and validation of models.

1.1.4 Examples of ABMs in Ecology

A stochastic movement simulation (SMS) is a class of individual-based model developed by Palmer et al. (2011). This model is similar to a least-cost path model, in that the environment comprises a grid of squares, with a cost value associated with each square. These models do not assume that individuals have complete knowledge of the study area, and individuals have two parameters: a direction bias and a perceptual range. The direction bias allows individuals to follow roughly the same heading, unless a very high cost square interferes with this, with the strength of this bias dictating the preference for staying on the same path. The perceptual range is the range of squares that the individual can assess around them. It should be noted that a perceptual range that includes the whole map would result in similar findings to a least-cost path model. In reality, most individuals would have a relatively small perceptual range, therefore SMS may provide a more accurate approximation of preferred corridors.

Aben et al. (2014) used an SMS model to predict movement behaviour of two species of forest bird within a tropical matrix, and evaluated this using telemetry data. They found that the model was able to predict bird movement behaviour relatively accurately. However, SMS models are simple models, based on two parameters and a cost surface, and although this solves some of the problems associated with least-cost path models, it still constitutes a very simplified representation of reality. Although they can accommodate for inter-individual variation and stochasicity, one can only represent inter-specific interactions as a static characteristic of a grid square. This ignores the spatially-explicit and dynamic nature of the interactions in real ecosystems.

HexSim is a spatially-explicit individual-based model that uses a grid of hexagonal cells (Schumaker et al., 2014). It derives from the PATCH model (Schumaker, 1998), which appear in over 30 publications (Stronen et al., 2012). HexSim allows individuals to create territories (Schumaker et al., 2014). These territories consist of a selection of cells, the quantity and choice of which depends on the characteristics of that cell in terms of resources and suitability. Individuals within a territory may reproduce. Offspring disperse a certain distance of cells. Floaters, those who were unable to form a territory in their patch, may also disperse. HexSim is useful for modelling the dispersal of individuals who must have a territory to breed. HexSim can take survival, reproduction, movement, resource acquisition, and species interactions into account (Schumaker et al., 2014). However, as territories are static once formed, it may not be as useful for species whose home ranges change over time. In addition, it does not consider the effect of home-range-level movement of resident individuals on dispersing individuals.

FunCon is a spatially-explicit individual-based model that differentiates between different types of movement (dispersal and short-range movements within home-range), different methods of moving through matrix (random walk or gap crossing), and different reactions to the presence of habitat edges (Pe’er et al., 2011). Pe’er et al. (2011) showed that considering these differences influenced the results of their study, as did the choice of connectivity measure. However, it is notable that this model does not consider population dynamics, demographic processes, or the effect of local interactions. Furthermore, although it did account for different methods of movement, the movement type given a particular parameter was predisposed rather than emerging from individual-level rules, such as requirement for food or mates.

The final example of a spatially-explicit IBM is J-walk. This model simulates animal dispersal in relation to landscape heterogeneity, amount of prey, predation risk, and energy requirements (Gardner and Gustafson, 2004). As with previous models, it runs on a grid-based platform. The movement algorithm has four steps: defining the direction of movement, calculating a random angle that curves the direction of movement, calculation of probability of moving into a neighbouring cell from habitat characteristics, and a random choice of movement based on those probabilities (Gardner and Gustafson, 2004). The movement decision rule, energy reserves of an individual at that point in time, and surrounding habitat types shape the movement of that individual. This is a complex model that considers metabolic requirements of individuals, as well as the risk of predation. However, land cover type defines the amount of prey, and although Gardner and Gustfason (2004) outlined six different rules for predation in their J-walk model, these interactions were also homogeneous over certain land cover types.

1.2 Optimisation and parameterisation of agent-based models

1.2.1 Choice of model resolution for spatially-explicit ABMs

Spatially-explicit agent-based models are particularly useful for evaluating how a species of conservation concern will respond to alternative management options. They typically base agents on a real population of animals that react to real-world environments rather than hypothetical or ideal environments. Environmental data generally comes from GIS or remote sensing, including altitude, categories of land cover, or distance to relevant features.

Optimizing the resolution of spatially explicit models, which is determined by the choice of grain size, remains an outstanding issue, with broad scale patterns of animal behaviour perhaps suiting a coarse resolution across a large area (Nezer et al., 2017). Kramer-Schadt et al. (2004), for example, used a grain size of 1×1 km to investigate the spread and dispersal of lynx across the entirety of Germany. In contrast, fine-scale movement decisions of individuals in a local area would suit a finer resolution. High resolution models allow us to examine how individuals interact with small or thin features, such as watering holes, river systems, or trail networks (Nezer et al., 2017). Fine-scale movement decisions determine how resident individuals move around their home range, and the movement paths of dispersing individuals. Even for long-distance dispersal, an individual’s path through the environment depends on fine-scale movement choices (Ahearn et al., 2017). Features that do not appear on coarser-resolution maps may form barriers to movement, resulting in real-world behaviour not predicted by coarse-grain maps (Nezer et al., 2017). Trail networks or river systems can enhance mobility or funnel individuals in particular directions (Latham et al., 2011; Whittington et al., 2011; Abrahms et al., 2015). Accurate evaluations of conservation initiatives require understanding how fine-scale features affect movement decisions. High-resolution models can complement coarser-grain models by providing insight on area-specific movement patterns. Coarse-grain models can then incorporate results from high-resolution movement models to build the full picture across a larger area.

We conducted a mini-review in order to determine the resolutions of agent-based or individual-based models of large-bodied carnivore movement behaviour. We limited the search to the genus *Panthera*, pumas, wolves, and bears. The search criteria yielded 116 returns on Web of Science. We narrowed these returns down to 15 studies that applied an agent-based or individual-based model of large-bodied carnivore movement behaviour to a named area. Of these, the average cell size was 1206 × 1206 m, ranging from 100 × 100 m to 10 × 10 km. None of these models had sufficient resolution to consider influences of fine-scale features such as trails or river systems, despite evidence that they do shape movement behaviours (Harmsen et al., 2009).

1.2.2 Parameterisation of spatially-explicit ABMs

Using empirical data to parameterise spatial mechanistic models increases the model's credibility in predicting responses to experimental scenarios, such as the response of a large mammal to increased deforestation. Pattern-oriented modelling uses real-world patterns to create and parameterise models with the aim of accurately replicating real-world patterns, and therefore aid in model design and calibration (Grimm et al., 2005; Grimm and Railsback, 2012). Approximate Bayesian Computation (ABC; Hartig et al., 2012) can facilitate the parameterisation of complex models (Van der Vaart et al., 2015). To parameterise models using ABC, researchers run the model with a large number of different sets of parameter values, and then isolate the set, or sets, of parameter values that best fit empirical data. For both of these techniques, the emphasis is on parameterising and building models that fit empirical data so as to increase the credibility of results from future studies that use the model.

Ground-truthing of movement algorithms requires spatial data from empirical studies. For example, Watkins et al. (2015) used results from empirical camera-trap studies to validate their movement model. To our knowledge, this study represents the only validation of a fine-scale ecological mechanistic model of mammalian movement against empirical data. Nevertheless, as we move into an era of next-generation modelling, it is likely that an increasing number of researchers will follow the example of Watkins et al. (2015) by attempting to ground-truth their movement models against spatial empirical data. These data may include summary statistics from radiotelemetry, occupancy, and camera-trap studies, all comprising observations taken at particular points in time and space. If we replicate these studies using a grid-based model, each of these points become the size of an individual cell. As an example, in a model with a spatial resolution of 100 × 100 m, each camera trap would cover an area of 100 × 100 m. Thus, summary statistics of virtual spatial studies may depend on the initial choice of spatial resolution. If we use these summary statistics as spatial patterns to parameterise and validate the spatial components of our model, our choice of movement algorithm may also depend on our initial choice of resolution. An argument for the use of complex mechanistic models is that their focus on mechanisms and processes allow them to exhibit greater predictability, as an agent's reaction to a situation is the result of behavioural algorithms. However, if the choice of algorithm depends on the choice of resolution, it calls into question the ability of the model to reflect reality as opposed to providing merely a reasonable fit to current data at a certain resolution. This may result in the introduction of conflicting models for the same species producing different answers to the same question, which would only serve to confuse the issues that such models are intended to inform, as well as reducing credibility in spatial models. Alternatively, researchers may decide to use best-fit parameter values or sensitivity analysis to draw conclusions about animal behaviour, as in Imron et al. (2012). However, if the choice of parameter values depends on the resolution of the model, inferences about animal behaviour based on those parameters will also depend on model resolution. Both modellers and empiricists require a greater understanding of how choice of resolution can affect the parameterisation process in order to draw appropriate conclusions from model outputs and identify potential sources of bias.

1.2.3 Conclusions

Mechanistic ABMs represent individuals as a set of interacting agents and allow real-world patterns to emerge from those interactions. Their predictive ability means that they will prove to be particularly important in analysing the impact of HIREC. Spatially-explicit ABMs are useful for evaluating the effectiveness of spatial conservation measures, such as wildlife corridors, and recent models use spatial data to parameterise mechanistic movement models.

As we move into a new generation of modelling, it is likely that more researchers will follow this example. However, parameterisation using spatial metrics may depend on the choice of resolution for the model. If so, spatial models may create a biased picture of animal behaviour, with low predictive power. We believe it is imperative to evaluate potential biases that may arise from parameterisation of mechanistic model using spatial metrics. In chapter 2, we investigate how initial choice of resolution affects parameterisation of spatially-explicit models.

1.3 Virtual ecology for developing empirical methodology

1.3.1 Virtual ecology

Virtual ecology uses simulation models to replicate empirical studies in-silico (Zurell et al., 2010). As experiments are conducted in a model with a known population, one can compare the result of the in-silico study with real-world data, thereby evaluating the effectiveness of this approach. Zurell et al (2010) list the two main applications of virtual ecology as 1) testing and improving sampling schemes and methods, and 2) testing and comparing models. Researchers have used virtual ecology in order to evaluate the conceptualisation and implementation of species distribution models (Miller, 2014), assess sampling designs (Albert et al, 2010; Ficetola et al., 2014; Lyashevska et al., 2016), and create risk maps where species-specific data are scarce (Osawa et al., 2016). Rodrigues and Coelho (2016) used simulated data in order to determine whether different capture methods were able to accurately capture male:female ratios. They found that differences in movement patterns and detectability between males and females resulted in biased sex ratio estimates.

Agent-based models treat populations as a collection of individuals that are driven by bottom-level rules. These basal individual-level rules and simple interactions then result in the kind of complex system-level behaviour discussed above. Furthermore, they represent a new method of modelling populations of species that we can use to compare density estimators, without relying on the same assumptions of those estimators. Due to the flexibility of agent-based models, we can capture heterogeneous home range size and shape, and movement patterns that differ from those assumed. By calibrating these models against empirical data, we can verify that the movement rules are representative of the species in question, and then use the modelled population to assess the effectiveness of telemetry study design and estimators. The complexity that one can include in these models may enable an assessment with a more realistic set of simulated data.

In the next section, we discuss two ecological metrics that we will evaluate using virtual ecology: step length for estimating animal movement, and minimum convex polygon for estimating home-range size.

1.3.2 Calculation of spatial metrics from telemetry data

1.3.2.1 Telemetry

Animal movement behaviours have been a key area of research in conservation biology for over 20 years (DeMars et al., 2013). Descriptions of animal movement can contribute to understanding how species utilise fragmented habitats and how they perceive risk (Morris, 2003). Patterns of movement determine the distribution of species, the transmission of disease, routes for animal migration, and responses to anthropogenic actions (Bradshaw et al., 2007; Beyer et al., 2013; Hosseini et al., 2006; Morris, 2003). Analyses of such patterns may augment our understanding of metapopulation dynamics, species persistence, and the effect of conservation measures (Schooley and Wiens, 2004; Loarie et al., 2009; Pittman et al., 2014; Jenks et al., 2015). Hence, conservation biologists may use knowledge of animal movement to develop effective strategies for conservation (Jenks et al., 2015).

Telemetry data allow researchers to understand movement by capturing individuals in space and time, and constitutes an active area of research (Kays et al., 2011; Ward and Raim, 2011). Researchers may use telemetry datasets to quantify metrics of movement at a variety of different scales, thereby identifying mechanisms such as scale-dependent foraging decisions and optimal searching behaviour (Bradshaw et al., 2007). Sources of telemetry data include: VHF radiotelemetry tags; fixed-position PIT tag detection arrays (Tew and MacDonald, 1994; Armstrong et al., 1996; Lucas et al., 1999), which use close-range proximity detection to detect locations (Harbicht et al., 2017); acoustic telemetry transmitters; and Global Positioning System (GPS) telemetry tags, which use satellites to obtain location data (Dana, 1989).

Studies on telemetry conventionally use Very High Frequency (VHF) radio-telemetry to provide location data. Radio antennae in fixed positions receive VHF signals and record the locations of tagged individuals (Harbicht et al., 2017). Modern amendments to VHF tags have made them smaller and cheaper than GPS tags (Harbicht et al., 2017). Nevertheless, conventional telemetry depends on factors such as personnel availability, field accessibility, light conditions, and local weather (Dussault et al., 2001).

Global Positioning System (GPS) was introduced by the U.S. Department of Defense as a satellite-based radio-navigation system (Dana, 1989). GPS trackers receive signals from at least three satellites and, by calculating the time taken for the signal to reach the sensor, computes latitude and longitude for that position (Bradshaw et al., 2007). Signals coming from three satellites allow for the computation of a 2D location, whereas signals from four satellites can determine the sensor's location in 3D space (Dana, 1989). The main advantage of GPS over VHF is that it can automate tracking and provide consistent, intense sampling for one radio-collar. In this manner, GPS technology has allowed researchers to collect a high abundance of accurate, fine-scale data on animal movement (Mills et al., 2006; Kie et al., 2010; Tomkiewicz et al., 2010). GPS is unaffected by weather conditions, which improves on traditional VHF radiotelemetry technology (Girard et al., 2002), although GPS tags are more expensive, which limits the number of individuals that the study can track (Otis and White, 1999; Harbricht et al., 2017).

Researchers have used telemetry data in order to develop their understanding in a number of areas, including studies on how animals respond to barriers on movement (Riley et al., 2006; Shepard et al., 2008), density estimation (for example, Soisalo and Cavalcanti, 2006), development of resource selection functions (for example, Johnson et al., 2004), and predator-prey relationships (Sevodkin et al., 2017). Munro et al. (2006), for example, used radio-telemetry data to understand seasonal food habits and activity patterns for grizzly bears in Canada. Hopcraft et al. (2016) used a long-term telemetry study to examine how hunting opportunities determine the distribution of lions in the Serengeti.

Although, data from telemetry studies have many uses, study design and data interpretation require considerable care. When designing telemetry studies, researchers must address a trade-off between the intensity of the sampling regime and the duration of the study (Kolodzinski et al., 2010). As the time interval between fixes on locations - hereafter referred to as the "fix interval" – increases, the study misses more intervening locations. This can lead to errors in calculations of space-use metrics. Multiple studies have found that long fix intervals underestimate both the distance travelled and the home-range area, as they miss tortuous movement and extreme points (Otis and White, 1999; Mills et al., 2006; Kolodzinksi et al., 2010). As an example, Kolodzinski et al. (2010) found that calculations of the minimum convex polygon (MCP) encompassing locations from telemetry with fix intervals of eight to twelve hours underestimated homes range by at least 50%. Furthermore, telemetry devices suffer from type II errors. In some cases, the success rate of fixes can be as low as 13% (Frair et al., 2004). This would change a sampling regime that takes location fixes every 2 hours to one that only samples locations every 16 hours, with implications for the accuracy of metrics.

1.3.2.2 Examples of spatial metrics calculated from telemetry data

Step length is the distance covered by a tagged individual between telemetry fixes. We can use it to calculate other metrics, such as cumulative distance covered over a study period and the average speed of individuals. Many movement models use step length and turning angles as parameters to simulate individual movement (Turchin, 1998). Telemetry provides the data to parameterise these models, which researchers may then use to draw conclusions about animal movement (Jerde and Visscher, 2005; Beyer et al., 2013; DeMars et al., 2013). Researchers have used step length in autocorrelation functions in order to investigate movement patterns (Boyce et al., 2010). As an example, Jenks et al. (2015) used autocorrelation functions and cluster analysis in order to compare the movement of a golden jackal and a dhole. Thus, it is important that researchers can obtain accurate estimates of step length so as to reduce bias in models used at later levels of abstraction.

The home range of an animal is the area that an individual uses regularly during quotidian activities such as foraging or hunting (Burt, 1943). Knowledge of the size of home ranges informs the construction of conservation measures by allowing the estimation of space required for that conservation measure to be successful. Telemetry data are often used to determine home range size and boundary (Otis and White, 1999). Calculations of home range using telemetry data commonly use either kernel analyses or minimum convex polygon (MCP) (Kolodzinski et al., 2010), both of which depend on the sampling regime used to collect telemetry data, with the latter being more sensitive than the former to the intensity of the sampling regime (Kolodzinski et al., 2010). As stakeholders use home range to indicate how much habitat a species requires, it is imperative that estimates are accurate, or at least that managers have a clear understanding of the strength and direction of potential bias.

1.3.3 Conclusions

Researchers can use empirical or simulated data to assess the effectiveness of study designs. Simulated data have the advantage of comparing a known “truth” against the results of simulated studies. This is the virtual ecologist approach. We suggest using a high-resolution mechanistic model that incorporates movement decisions in order to evaluate the accuracy of calculations for step length and MCP from telemetry data. These methodologies have caveats and trade-offs that warrant further investigation. ABMs have particular potential in virtual ecology as they model the behaviour of agents based on simple rules and allow patterns to emerge. In chapter 3, we use an ABM to define the relationship between fix interval and error using known values for step length and MCP. We can use this definition to develop a methodology for correcting biases in step length and MCP calculation.

1.4 Mechanistic models in conservation

At the turn of the millennium, extinction rates were between 1000 – 10,000 times the background rate (Rosser and Mainka, 2002), and this is likely to get worse, with many future scenarios projecting further high rates of extinction and habitat loss during the course of this century (Secretariat of the Convention on Biological Diversity, 2010). There exists great uncertainty concerning both the total number of species on Earth and extinction rates (Monastersky, 2014). Current extinction rate estimates, representative percentages of the proportion of species becoming extinct per annum, range from 0.01 – 0.7% (Monastersky, 2014). At the higher end of this estimate, a sixth mass extinction of species, an event categorised by the loss of 75% of species on Earth, could occur by 2200 (Monastersky, 2014). Such an event is likely to be exacerbated due to a phenomenon known as co-extinction, or extinction cascades, whereby the interactions between species mean that when one species is lost, others that depend on its existence may also become extinct (Dunn et al., 2009). Furthermore, the ‘ecosystem services’ that are provided by wildlife and which can be beneficial to humans, such as pollination and coastal protection, may disappear as biodiversity decreases globally (Mace et al., 2012; Worm et al., 2006).

Butchart et al. (2010) used 31 indicators to assess the progress towards international biodiversity conservation targets set for 2010. Although there were some successes locally, they found that biodiversity generally decreased, with various pressures that contribute to biodiversity loss increasing over the past four decades. The Convention of Biological Diversity (CBD) laid out the Aichi Biodiversity Targets for 2020, which are a set of twenty targets, divided into five strategic goals, the main focus of which is on the conservation of biodiversity and ecosystem services and the promotion of sustainable living. In 2014, the CBD released the Global Biodiversity Outlook 4, which assessed the progress of the 2020 targets. Although the response to biodiversity loss has increased notably, the pressures on biodiversity are still worsening, and in general the targets are unlikely to be met by 2020 (Secretariat of the Convention on Biological Diversity, 2014; Tittensor et al., 2014).

As human populations continue to grow in density and in economic development, ecological systems experience increasing pressure from human-induced rapid environmental change (HIREC; Fahrig, 2003; Parmesan, 2006; Sih, 2013). The projection of a potential sixth mass extinction (Monastersky, 2014), combined with a growing knowledge of the benefits that humans gain from biodiversity (Mace et al., 2012), means that conservation actions to protect the world's most vulnerable species are increasingly important.

Agent-based models use agent-level rules to simulate the emergence of population dynamics. They have the potential to offer insights into conservation actions and strategies where empirical experiments are impossible or unethical. These kind of population models help scientists to understand how ecological systems react and adapt to HIREC (Evans et al., 2013a; Sih et al., 2016). They complement empirical data by highlighting data gaps, generating hypotheses, and predicting alternative futures.

Spatially explicit mechanistic models are particularly useful for evaluating how a species of conservation concern will respond to alternative management options. They typically structure the agents on real animals in populations that react to real-world environments rather than hypothetical or idealized environments (DeAngelis and Yurek, 2017). For example, the spatially-explicit population model of Watkins et al. (2015) was designed to simulate jaguar movements across the Central Belize Corridor, connecting the

Selva Maya forest block in the north of Belize to the Mayan Mountain forest block in the south (Figueroa, 2013). They found that jaguars in protected areas had higher fitness in terms of fecundity, energy reserves, age and life expectancy than those outside the reserves.

Population models of such species are of particular importance due to both the role of apex predators in ecosystem regulation and maintenance (Kelly, 2003; Watkins et al., 2015) and the way in which HIREC has led to a global decrease in range for the majority of large carnivores (Parmesan, 2006; Sih, 2013; Wolf and Ripple, 2017). Indeed, 77% of predators with a body mass greater than 15 kg are suffering population declines, and 61% have an IUCN status of either vulnerable, endangered, or critically endangered. (Ripple et al., 2014). Important factors in the vulnerability of large predators to HIREC include their large body size, low densities, and large home ranges (Cardillo et al., 2004; Marshall et al., 2015). The decrease in large-bodied predators has led to the global disruption and degreadation of ecosystems and processes (Estes et al., 2011; Ripple et al., 2014). These declines could even impact local cultures, due to the way in which large predators have cultural significance as important symbols in cultures worldwide (Di Minin et al., 2016).

The next three sub-sections will focus on three threats of particular concern to predator conservation: deforestation, wildmeat hunting, and direct persecution in response to livestock depredation. Chapter 5 will involve developing a model to evaluate their interacting effects.

1.4.1 Deforestation

Anthropogenic land-use change is one of the drivers of biodiversity loss. Many predict that land-use change will have the biggest effect on biodiversity this century, with climate change and nitrogen deposition also having large effects (Sala et al., 2000). Humans have converted 40-50% of the global ice-free land surface into agricultural or urban terrain (Chapin et al., 2000). Activities associated with agriculture may be responsible for 70% of projected biodiversity loss in terrestrial taxa (Secretariat of the Convention on Biological Diversity, 2014). The resultant habitat loss and fragmentation, the change of configuration of a landscape, are major drivers of biodiversity loss (McGarigal and Cushman, 2002; Fahrig, 2003).

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The effects of fragmentation include reduced gene flow between populations, which may then lead to a decrease in effective population size and lower adaptive fitness due to factors such as inbreeding (MacArthur and Wilson, 1967; Soulé and Mills, 1998). This isolation of populations accompanies other effects of fragmentation, such as edge effects, invasions and increased anthropogenic use of the forest due to better access (Marsh, 2003), which may interact with other threats to species, including over-exploitation of ecosystems, and fires (Laurance et al., 2002). The extent and character of these effects are not uniform, and vary by organism, as well as by habitat type and environment (Haila, 2002). Furthermore, studies have been known to confound fragmentation and habitat loss. Fahrig (2003), for example, found that habitat loss had more of an impact on biodiversity than fragmentation when decoupled from each other.

Land-use change is associated with massive deforestation, and anthropogenic land-use change or natural causes destroyed around 130,000 km^2 of forest between the years 2000 and 2010, with South America and Africa suffering the largest net loss of forest habitat (Secretariat of the Convention on Biological Diversity, 2010). A study on deforestation in the Amazon, conducted over three decades, found that up to 1,200 km^2 of conservation land were logged per year (Asner et al., 2005). Although good logging practices reduce both environmental damage and costs, destructive and illegal logging is still very common in the tropics (Putz et al., 2000), resulting in habitat loss and fragmentation. Indeed, illegal logging, drug trafficking and agricultural development represent the main causes of high deforestation rates in Mesoamerica (Wultsch et al., 2016). Although some predators are able to inhabit unprotected areas (Boron et al., 2016), contact with agricultural areas increases the risk of livestock depredation and persecution as pests. These issues have a significant impact upon large-bodied mammals, which often have large home ranges. Female jaguars, for example, have been estimated to require patches of at least 180 km^2 of primary forest to meet their space requirements (de la Torre et al., 2017). Such species therefore often find themselves in competition with humans for space and food, as well as being victims of human encroachment (Urquiza-Haas et al., 2009).

A metapopulation is a set of populations connected by gene flow. The rescue effect hypothesis proposes that immigration between these populations may reduce the probability of extinction of individual populations, and allow re-establishment of locally extinct populations (Gonzalez et al., 1998; Tewksbury et al., 2002). A lack of gene flow between populations can lead to extinction risk as a result of inbreeding and local stochasticity, especially when these isolated populations are small (Swift and Hannon, 2010). The viability of a metapopulation does not depend on habitat loss alone, but also on the spatial distribution of habitat (Ewers and Didham, 2006). As an example, Coulon et al. (2004) found that roe deer tended to stick to areas of woodland during dispersal, which meant that habitat connectivity strongly affected the gene flow between populations.

Corridors, in the context of habitat fragmentation, are sections of habitat that connect separate patches (Tewksbury et al., 2002). The advantages and disadvantages of man-made wildlife corridors are summarized in Table 1, below.

Table 1. The advantages and disadvantages of man-made wildlife corridors for use in increasing habitat connectivity.

Advantages	**Disadvantages**
Corridors may improve genetic diversity (Petracca et al., 2013).	The structural design of corridors may have important effects on their effectiveness (Sieving et al., 2000).
Corridors may allow the re-colonisation of extinct populations in the metapopulation by the “rescue effect” (e.g., Gonzalez et al., 1998).	Corridors may aid the spread of disease, invasive species and environmental disturbances, such as wildfires (Simberloff and Cox, 1987).
Corridors may facilitate large-scale migrations in the wake of climate change (Ewers and Didham, 2006).	It may be more economically viable to use alternative conservation measures, such as moving species manually between habitat fragments (Simberloff and Cox, 1987) or simply increasing amount of protected area.
Corridors may benefit associated plant species through increased pollination and seed dispersal (e.g., Tewkesbury et al., 2002).	Corridors are logistically-complicated long-term projects, requiring negotiation with stakeholders and substantial funding (Salom-Pérez et al., 2010).

Beier and Noss (1998) assessed previous studies on corridors and found that none of them had properly investigated the benefits of corridors correctly, with many lacking proper experimental procedures. This meant that many corridors set up before and during this period in time were created without any adequate scientific consensus, and based on pure intuition (Tewksbury et al., 2002; Gilbert-Norton et al., 2010). However, recent studies have managed to effectively assess the benefits and design flaws of corridors, allowing construction with proper scientific backing (Gilbert-Norton et al., 2010). It should be noted, nevertheless, that Beier and Noss (1998) emphasised that the few reliable studies they did find pointed towards a positive effect of corridors, rather than neutral or detrimental effects.

1.4.2 Wildmeat hunting

The world is suffering a wildmeat crisis (Ripple et al., 2016), which has already led to multiple extinctions (Fa et al., 2002; Milner-Gulland and Bennett, 2003; Darimon et al., 2015). Wildmeat (often referred to as 'bushmeat' on the African continent), is animal protein obtained by hunting wild species. In the past few decades, the consumption of wildmeat has increased (Milner-Gulland and Bennett, 2003). Land-use change (LUC), the construction of roads, commercialisation of hunting and the technological advance in hunting weapon technology have all led to the increase in wildmeat hunting (Peres, 2000; Wilkie et al., 2000; Milner-Gulland and Bennet, 2003; Wolfe et al., 2005). Wildmeat can contribute a significant portion of protein to the diet of people in the tropics (Bennett and Robinson, 2000; Peres, 2000). In addition to subsistence, wildmeat can provide a role in household income (Beier and Noss, 1998; Wilkie and Carpenter, 1999; de Merode et al., 2004).

The hunting of wild species, whether for subsistence or commercial uses, is sometimes a more significant cause of biodiversity loss than deforestation (Redford 1992). Indeed, hunting has been responsible for the extinction of 12 species of vertebrate in Vietnam over the past five decades (Bennet and Rao, 2002). The result of these local and global extinctions is the presence of "empty forests" or "half-empty forests", where there are no outward signs of ecosystem destruction but where defaunation from hunting has left the forest devoid of large vertebrates (Redford and Feinsinger, 2001). Most target species are large, K-selected mammals, whose low reproductive rates cause them to be more susceptible to hunting than smaller r-selected species (Mangel et al., 1996; Peres and Palacios, 2007).

Hunting interacts with deforestation and fragmentation to further impact large-bodied animals, as larger species are often the first targets for wildmeat hunters (Ripple et al., 2014; Ripple et al., 2015). Population declines in large birds and mammals can impact species at other trophic levels through trophic cascades, disrupting entire communities (Peres, 2000; Andresen and Laurance, 2007; Stoner et al., 2007).

Wildmeat hunting in Latin America is less frequent than in the already heavily defaunated continents of Africa and Asia (Fa and Peres, 2001). Nevertheless, estimates of wildmeat hunting in the Brazilian Amazonia reach 165, 000 tons a year (Peres, 2000). In numbers of individual animals, this may equate to 23.5 million from multiple taxa (Peres and Palacios, 2007). Although the extent and current consequences of wildmeat hunting in the Amazon may not be as great as those in Africa, it appears that the wildmeat crisis extends to the Neotropics and its people.

Wildmeat consumption puts apex predators in competition with humans. In Belize, for example, 7% of protein-containing meals include meat from one of six wild species (Foster et al. 2016). These species are the nine-banded armadillo, paca, collared peccary, white-lipped peccary, red brocket deer and white-tailed deer, species that make up large proportions of the diets of jaguars and pumas in Belize (Foster et al. 2016). Hence, humans are in competition with these large felids, with implications for jaguar and puma abundance, and predation by these species on livestock.

1.4.3 Direct persecution of jaguars

Livestock frequently appear in the diets of in big cats across the globe (Ghouddousi et al., 2016; Babrgir et al., 2017). Local farmers may opt to poison or shoot big cats in order to protect their livestock (Trinkel et al., 2016). In some areas, direct persecution may represent a large proportion of felid mortalities. For example, Trinkel et al. (2016) found that within their study period human-wildlife conflict caused almost 50% of lion mortalities on the border of Etosha National Park. Subadult males and adult females represented the majority of persecuted individuals, and this had second-order effects on the population structure of lion prides (Trinkel et al., 2016). Moreover, Tortato et al. (2017) suggest that depredation of large livestock may lead to a greater risk of infanticide due to attraction of multiple individuals to a carcass, including females with cubs.

Predators may rely on livestock as a food source where stocks of wild ungulates are low (Meriggi and Lovari, 1996; Dahle et al., 1998). The findings of Newsome et al. (2016), for example, indicated that wolves in Europe may change their diet in response to populations of wild prey. Hence, low populations of wild prey may contribute to the depredation of livestock (Khorozyan et al., 2015). Nevertheless, livestock present easy targets for wild predators as the process of domestication has left them without natural behaviours and agility (Linnell et al., 1999).

Livestock losses due to big cat depredation affect small economies and livelihoods (Inskip and Zimmerman, 2009). As a result, large carnivores are often viewed as pests by local people (Babrgir et al., 2017). Attitudes towards large carnivores may depend on level of education and knowledge of predators (Mkonyi et al., 2017). A study on Persian leopard depredation found that 80% of survey respondents in northern Iran considered leopards a pest and 45% supported either legal hunting or culling of the Persian leopard population. Public perception and the media may often drive precautionary lethal control of populations (Fernández-Gil et al., 2016). For example, Fernández-Gil et al. (2016) found no correlation between coverage in the media of damages caused by wolves and the actual damages. However, coverage in the media correlated with the level of culling. Thus, although media coverage was unrelated to actual damages, it impacted the perception of stakeholders and determined measure of control. Furthermore, stakeholders may persecute one species or individual for the actions of another, despite the ineffectiveness of this lethal measure (Knowlton et al., 1999).

Entities involved in lethal control include governments, agencies, or individual stakeholders (Wirsing and Ripple, 2010). Nevertheless, the persecution of apex predators has raised ethical concerns, given the ecological impact of the removal of large-bodied species and the questionable effectiveness of lethal methods (Vucetich and Nelson, 2014; Eklund et al., 2017). Poudyal et al. (2016) found that that the number of sheep killed increased by 2.2% for each wolf killed, indicating that lethal control of wolves may have undesirable effects. Black bears, pumas and wolves have also shown unexpected reactions to lethal control (Treves et al., 2010; Peebles et al., 2013; Wielgus and Peebles, 2014). Explanations for these effects include source-sink dynamics (Peebles et al., 2013) and social disruption (Borg et al., 2015). Lethal intervention may create gaps in communities, allowing smaller predators to take the place of large predators (Prugh et al., 2009). Moreover, predators may respond in an unintuitive way to lethal control. For example, Knowlton et al. (1999) found that coyotes compensated for reductions in population from persecution by increasing their rate of reproduction.

There are two general non-lethal pathways to combatting direct persecution of felids as pests. The first is to initiate compensation schemes (for example, Bauer et al., 2017), which are motivated by the theory that compensation creates a win-win situation, benefitting all stakeholders (Dickman et al., 2011). However, these are only feasible when funding is both available and sustainable, and although compensation schemes are a frequently used method for reducing human-wildlife conflict (Naughton-Treves et al., 2003; Treves et al., 2009), they may not be effective (Fernández-Gil et al., 2016). Attitudes towards large carnivores may not be linked to depredation events, but to socio-economic factors (Rust et al., 2016; Mkonyi et al., 2017). In some areas, negative perceptions of predators may be linked to personal safety rather than economic factors (for example, Porfirio et al., 2016), and where fear drives negative opinions of predators, compensation schemes are unlikely to prove successful. Moreover, compensation may actually create an incentive not to prevent depredation events (Bauer et al., 2017).

A second pathway is improving animal husbandry. Penning and the use of guard dogs or donkeys can reduce levels of felid depredation (Ghoddousi et al., 2016). Felids may target straggling individuals, hence good veterinary standards may aid in improving herd safety (Ghoddousi et al., 2016). Indeed, Treves et al. (2016) found that non-lethal methods of protection were more effective than lethal methods, in particular the use of guard dogs and ‘fladry’, a visual deterrant to predators. Other non-lethal methods include electric or audio deterrants (Musiani et al., 2003; Shivik et al., 2003). In Miller et al. (2016), husbandry and deterrants proved the most effective measures of control. However, both suffered from high variation, in comparison to lethal control, which although on average less effective, had low variation.

1.4.4 Conclusions

Deforestation, wildmeat hunting, and direct persecution represent three key anthropogenic threats to predators. These three threats also interact with one another, in that deforestation increases the availability of previously inaccessible areas to hunters, a reduction in natural prey may result in an increased rate of livestock depredation, and deforestation puts predators in closer contact with livestock. ABMs are mechanistic, and hence have the potential to model the interactions between factors and predict potential behaviour of animals in response to HIREC, which disproportionately affects apex predators. They may hence provide insights that can augment current conservation research. Despite their promise, none have attempted to utilise an ABM to simulate these interacting effects on the movement of large felids. In chapter 4, we employ an ABM to investigate how interacting effects affect the movement of large felids through a movement corridor.

1.5 Thesis aims

Highly complex, mechanistic models have the potential to contribute to the conservation of species impacted by HIREC. Given the promise of 'next-generation modelling' (Grimm and Berger, 2016) and the increasing availability of high-powered computing tools, we predict that researchers will follow the examples of Watkins et al. (2015) in developing complex, spatially explicit mechanistic models of animal movement and habitat choice in a landscape, in order to augment current knowledge, and provide mechanisms and evidence for predictions.

This thesis presents the development of one such complex, mechanistic model, and its parameterisation using modern techniques. Our main aim is to employ it as an exemplar for evaluating applications and limitations of complex, spatially explicit mechanistic models, in order to provide others with both an inspiration for future work and an understanding of potential biases.

Chapter 2 presents a spatially explicit, fine-grain ABM of jaguar movements within the Cockscomb Basin Wildlife Sanctuary in Belize. The ABM includes gender-specific interactions between jaguar agents and fine-scale features such as trails, river systems and cell-specific slopes in hilly terrain. I calibrate the model using real-world patterns from empirical camera-trap and telemetry data, in accordance with pattern-oriented calibration

(Grimm and Railsback, 2012). In doing so, I reveal a caveat of parameterisation using spatial point data, whereby the selection of best-fit parameter values then depends on the original choice of resolution. The next two chapters demonstrate two different applications of the high-resolution model: (a) to develop and evaluate a new empirical method of measuring animal movement from GPS data, using a virtual ecology approach (Zurell et al., 2016); (b) to evaluate the effects of interacting threats on jaguars in a manmade wildlife corridor.

Chapter 3 uses the model developed in chapter 2 to evaluate the reducing accuracy of spatial metrics derived from telemetry data as fix intervals increase. I use results from the simulation to introduce a method for correcting for bias caused by long fix intervals. I show that the mechanistic model was essential to evaluating and developing this empirical methodology.

Large felids are under threat from deforestation, wildmeat hunting, and direct persecution due to livestock depredation. They require large areas of forest for their home range and, although often able to live in agricultural environments, this puts them into contact with livestock, increasing the risk of livestock depredation. Deforestation enables hunters to have greater access to new hunting grounds. Moreover, depletion of prey may cause jaguars to look for other prey sources, such as livestock. Thus, the anthropogenic impacts interact in a manner that is difficult to quantify in reality due to the presence of other confounding factors. In chapter 4, I employ the high-resolution model I developed in chapter 2 to evaluate the effects of interacting factors (deforestation, wildmeat hunting, and direct persecution) on large-felid movement across a corridor area in Belize. To the best of my knowledge, this represents the first mechanistic model to evaluate the effect of interacting anthropogenic threats on a felid population.

The applications to real-world problems developed in this thesis have demonstrated the utility of complex, mechanistic models in different areas of conservation biology. In chapter 5 I synthesise these results by presenting limitations of the model and outlining potential future work. Although I identify caveats that influence the predictive ability of some spatially-explicit models, I remain hopeful that advancements in computing will overcome some of the current hurdles to creating complex models.

Chapter 2.

Effects of model resolution on fit to empirical data

Ball, A.E, Foster, R.J., Harmsen, B.J., Doncaster, C.P. Author contributions: A.E.B. conceived the original idea, developed and ran the models, designed and executed the analyses, and wrote the chapter; R.J.F. and B.J.H. provided telemetry data and subject matter expertise, and revised later drafts of the manuscript; CPD advised on study design and revised earlier drafts of the manuscript.

Chapter 2. Effects of model resolution

Abstract

Agent-based models allow population-level processes to emerge from individual-level behaviours. They will play a major role in next-generation mechanistic modelling of organismal responses to human-induced rapid environmental change. Choice of resolution remains an outstanding issue for these models. Although fine-grain models can represent fine-scale point and line features, such as trails and rivers, they require large amounts of computing power. More fundamentally, the choice of resolution influences the values of output parameters estimated by the in-silico experiments, which researchers may then use to validate their models or to inform virtual- or field-ecology studies. We developed and validated an agent-based model of fine-scale movement decisions by jaguars (*Panthera onca*), based on camera trap and radio tracking data from a wildlife reserve in Belize. We used the model to investigate the effect of resolution on model outputs from in-silico experiments. All summary statistics depended on resolution. Models with coarser resolutions had double the number of detections by virtual camera-traps and a higher number of virtual captures of individuals than models with finer resolutions, and they overestimated minimum convex polygon sizes of territories. Best-fit parameter values for the models differed when calculated using different resolutions. Thus, the resolution dictated how agents used their home ranges and interacted with one another. We caution against drawing inferences that depend on model resolution, when researchers apply outputs from agent-based models to real scenarios. The dependence of the model on choice of resolution raises questions about the ability of spatially-explicit mechanistic models to truly replicate species behaviour, and hence to predict how species will react to our changing world.

Key words: animal movement; fine-grain; model validation; pattern-oriented modelling; radiotelemetry

2.1 Introduction

As human populations continue to grow in both density and economic development, ecological systems experience increasing pressure from human-induced rapid environmental change (HIREC) (Fahrig, 2003; Parmesan, 2006; Sih, 2013). Deforestation and human encroachment disproportionately impacts large-bodied mammals, which often have large home ranges that bring them into competition with humans for space and food (Urquiza-Haas et al., 2009). Population models help scientists to understand how ecological systems react and adapt to HIREC (Evans et al., 2013a; Sih et al., 2016). They complement empirical data by highlighting data gaps, generating hypotheses, and predicting alternative futures. Recent developments in mechanistic, process-based models have incorporated a high level of complexity (Singer et al., 2016; Synes et al., 2016), reflecting a change in mind-set from the previously favoured simpler models (Evans et al., 2014). Evans et al. (2013b) have argued that simpler models often have less predictive power than complex models, and that over-simplified models risk incorrect predictions by ignoring key ecological processes. In contrast, mechanistic models aim for a realistic depiction of individual choices and interactions (Singer et al., 2016). Grimm and Berger (2016) coined the term "next-generation modelling" in describing the proliferation of these models. In doing so, they identified their essential elements as structural realism, emergence, and predictions. Here, we investigate the issues that modellers may encounter when attempting to parameterise spatially-explicit mechanistic models using empirical data.

Spatially explicit mechanistic models are particularly useful for evaluating how a species of conservation concern will respond to alternative management options. They typically structure the agents on real animals in populations that react to real-world environments rather than hypothetical or idealized environments (DeAngelis and Yurek, 2017). Watkins et al. (2015), for example, modelled a specific jaguar population in Belize in order to assess how different landscape scenarios would affect jaguar movement through a corridor area. Two components of spatially-explicit ecological models are the environment, which modellers most commonly represent using a grid of cells, and the agents, which navigate the grid using a movement algorithm. Examples of algorithms include random correlated walks and diffusion models of movement (Beyer et al., 2013; Bernal-Escobar et al., 2015). The choice of movement algorithm in a spatial model determines how agents respond to their environment, and therefore, how they will respond to experimental scenarios. If stakeholders use the results of the model to inform their decisions, the choice of movement algorithm may impact on the decisions of those stakeholders; and hence on the conservation of a species or ecosystem.

Optimizing the resolution of spatially explicit models remains an outstanding issue for agent-based models (ABMs). The resolution is determined by the choice of grain size, and the optimum size depends on the scenario under consideration. Broad scale patterns of animal behaviour may suit a coarse resolution across a large area (Nezer et al., 2017). Kramer-Schadt et al. (2004), for example, used a grain size of 1×1 km to investigate the spread and dispersal of lynx across Germany. A finer resolution may better suit fine-scale movement decisions of individuals in a local area. High-resolution models allow us to examine how individuals interact with small, thin, or linear features; such as watering holes, habitat boundaries, river systems or trail networks (Nezer et al., 2017). Trail networks or river systems can enhance mobility or funnel individuals in particular directions (Abrahms et al., 2015; Latham et al., 2011; Whittington et al., 2011). The choice of spatial resolution for the model depends either on the question the model wishes to address or on the spatial resolution of available environmental data, which generally come from GIS or remote sensing; including altitude, categories of land cover, or distance to relevant features. Hence, choice of resolution often occurs at an early stage of modelling.

Using empirical data to parameterise spatial mechanistic models increases credibility in that model's ability to predict responses to experimental scenarios; such as the response of a large mammal to increased deforestation. Pattern-oriented modelling uses real-world patterns to create and parameterise models with the aim of accurately replicating real-world patterns, and therefore aid in model design and calibration (Grimm et al., 2005; Grimm and Railsback, 2012). Approximate Bayesian Computation (ABC; Hartig et al., 2012) aids the parameterisation and validation of complex models (Van der Vaart et al., 2015). To parameterise models using ABC, researchers run the model with a large number of different sets of parameter values, and then isolate the set, or sets, of parameter values that best fit empirical data. For both of these techniques, the emphasis is on parameterising and building models that fit empirical data so as to increase the credibility of results from future studies that use the model.

Ground-truthing of movement algorithms requires spatial data from empirical studies. For example, Watkins et al. (2015) used results from empirical camera-trap studies to validate their movement model. To our knowledge, this study represents the only validation of an ecological mechanistic model of mammalian movement against empirical data. Nevertheless, as we move into an era of next-generation modelling, it is likely that an increasing number of researchers will follow the example of Watkins et al. (2015) by attempting to ground-truth their movement models against spatial empirical data. These data may include summary statistics from radiotelemetry, occupancy, and camera-trap studies, all comprising observations taken at particular points in time and space. If we replicate these studies using a grid-based model, each of these points become the size of an individual cell. As an example, in a model with a spatial resolution of 100 × 100 m, each camera trap would sample an unfeasibly large area of 100 × 100 m. Thus, summary statistics of virtual spatial studies may depend on the initial choice of spatial resolution. If we use these summary statistics as spatial patterns to parameterise and validate the spatial components of our model, our choice of movement algorithm may also depend on our initial choice of resolution. An argument for the use of complex mechanistic models is that their focus on mechanisms and processes allow them to exhibit greater predictability, as an agent's reaction to a situation is the result of behavioural algorithms. However, if the choice of algorithm depends on the choice of resolution, it calls into question the ability of that model to reflect reality rather than merely being a good-enough fit to current data at a certain resolution. This may result in the introduction of conflicting models for the same species producing different answers to the same question, which would only serve to confuse the issues that such models are intended to inform, as well as reducing credibility in spatial models. Alternatively, researchers may decide to use best-fit parameter values or sensitivity analysis to draw conclusions about animal behaviour; as in Imron et al. (2012). However, if the choice of parameter values depends on the resolution of the model, inferences about animal behaviour based on those parameters will also depend on model resolution. Both modellers and empiricists require a greater understanding of how choice of resolution can affect the parameterisation process in order to draw appropriate conclusions from model outputs and identify potential sources of bias.

Despite the increasing importance of spatially-explicit ABMs in conservation biology, no study has yet investigated the dependence of the parameterisation process on the choice of spatial resolution for models. Our aim is to use an ABM to investigate how changing resolution affects a) model fit to empirical data given a predetermined set of parameter values, and b) which parameter values best fit empirical data. To this end, we developed a spatially-explicit ABM of jaguar movements through the Cockscomb Basin Wildlife Sanctuary in Belize. We based our model on the ABM presented in Watkins et al. (2015), which includes gender-specific interactions between agents and their environment. We restructured the model to accommodate fine-scale features to the modelled environment, including trail and river systems, and cell-specific slopes, in order to evaluate the effect of resolution on movement models for animals that navigate using environmental cues.

In accordance with the principles of pattern-oriented calibration (Grimm and Railsback, 2012), we calibrated the movement model at a spatial resolution of 40 × 40 m using real-world patterns from empirical camera-trap and telemetry data. We ran the model at each of three resolutions using the parameter values derived from calibration: 40m × 40 m, 100 × 100 m, and 200 × 200 m. We investigated the influence of resolution on model outputs for five summary statistics: number of detections during each camera-trap study; absolute number of different male/female individuals caught on camera; size of male/female minimum convex polygon (MCP).

2.2 Methods

2.2.1 Study site

Belize covers a mainland area of 21,800 km^2 (Lands and Survey Department, 2015; United Nations Development Program, 2015). It has the highest percentage of forest cover of any country in mainland Central America, at 61% (FAO, 2010), with current or candidate protected areas taking up 43% of its mainland (Foster et al. 2016).

The study area of Cockscomb Basin Wildlife Sanctuary (CBWS, 425 km^2) lies in the south of the country (Figure 1). Its position in the Mayan mountains makes the terrain in CBWS hilly and rugged. The land-cover types in CBWS are lowland broad-leaved moist forest, sub-montane broad-leaved moist forest, and shrub-land. CBWS supports sympatric populations of jaguars and pumas (Harmsen et al., 2009; Harmsen et al., 2011).

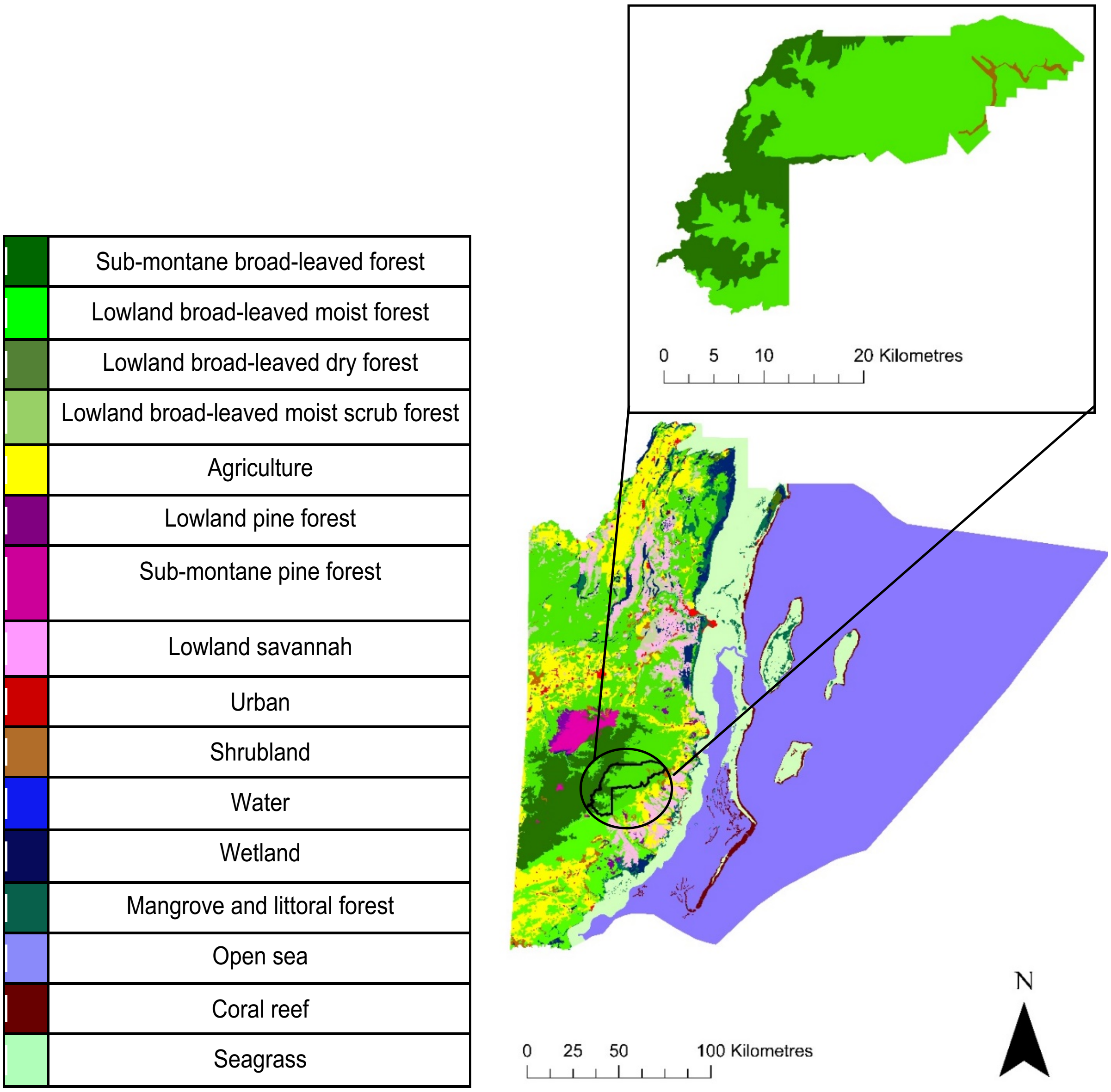

Figure 1. The location of the study site, Cockscomb Basin Wildlife Sanctuary (CBWS), within Belize.

2.2.2 Study species

Jaguar density estimates in CBWS vary from 3.5 to 11.0 adults per 100 km^2, suggesting a high density compared to other areas across the range (Harmsen et al., 2010a). Jaguars prey mostly on medium-sized mammals (Harmsen et al., 2011). Armadillos make up 50% of jaguar diet in CBWS (Foster et al., 2010), and their high availability may contribute to the high densities of jaguars in the reserve (Foster et al., 2010).

2.2.3 Empirical data

The telemetry data tracked two male jaguars over 226 and 376 days, and one male puma over 320 days. We used these data to estimate home ranges by minimum convex polygon. We estimated measurements for female minimum convex polygon by dividing male MCPs by 2.5, an approximation of the dividend between average male MCP and average female MCP in both Figueroa (2013) and Rabinowitz and Nottingham (1986). Annual MCP for male and female jaguars in Figueroa (2013) was 257 km^2 and 111 km^2, respectively. Minimum home ranges for male and female jaguars in Rabinowitz and Nottingham (1986) were 28 km^2 and 10 km^2, respectively. Hence, we approximated female home range by dividing our calculated home range for male jaguars by 2.5. The camera-trap data covered once-yearly surveys in CBWS from 2011 to 2015, each lasting ~3 months during the dry season. Unique pelt patterns allowed identification of individual jaguars (Silver et al., 2004). These data yielded detection frequencies and numbers of individuals of each sex, per camera, and in total within CBWS.

2.2.4 The model

We used Python to write the simulation model, and a combination of Python and R for data handling and statistical analysis. Appendix I describes the Overview, Design concepts, and Details (ODD; Grimm et al., 2006) for the model. For each set of parameter values, the model ran for 21,900 time steps, each simulating 12 min and totalling a 6-month period. Figure 3 shows a flow chart of the full model.

2.2.4.1 Background grid

The simulation model ran on a grid of cells, each representing 40 × 40 m. Each cell stored the following attributes: cell identity, *x* coordinate, *y* coordinate, terrain type, slope, distance to water, distance to trail, altitude, camera identity, jaguar occupant identity, female jaguar pheromone level, male jaguar pheromone level, the last female jaguar on the cell, the last male jaguar on the cell, neighbouring cells and attributes of cell graphics.

Information on terrain came from GIS data by Meerman (2011). We used the ArcMap tool *Euclidean Distance* to calculate distance to river and distance to trail, and the *Slope* tool to calculate slope from altitude data. We converted all terrain files to raster files, where necessary, and then to ASCII files. Panthera Belize provided GIS files for camera stations within CBWS. We converted the camera station GIS file to an ASCII file. The model read all ASCII files at the beginning of each replicate. Terrain- and camera-related attributes were static throughout each replicate.

Agents within the model used a proxy for pheromones to represent the various ways in which jaguars communicate with each other, including scent marking, scrapes, and vocalisations (Harmsen et al., 2010b).

2.2.4.2 Agents

The model initiated a new population of agents at the beginning of each replicate (Figure 2). It assigned initial agent locations, at random, from a selection of all cells within CBWS.

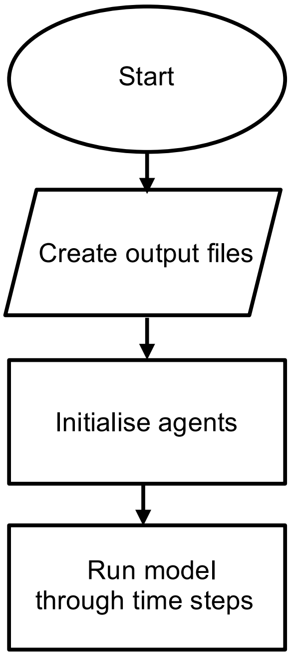

Figure 2. Process for each replicate. The model creates two output files, one representing a virtual telemetry study and the other a virtual camera-trap study.

Agents represented jaguars within the model. Each agent had the following attributes: identity, location, graphics attributes (colour, shape and size of agent in graphical representation), gender, current direction, and the agent's last position.

The agents had an equal chance of being male or female. Identity, graphics, and gender remained static throughout the replicate. Current direction, location, and the agent's last position changed as the time steps progressed. Directional persistence, the likelihood of an agent maintaining its current direction, differed between genders. The model did not incorporate birth and death as the simulation ran for too short a timescale to warrant its inclusion.

At the beginning of each time step, each agent placed pheromones on their current cell. The program then entered the *Move* function, *Re-entry* function, and lastly, the *Decay pheromones* function (Figure 3). After these functions, the model decayed pheromone levels in all cells and wrote data to output files.

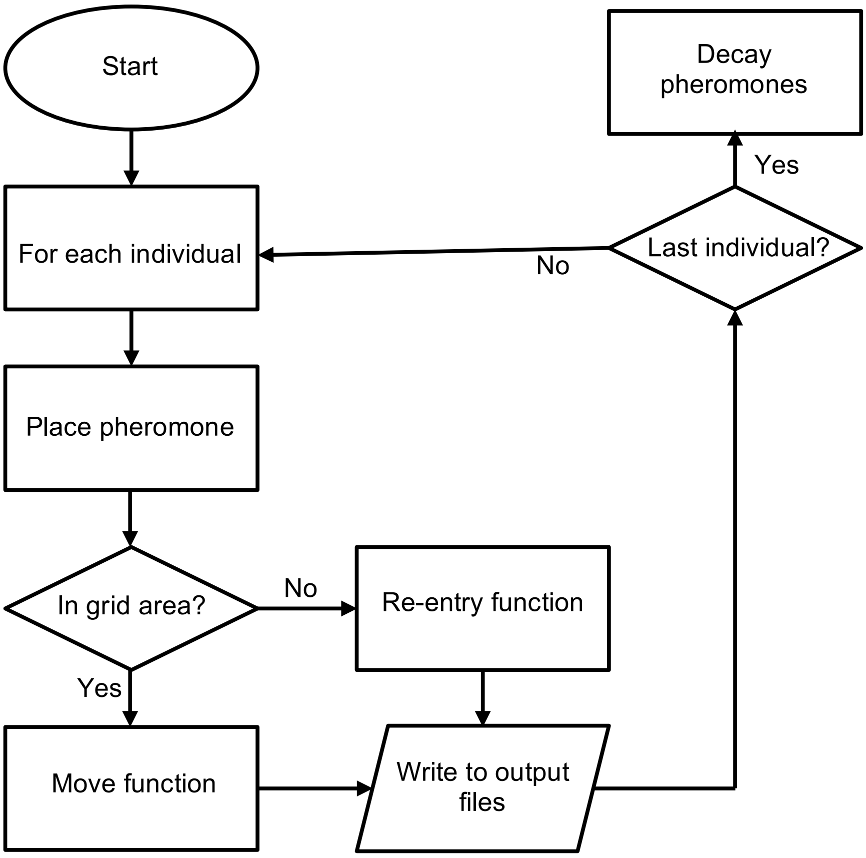

Figure 3. Flowchart for each time step. Squares contain process commands and diamonds contain conditional *if* statements.

2.2.4.3 Move function

For each agent within CBWS, the *Move* function (Figure 4) created a random probability between 0 and 1. If this did not exceed a pre-set probability of random movement, the agent randomly selected one of the eight neighbouring cells for its next cell. Otherwise, the model created another random probability between 0 and 1. If this did not exceed a pre-set probability of directional persistence, the agent continued moving in the same direction it had moved previously. If an agent did not move randomly, or in the same direction as previously, the model calculated the gender-specific cost values of all neighbouring cells. The cost value was calculated as per Equation (1), which represents cost calculation for male agents (C_M), and Equation (2), which represents cost calculation for female agents (C_F).

$$C_M = Ph_M + CFM + MDW \cdot dW + MDT \cdot dT + MS \cdot S + MA \cdot A + MTr \tag{1}$$

$$C_F = Ph_F + CMF + FDW \cdot dW + FDT \cdot dT + FS \cdot S + FA \cdot A + FTr \tag{2}$$

Table 1 contains the definitions for the majority of parameters in Equations 1 and 2. Ph_M is total pheromone placed by male agents in the cell. Ph_F is total pheromone placed by female agents in the cell. dW is the distance between the cell and a water feature. dT is the distance between the cell and a trail. S is the slope associated with the cell. A is the altitude associated with the cell. The gender-specific values *MTr* and *FTr* were only included in the equation when an agent was located on a trail square. *CFM* was only included in the cost calculation for male agents (Equation 1) if the amount of female pheromone associated with the cell was greater than 0. Similarly, *CMF* was only included in the cost calculation for female agents (Equation 2) if the amount of male pheromone associated with the cell was greater than 0. The agent then chose the least-cost neighbouring cell. Once the agent selected a cell, the model removed the agent from the cell occupancy list and changed the x and y coordinates of the agent. Graphical information also changed to reflect the new location.

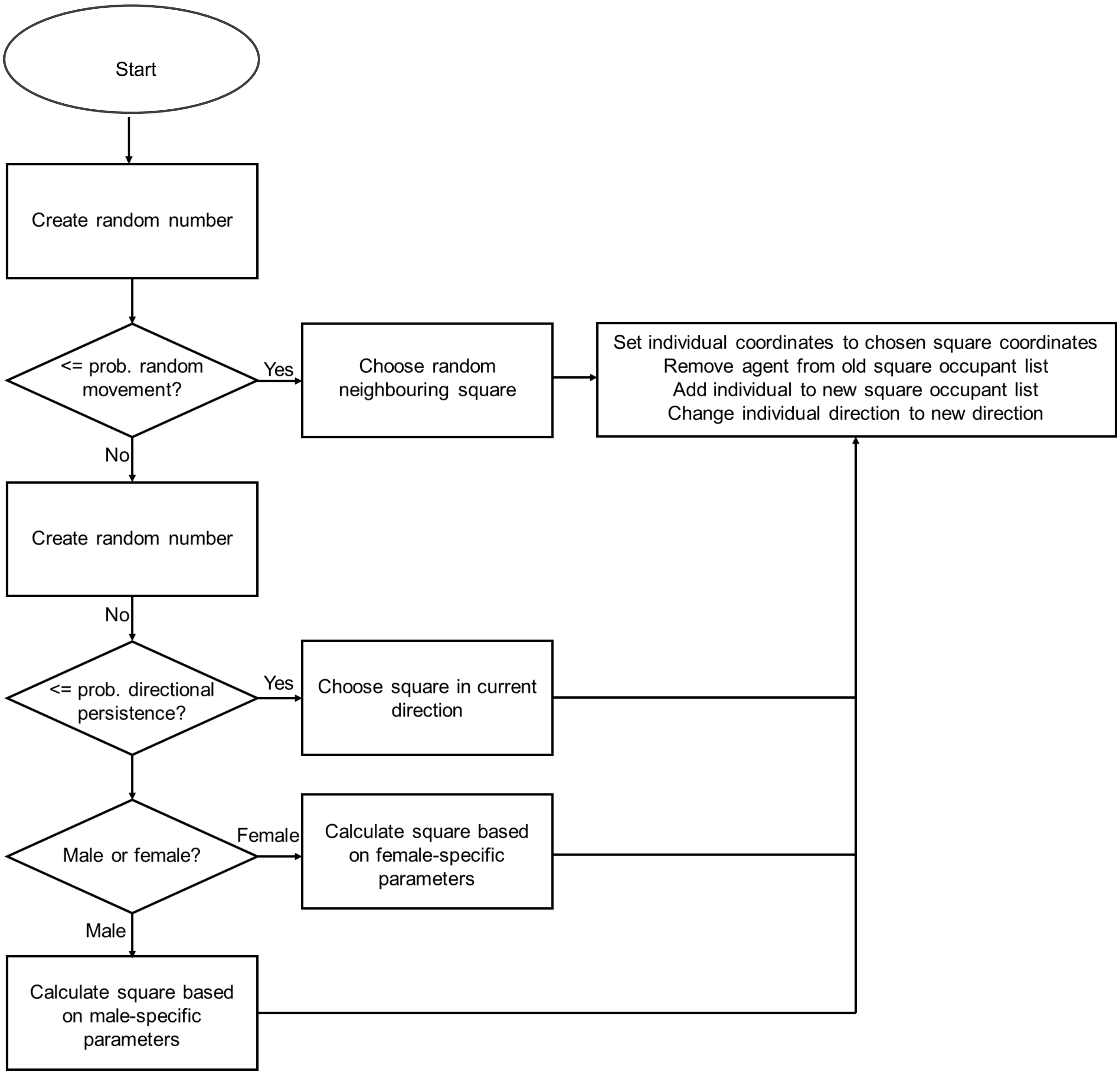

Figure 4. The process for the move. The model chooses whether to move in a random direction, move in the same direction or move based on habitat attributes. If it uses habitat attributes, it calculates the chosen square based on gender-specific costs. Squares contain model commands and diamond shapes contain *if* statements.

2.2.4.4 Re-entry function

If a resident was outside the boundaries of CBWS, the model entered a *Re-entry* function. The model created a selection of cells consisting of the last non-null cell the agent stepped on and any border cells within 250 m of that last cell. The model selected one of these cells at random and moved the agent to this cell.

2.2.5 Raw data format

The model stored data in two text files, one representing a virtual camera-trap study and one representing a virtual telemetry study. It wrote to these files at the end of each time step.

If an agent was in the same cell as a camera-trap, the model wrote the camera location, replicate number, time step, coordinates and agent gender to the file.

The model wrote each agent's location and attributes to the telemetry file. The telemetry file also included information on the time step and replicate number.

2.2.6 Validation

We used Latin Hypercube Sampling to select 2500 parameter sets (Carnell, 2016). We ran each of these parameter sets using a combination of the Iridis supercomputer at the University of Southampton, 2 desktop computers and 1 laptop. One replicate of the model took approximately 4 hours to run.

We sampled the virtual telemetry data to points occurring every simulated 24 hours, in order to match the empirical data. For each model, we calculated the following: number of detections during each camera-trap study; absolute number of different male individuals caught on camera; absolute number of different female individuals caught on camera; male minimum convex polygon (MCP) size; female MCP size.

We used absolute values for number of males, number of females, male MCP and female MCP. MCP data came from the virtual telemetry study, so did not depend on camera-trap success rate. We assumed that the cameras would eventually catch every male or female resident individual in the area, hence a perfect camera-trap rate would not bias the absolute male or female values.

2.2.7 Summary statistics as a function of resolution

We selected a set of parameter values for the model using a resolution of 40 × 40 m. The set of parameter values was the set that had the best fit to empirical data out of 2500 sets of parameter values.

We ran the model with the selected set of parameter values for 50 replicates at resolutions of 40 × 40 m, 100 × 100 m, and 200 × 200 m. The choice of resolutions derived from both the resolution of the GIS data (40 × 40 m) and the size of the study area. The higher resolutions represented approximately double, and then quadruple, the size of the resolution of the GIS data. Any resolutions in excess of 300 × 300 m would have resulted in a crowded grid, given the relatively small study area and the number of agents within the grid. The sample of resolutions was limited to three due to the time taken to run through the set of parameter values for each.

We calculated summary statistics from each of the models and used the non-parametric Kruskal-Wallis test in order to investigate the dependency of simulated summary statistics on the model resolution.

2.2.8 Parameter values as a function of resolution

We ran the model again for each of the 2500 sets of parameter values for both 100 × 100 m and 200 × 200 m resolutions, and chose the set of parameter values that best fit summary statistics from empirical data. We normalised each parameter value by dividing by the mean from parameter values calculated for the three resolutions and plotted them for comparison between resolutions.

2.3 Results

2.3.1 Selection of parameter values for model at 40 × 40 m resolution

We parameterised the first model using a 40 × 40 m resolution (Table 1). The model included attraction of male and female agents to agents of the opposite gender (CFM and CMF). The best-fit parameter values obtained from parameterisation against empirical data determined that agents in the model moved in a random direction for approximately half the time-steps, that male agents were more likely to move in a constant direction than female agents and that female agents avoided trail cells, whereas male agents preferentially chose trail cells.

Table 1. Input parameters for the ABM, showing the range of values tested, and the values that fitted best to the empirical data.

Parameter	Abbreviation	Range	Best-fit
(a) *Pheromone-related, determining interactions amongst individuals*			
Population size	Po	1 to 100	50
Pheromone placed by agent each turn	Ph	0.00 to 100.00	77.00
Pheromone decay rate	PhD	0.80 to 1.00	0.92
Cost of females to males	CFM	-50.00 to 50.00	-39.00
Cost of males to females	CMF	-50.00 to 50.00	-1.00
(b) *Movement, determining type of algorithm for choosing next cell*			
Probability of random movement	R	0.00 to 1.00	0.46
Male probability of directional persistence	MDP	0.00 to 1.00	0.62
Female probability of directional persistence	FDP	0.00 to 1.00	0.16
(c) *Environmental parameters, determining interactions with the abiotic environment*			
Male distance to water multiplier	MDW	-1.00 to 1.00	-0.18
Female distance to water multiplier	FDW	-1.00 to 1.00	-0.06
Male distance to trail multiplier	MDT	-1.00 to 1.00	0.39
Female distance to trail multiplier	FDT	-1.00 to 1.00	0.05
Male trail square cost	MTr	-50.00 to 50.00	-6.00
Female trail square cost	FTr	-50.00 to 50.00	14.00
Male slope multiplier	MS	-5.00 to 5.00	2.51
Female slope multiplier	FS	-5.00 to 5.00	3.00
Male altitude multiplier	MA	-1.00 to 1.00	0.47
Female altitude multiplier	FA	-1.00 to 1.00	0.48

Summary statistics from the model runs using 40 × 40 m cells were broadly similar to summary statistics from empirical studies (Table 2). Although output values for summary statistics from the model were feasible, the model failed to capture the empirical level of difference between males and females. Moreover, the average number of detections in the model was approximately three times less than the average from empirical studies.

Figueroa (2013) calculated much larger MCPs than the empirical MCPs used for comparison in this study. However, his study was conducted in the corridor area of Belize, which incorporated large open areas, rather than within a reserve. This explains the discrepancy between empirical MCPs. Figueroa (2013) used data from 6 male jaguars and 1 female jaguar. The female MCP calculated from simulation data is more similar to the Figueroa data than our empirical data. The male MCP calculated from simulation data is more similar to our empirical data than the Figueroa empirical data. As MCP data are broadly similar to both sets of empirical data rather than being several orders of magnitude higher or lower than the empirical datasets, the Figueroa data provide further evidence that the model represents a good enough approximation of empirical patterns to use for further analysis.

Table 2. Comparison between summary statistics from empirical camera-trap and telemetry studies in CBWS and outputs from the best-fit ABM of jaguar movement. The table includes MCP values calculated in Figueroa (2013).

Summary statistic	**Empirical**	**Empirical (Figueroa, 2013)**	**Model**
Number of male agents captured	16.4 +/- 0.87	n/a	14.5 +/- 0.3
Number of female agents captured	9.6 +/- 1.8	n/a	14.84 +/- 0.3
Male minimum convex polygon size	147.6 +/- 11.7 km^2	257 +/- 48.8 km^2	125.7 +/- 0.6 km^2
Female minimum convex polygon size	57.0 +/- 11.1 km^2	111 +/- 0.0 km^2	97.4 +/- 0.7 km^2
Number of detections	334.8 +/- 89.1	n/a	119.36 +/- 1.0

The empirical data for number of male individuals captured had a narrow distribution, which lay within the distribution for modelled data, but not within the interquartile range

(Figure 5a). Distributions for male MCP size (Figure 5c) and number of detections (Figure 5e) from the model lay within distributions for corresponding empirical data, despite the difference in average number of detections between empirical and model data. Lower values for number of female individuals captured lay within the interquartile range for number of female individuals captured in empirical studies (Figure 5b). Female MCP size showed the greatest difference between model and empirical data, with none of the values from the model lying within the distribution from empirical data (Figure 5d). None of the summary statistics from the model had distributions that aligned well with empirical data. Nevertheless, the results were consistent amongst model runs and the model values were of similar orders of magnitude to empirical data, which allowed us to use the model for further analysis.

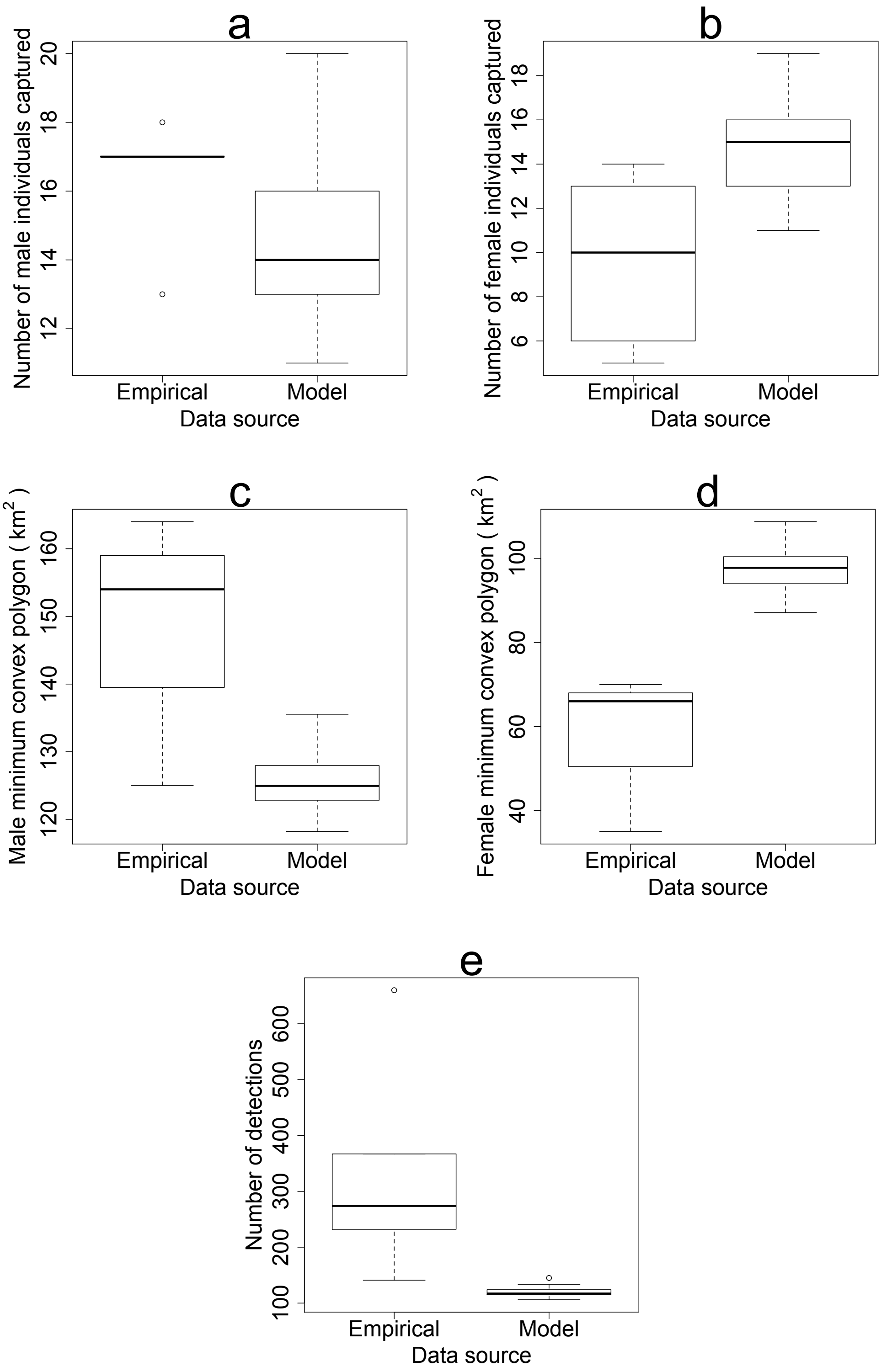

Figure 5. Summary statistics from empirical and modelled data.

2.3.2 Summary statistic outputs as a function of resolution

All summary statistics from model runs depended on resolution of the model (Figure 6). There was an almost twofold difference between number of detections for models using a 40 × 40 m resolution and models using a 200 × 200 m resolution. Female minimum convex polygon sizes for models using 200 × 200 m cells were approximately 1.5 times the size of those from models using 40 × 40 m cells. Models using a resolution of 40 × 40 m generally had smaller ranges and smaller values. Models at every resolution underestimated the number of detections during camera-trap studies (Figure 6e). The 40 × 40 m resolution model most accurately simulated female jaguar movement (Figures 6b and 6d). Empirical values for number of male individuals captured and male minimum convex polygon size lay between the results from the 40 × 40 m and 100 × 100 m models. Changing resolution appeared to have little effect on the ability of the model to capture male and female differences in summary statistic values.

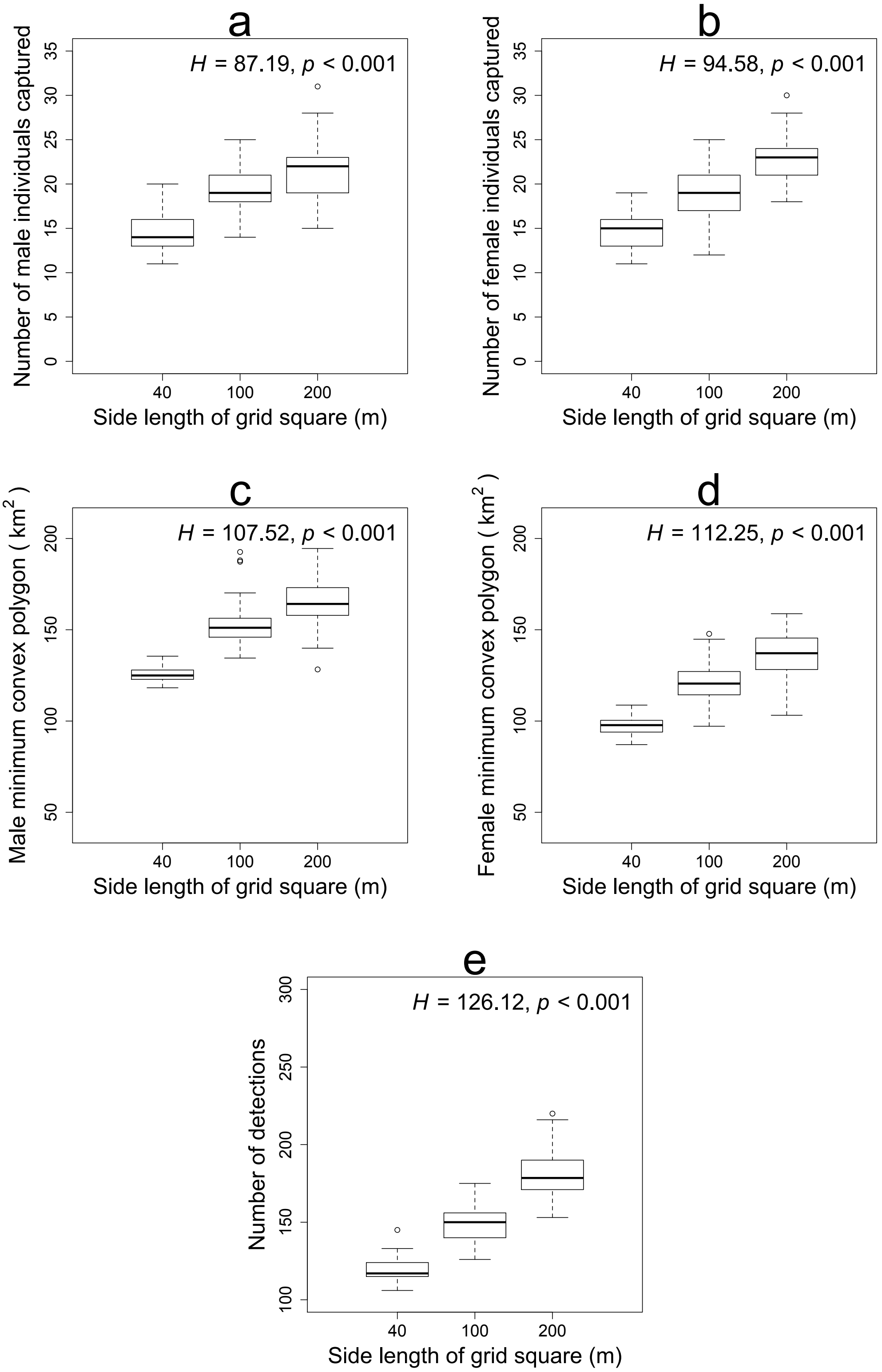

Figure 6. Summary statistics as a function of cell size. *H* and *p* values are from K-S tests for each relationship.

In our coarse-grain model (200 × 200 m), each section of trail covered a width of 200 m. This increased the amount of trail available to the agents within the area. Virtual camera-traps were each able to cover areas of 200 × 200 m, something impossible in most empirical studies. This increased the number of detection incidents in coarser resolution models and allowed them to capture a greater number of agents.

Coarse-grain models had greater MCP sizes for both male and female agents. For empirical data, we calculate MCP using points within a landscape (Figure 7a). If an agent in a grid-based model moves to similar locations within the model, we include entire grid squares in the MCP calculation. This results from the fact that the model cannot pinpoint where an agent has stepped within a grid square when it moves into the square (Figure 7b). As the grain of the model becomes coarser, the grid squares that we include as points in MCP calculation become larger, inflating MCP estimates (Figure 7c). In the most extreme example in Figure 7, changing resolution from 50 × 50 m (Figure 7b) to 200 × 200 m (Figure 7d) inflates MCP estimates by 33%.

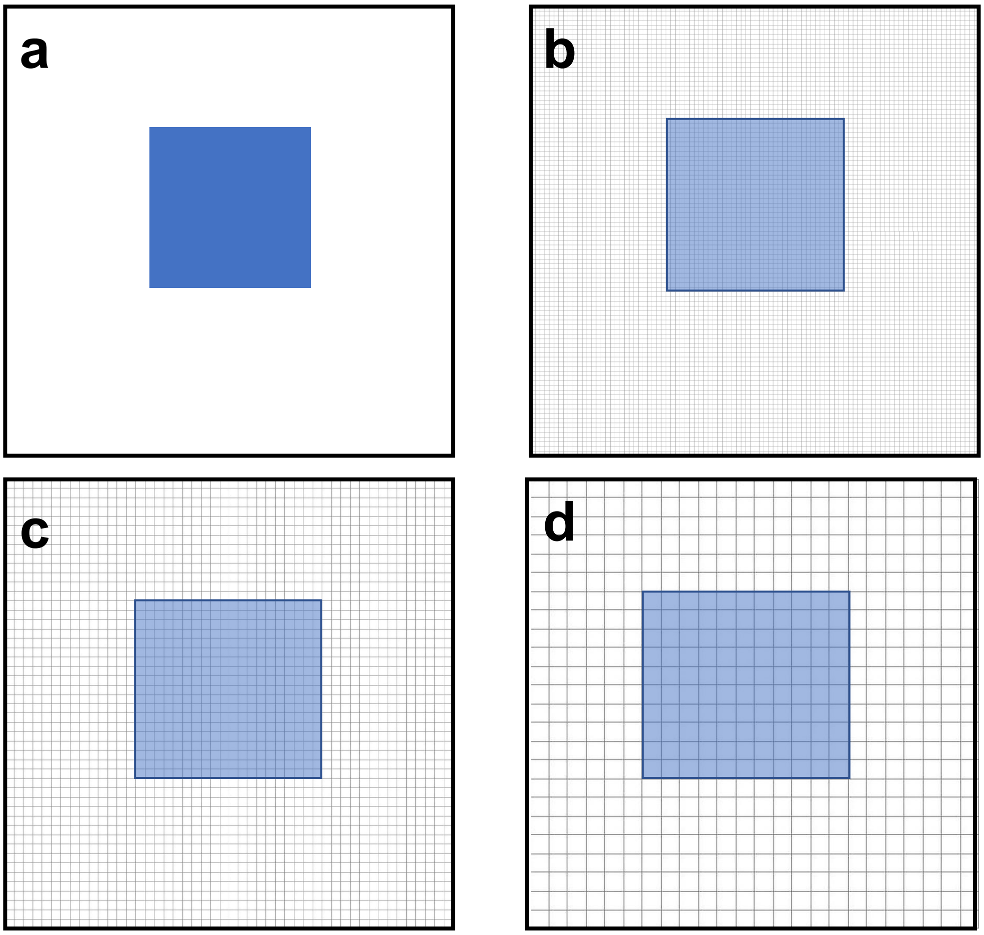

Figure 7. MCP size as a function of grid cell size: a) MCP = 3.2 km^2 control MCP calculation with no grid cells, b) MCP = 3.6 km^2 calculated using a grid of 50 × 50 m cells, c) MCP = 4.0 km^2 using a grid of 100 × 100 m^2, d) MCP = 4.8 km^2 calculated from a model using a grid of 200 × 200 m cells.

2.3.3 Resolution determines model behaviour

Values of model parameters selected using the parameterisation process depended on choice of resolution (Figure 8). The cost of female agents to males (CFM) and the cost of male agents to females (CMF) differed broadly when using the parameterisation process for different resolutions. In both the 40 × 40 m and 200 × 200 m models, male agents were strongly attracted to female pheromone. For the 100 × 100 m model in contrast, male agents strongly avoided female agents. This resulted in models with very different movement processes, depending on which resolution we selected initially. The cost of male agents to female agents differed less, although female agents were attracted to male agents in the 40 × 40 m model, while avoiding them in the 100 × 100 m and 200 × 200 m model. In the 40 × 40 m model, males strongly avoided water sources, but were attracted to them in the 100 × 100 m and 200 × 200 m models. Male agents in both the 40 × 40 m and 100 × 100 m models avoided trails; particularly in the latter case. However, in the 200 × 200 m model, they appeared to be strongly attracted to trail squares. Likewise, female agents were attracted to trail for the 40 × 40 m model, but avoided trail for the 100 × 100 m model. Male agents were attracted to high altitude areas in the 40 × 40 m model, but avoided them in the 100 × 100 m and 200 × 200 m models. In short, varying the initial resolution of the model results in very different movement processes.

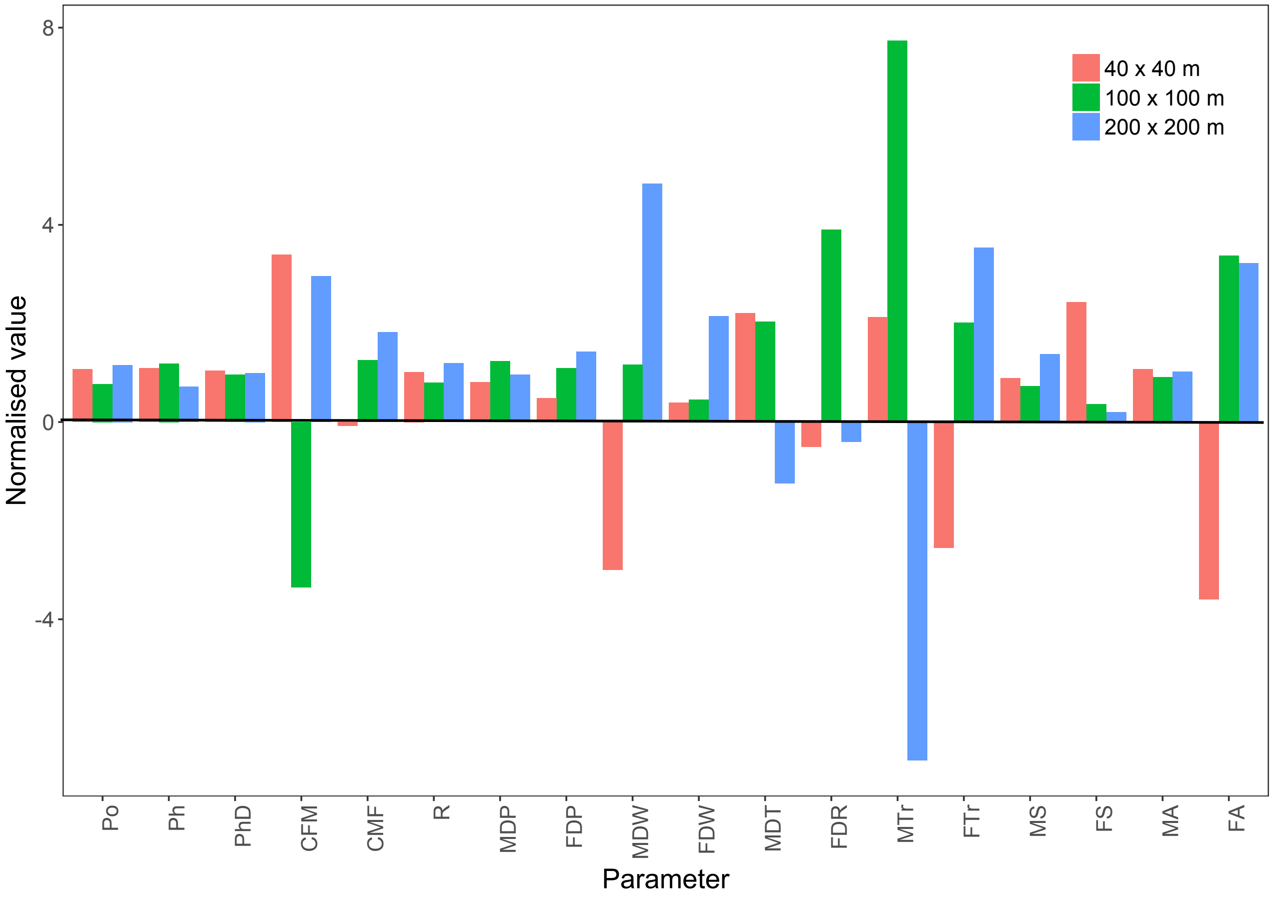

Figure 8. Normalised parameter values selected by the parameterisation process for three different resolutions. See Table 1 for definitions of abbreviations.

Probabilities of random movement and directional persistence selected using the parameterisation process depended on resolution of the model (Table 3). The probability of random movement was 36% for the 100 × 100 m model and 54% for the 200 × 200 m model. Thus, there was 1.5 times more random movement within the 200 × 200 m model than in the 100 × 100 m model. This resulted in every agent in the 200 × 200 m model taking 3,942 more random steps than the agents in the 100 × 100 m model. Female agents in the 40 × 40 m model continued in the same direction 9% of the time, taking into account the probability of random movement. Female agents in the 100 × 100 m model continued in the same direction 23% of the time. Hence, female agents in the 100 × 100 m model chose to move in the same direction as the previous step 2.6 times more often than female agents in the 40 × 40 m model. Likewise, male agents in the 100 × 100 m model chose to move in the same direction 1.8 times more frequently than male agents in the 200 × 200 m model. Thus, the parameterisation process yielded different parameter values for best-fit models depending on resolution, which resulted in very different mechanistic models for animal movement, despite using the same empirical data. The movement processes that best fit the empirical data depended on the resolution of the model.

Table 3. Parameter values selected from parameterisation process for the same model at three resolutions.

Parameter	40 × 40 m	100 × 100 m	200 × 200 m
(a) *Pheromone-related, determining interactions amongst individuals*			
Population size	50	36	54
Pheromone placed by agent each turn	77.00	83.46	50.46
Pheromone decay rate	0.92	0.85	0.88
Cost of females to males	-39.00	38.54	-34.04
Cost of males to females	-1.00	16.74	24.37
(b) *Movement, determining type of algorithm for choosing next cell*			
Probability of random movement	0.46	0.36	0.54
Male probability of directional persistence	0.62	0.95	0.74
Female probability of directional persistence	0.16	0.36	0.47
(c) *Environmental parameters, determining interactions with the abiotic environment*			
Male distance to water multiplier	-0.18	0.07	0.29
Female distance to water multiplier	-0.06	-0.07	-0.33
Male distance to trail multiplier	0.39	0.36	-0.22
Female distance to trail multiplier	0.05	-0.39	0.04
Male trail square cost	-6.00	-21.78	19.33
Female trail square cost	14.00	-11.07	-19.40
Male slope multiplier	2.51	2.06	3.90
Female slope multiplier	3.00	0.45	0.25
Male altitude multiplier	0.47	0.40	0.45
Female altitude multiplier	0.48	-0.45	-0.43

2.4 Discussion

In this study, we have demonstrated that changing the resolution of a model can affect its fit to empirical data. We found that all chosen summary statistics depended on model resolution, and that parameterising the model under three different resolutions using spatial statistics from point data resulted in three very different movement algorithms. Spatial statistics, such as telemetry and camera-trapping data, are often the only empirical data available to researchers studying large and elusive species. Our results have direct implications for the development of simulation models for these species, and therefore on their conservation, and they suggest implications for all single species ABMs.

Next-generation ecological models will incorporate enough realism to predict the effects of future HIREC on ecological systems (Grimm and Berger, 2016). Mechanistic models have the potential to predict responses to environmental change as they model a process, and allow responses to emerge from that process (Stillman et al., 2015). If we use our models to test a future scenario of human-induced environmental change, how will their results differ? Consider a scenario of potential deforestation. Agents that display more random movement, or who persist in the same direction more often, may react less to the presence of environmental cues than other agents, and would therefore appear less affected by loss of pristine habitat. Likewise, when deforestation leads to construction of trails in an area that was previously inaccessible, which of these models would capture the correct interaction between agents and trail? The reaction could either be canalisation or avoidance, depending on which resolution we chose while parameterising our model. The results of future studies using this model will depend on the processes and behaviour used in the final model, and hence on the initial choice of resolution. If selection of specific movement algorithms relies on the spatial resolution of the model, the movement algorithms may not actually capture the behaviour of the species. When we run the model with a scenario in order to investigate the effect of future HIREC on our agents, the agents may not react in a similar fashion to our study species. Moreover, models parameterised with different resolutions may produce very different predictions. If modellers offer contrary predictions to the same situation, this may only work to fuel the divide between modellers and empiricists (Jeltsch et al., 2013).

Parameter choice may depend on model resolution when modellers use fine-scale empirical data to parameterise their model (e.g., Watkins et al., 2015). Camera-trap studies and radiotelemetry studies rely on point data. When in an environment with poor visibility, such as a rainforest, each empirical camera-trap can cover an area far less than 40 × 40 m. The grain of the available empirical data is therefore finer than the finest resolution we used in our study. We caution that researchers cannot change the model resolution once they have decided on a parameter set, or re-parameterise the model if they wish to change the resolution, without also re-evaluating the fit of the new model to empirical patterns.

Both virtual camera-trap and radiotelemetry summary statistics depended on the choice of resolution. Models with fine resolutions can represent point or line features, such as trails or river systems (Nezer et al., 2017), that influence how animals select movement paths through the landscape (Abrams et al., 2016). When animals move through their landscape, their movement paths form a line feature. Any factors in the model that depend on movement paths will hence depend on the resolution of the model. As an example, if we want to investigate how often two agents living in the same vicinity interact, the results of our model may depend on the paths the agents take through their landscape. If we used a model with a large cell size, the agents would have coarser movement paths, and hence, may interact more often than if we were to use a model with a small cell size. Questions of this sort may necessitate running the experiment under multiple resolutions in order to evaluate the sensitivity of results to model resolution.

Researchers often draw inferences about species behaviour from the output values of the parameterisation process. For example, some studies have used the results from sensitivity analyses of parameter values (e.g. mortality) to draw conclusions about the behaviour of species or groups (Kanagaraj et al., 2013; Imron et al., 2012). In our study, we could have concluded that the difference between males and females in directional persistence values indicated that male and female jaguars show different levels of patrolling behaviour. While this may be true, the difference in directional persistence parameters could result from resolution bias. The directional persistence values that best fit empirical data when using a 40 × 40 m model resolution may be different from those that best fit empirical data when we use a finer or coarser grain. We must therefore treat any conclusions that we draw from model parameterisation with caution.

Virtual ecology focuses on recreating empirical experiments in-silico, often with the aim of considering alternative empirical methodologies (Zurell et al., 2010). Rodrigues and Coelho (2016), for example, used a mechanistic simulation model in order to assess how different movement patterns and detectability between male and female agents affected estimates of sex ratio from both active and passive capture methods. Our study shows that virtual ecology studies need to investigate the potential for bias due to choice of resolution, in order to draw conclusions that can inform empirical study. Consideration of potential bias is especially important when attempting to recreate fine-grain spatial experimental data, such as camera-trap or radiotelemetry data.

Although direct parameterisation is the best solution to the problem of resolution-dependent predictions, often the species we wish to model are elusive, and little is known about their behaviour in the wild. Choice of resolution often becomes fixed at an early stage in model development, as a function of the study aims, the available environmental data, and the computing power required to run the model. In these cases, we advise conducting robustness analysis (Grimm and Berger, 2016) by running the model under different resolutions to investigate whether changing spatial resolution breaks the model. Any parameter values that vary significantly between one resolution and the next may not be important for model fit, or may be indicative of bias caused by the scaling up of point data to grid cells.

We have shown that spatial statistics that use point data result in biased approximations. It may be better to focus on qualitative rather than quantitative patterns (Jakoby et al., 2014), or a mixture of qualitative patterns and ratios; such as the level of overlap between home ranges or the ratio between male and female home ranges, for example. Where data on species are lacking, it may be advisable to run the scenarios under multiple possible movement algorithms or address only a hypothetical species with a certain movement algorithm.

The scientific world has yet to obtain a full understanding of what drives animal movement decisions. It is highly likely that decisions derive from multiple cues (Sih et al., 2016). The future of ecological modelling lies in complex mechanistic models that incorporate fine-scale movement decisions, models of dispersal, genetics, demographics and models of human activity at the small- and large-scale in order to provide predictions on organism response to HIREC (Sih et al., 2016). ABMs parameterised using empirical data will likely become increasingly popular and useful tools for the conservation of elusive mammals. Empirical data for these species will continue to come from point data, such as camera-trap and radiotelemetry data. If model parameter sets depend on the resolution of the model, we must ask whether spatially-explicit mechanistic models do accurately replicate the behaviour of a species. This has implications for the ability of spatially-explicit models to predict how ecological systems adapt to change, which is one of the three essential elements of next generation modelling (Grimm and Berger, 2016). With mechanistic movement modelling still in its infancy, it is imperative to bring out potential biases in the methodology in the early stages of what will doubtless become an important and insightful discipline.

2.5 Appendix I. Overview, Design concepts and Details

Appendix I follows the protocol of Overview, Design concepts and Details suggested by Grimm et al (2006).

2.5.1 Purpose

The model simulated fine-scale movement decisions of jaguars in Cockscomb Basin Wildlife Sanctuary (CBWS), Belize. Our purpose was to capture the movement of resident agents around their home-ranges and use pattern-oriented calibration in order to parametrise the model. We present the parameterisation and validation here. We then use this model to investigate the effect of resolution choice on model fit and validation. We seek to use this model in order to undertake further theoretical experiments on jaguar responses to anthropogenic impacts.

2.5.2 State Variables and Scales

The model background consisted of 1071 × 750 grid cells. Each grid cell represented an area comprising 40m × 40m. This grid includes “Null” cells that lay outside CBWS. The area of CBWS comprises a modelled 425 km^2. GIS data (Meerman, 2011) informed data on static aspects of the cells: habitat type, distance to river, distance to trail, altitude, slope, presence of camera-trap and camera-trap ID. We used results from in-silico camera-trap and telemetry experiments to validate the model. The agents occupied a single cell at a time. The model allocated each agent with a gender, identity, location and graphics information. At the beginning of each time step, the agent would deposit an amount of “pheromone”. Pheromone represented the ability of agent to signal to each other. In reality, jaguars communicate using scrape markings, scent markings and vocal calls. The model stored pheromone levels as a feature of grid cells. Pheromone levels were gender-specific.

We ran the model through a series of parameter sets. Each replicate consisted of 21,900 time steps that represented 6 months. Each time step equated to 12 minutes.

2.5.3 Process overview and scheduling

At the beginning of each parameter set run, the model created the background grid and set staticcell attributes: terrain type, distance to river, distance to trail, altitude, slope, coordinates and graphics information. The model then ran through replicates.

At the beginning of each replicate the model created output files and initialised a population of agents. The agents had an equal chance of being male and female. All agents created at the beginning of the simulation were "resident" agents. After initialisation, the model ran through a series of time steps.

The model placed an amount of pheromone at the beginning of each time step. It then looped through all agents. If an agent was in CBWS, the agent would undergo the move function. If an agent was a "resident" and outside CBWS, it would undergo the re-entry function. At the end of the time step, the model would write to output files and decay pheromone levels. The model continuously updated all information on cell pheromone levels and jaguar locations.

2.5.4 Design concepts

2.5.4.1 Emergence

Agent home ranges emerged from the communication between agents via pheromone levels. The constant decay and placement of pheromone allowed home ranges to be dynamic.

2.5.4.2 Adaptation

Agents chose the least-cost neighbouring cell based on cell attributes. These attributes were both dynamic (for example, distance to river) and dynamic (pheromone levels). The parameter sets each had specific values for how an agent responded to each of the cell attributes.

3.5.4.3 Fitness

The model did not include mortality or fecundity, however this model represents a base model for future investigations of how movement decisions affect mortality and dispersal in a human-influenced environment.

2.5.4.4 Sensing

All agents could access information on neighbouring cell attributes. This information included environmental attributes (terrain type, distance to river, distance to trail, altitude and slope) and agent-related attributes (amount of male pheromone, amount of female pheromone, jaguar occupancy). The agent did not access camera-related cell data. Each cell had eight neighbours, representing north, north-east, east, south-east, south, south-west, west, north-west and north cells.

2.5.4.5 Interaction

Agents interacted using pheromone. Pheromone was gender-specific. Gender-specific parameters dictated how agents respond to same-gender, opposite-gender and own pheromone. Agents responded to pheromone levels by having an increased or reduced cost proportional to the amount of pheromone. Hence, pheromone resulted in avoidance or attraction to the same- and opposite genders, dependent on the parameter set.

2.5.4.6 Stochasticity

The model included parameters for probability of random movement, and probability of directional persistence. Hence, an agent could move in a random direction, in the same direction as previously or in a direction dictated by cost of neighbouring cells. The probability of these movement types depended on the parameter values and random number generation. The model allocated gender based on a 50% chance of being male or female.

2.5.4.7 Observation

The model used the Python package Tkinter for graphical representation during testing. The graphics provided information on environmental attributes and gender-specific pheromone levels in each cell, and agent movements around the grid.

2.5.5 Initialisation

The model reset all landscape and agent attributes at the beginning of a new parameter set. At the end of each replicate, the cell pheromone-related attributes reset. The model removed all agent and created a new population. The number of agents in the new population depended on the value of the population parameter. Agents could then establish new home ranges.

2.5.6 Submodels

2.5.6.1 Pheromone placement

At the beginning of each time step, each agent placed an amount of pheromone in its current cell equal to the pheromone placement parameter value. This allowed agents to communicate with each other.

2.5.6.2 Move

The function ran through each agent in the population, provided the agent was within the CBWS area. It first created a random probability. If this did not exceed a pre-set probability of random movement, the agent selected a random neighbouring cell as its next cell. There were eight neighbouring cells for each cell. This cell may be outside CBWS. If the agent did not undertake random movement, the model created another random probability. If this did not exceed a pre-set probability of directional persistence, the agent continued moving in the same direction it had moved previously. If an agent did not move randomly or in the same direction as previously, the model calculated the gender-specific cost values of all neighbouring cells. The agent chose the least cost neighbouring cell. Once the agent selected a cell, the model removed the agent from the cell occupancy list and changed the *x* and *y* coordinates of the agent. Graphics information also changed.

2.5.6.3 Re-entry

If an agent was a "resident" and outside the boundaries of CBWS, the model entered a re-entry function. The program created a random probability. If this did not exceed a pre-set probability of re-entry, the model created a selection of cells consisting of the last non-null cell the agent stepped on and any "border cells" within 250m of that last cell. The model selected one of these cells at random and moved the agent to this cell.

2.5.6.4 Pheromone decay

At the end of each time step, the model decayed pheromone levels in all cells by a multiplier equal to the pheromone decay parameter.

2.5.6.5 Take photo

At the end of each time step, if an agent was present on a cell with a camera, that cell object would write the following to an output file: time, agent ID, location, camera type and gender of agent.

Chapter 3.

A method for correcting estimates of metrics derived from radiotelemetry movement data

Ball, A.E, Foster, R.J., Harmsen, B.J., Doncaster, C.P. In preparation for 'Biological Conservation'. Author contributions: A.E.B. conceived the original idea, developed and ran the models, designed and executed the analyses, and wrote the chapter; R.J.F. and B.J.H. provided telemetry data and subject matter expertise; CPD advised on study design and revised earlier drafts of the manuscript.

Chapter 3. Correcting telemetry metrics

Abstract

The calculation of accurate movement metrics from telemetry data has consequences both for modellers, who incorporate metrics as parameters in their models, and managers who consider metrics in the development of conservation strategies. Despite recent advances using GPS satellites, a trade-off exists between fix interval (the number of hours between fixes) and the length of a telemetry study set by the battery life of telemetry devices. Although studies have shown that longer fix intervals result in greater errors when calculating metrics, none have attempted to provide a standard method for correcting movement metrics derived from telemetry data. Here we use a mechanistic model to demonstrate a method for correcting estimates of movement metrics, by employing a combination of subsampling and non-linear regression to define the relationship between fix interval and estimate for two metrics: step length and MCP. We repeat this for six different movement models, including a random movement model and five models representing agent 'choice' with varying levels of directional persistence to determine whether movement type affects the accuracy of the method. At a fix interval of 2 hours, the estimated step length was 25% less than the actual step length. The correction method reduced this error to 14.5%. By tailoring the method to movement types, we further reduced the error to 11% for some simulations. Fix intervals of 2 hours had an error in MCP estimation of approximately 50%. The correction method did not improve estimates of MCP when generalising an equation across all movement types. Tailoring the correction method to different movement types generally increased the accuracy of estimates, with a minimum error of 4%. The correction method we present here is particularly useful where researchers cannot narrow the fix interval in their study due to either research requirements or the interference of terrain with telemetry signal.

Key words: agent-based model; virtual ecology

3.1 Introduction

Movement of animals has been a key area of research in conservation biology for over 20 years (DeMars et al., 2013). Patterns of movement determine the distribution of species, the transmission of disease, routes for animal migration, and responses to anthropogenic actions (Morris, 2003; Hosseini et al., 2006; Bradshaw et al., 2007; Beyer et al., 2013). Analyses of such patterns may augment our understanding of metapopulation dynamics, species persistence and the effect of conservation measures (Schooley and Wiens, 2004; Loarie et al., 2009; Pittman et al., 2014; Jenks et al., 2015). Studying patterns of movement can therefore contribute to the conservation of endangered and threatened species.

Telemetry data allow researchers to understand movement by capturing individuals in space and time. Sources of telemetry data include VHF radiotelemetry tags, fixed-position PIT tag detection arrays (Tew and MacDonald, 1994; Armstrong et al., 1996; Lucas et al., 1999), which detect locations by close-range proximity detection (Harbicht et al., 2017), acoustic telemetry transmitters, and Global Positioning System (GPS) telemetry tags, which use satellites to obtain location data (Dana, 1989). GPS technology, in particular, has allowed researchers to collect a high abundance of accurate, fine-scale data on animal movement (Mills et al., 2006; Kie et al., 2010; Tomkiewicz et al., 2010). GPS is unaffected by weather conditions, which improves on traditional VHF radiotelemetry technology (Girard et al., 2002), although GPS tags are more expensive, which limits the number of individuals that the study can track (Otis and White, 1999; Harbricht et al., 2017). Researchers have employed telemetry data to in order to develop their understanding in a number of areas, including studies on how animals respond to barriers to movement (Riley et al., 2006; Shepard et al., 2008), density estimation (for example, Soisalo and Cavalcanti, 2006), development of resource selection functions (for example, Johnson et al., 2004), and predator-prey relationships (Sevodkin et al., 2017). In this paper, we will focus on two of the many outputs from telemetry data, namely step length and size of home range in order to offer methods to correct for bias caused by fix interval for two metrics that are frequently exploited in further conservation research.

Step length is the distance covered by a tagged individual between two sequential telemetry fixes. Knowing the value of step length allows calculation of other metrics, such as cumulative distance covered over a study period and the average speed of individuals. Many movement models incorporate step length and turning angles as parameters to simulate individual movement (Turchin, 1998). Telemetry provides the data to parameterise the models that researchers then use to make inferences about animal movement (Jerde and Visscher, 2005; Beyer et al., 2013; DeMars et al., 2013). Researchers have included step length in autocorrelation functions in order to investigate movement patterns (Boyce et al., 2010). For example, Jenks et al. (2015) used autocorrelation functions and cluster analysis in order to compare the movement of a golden jackal and a dhole. Thus, it is important that researchers can obtain accurate estimates of step length so as to reduce bias in models at later levels of abstraction.

A home range of an animal is the area that an individual inhabits regularly, during activities such as foraging (Burt, 1943). Knowledge of the size of home ranges informs the construction of conservation measures by allowing the estimation of space required for that conservation measure to be successful. Telemetry data is often employed to determine home range size and boundary (Otis and White, 1999). Calculation of home range using telemetry data commonly employ either kernel analyses or minimum convex polygon (MCP) (Kolodzinski et al., 2010). Both kernel and MCP calculation depend on the sampling regime applied to collect telemetry data, with the latter being more sensitive than the former to the intensity of the sampling regime (Kolodzinski et al., 2010). As stakeholders use home range to indicate how much habitat a species requires, it is imperative that estimates are accurate, or at least that managers have a clear understanding of the strength and direction of potential bias.

When designing telemetry studies, researchers must often address a trade-off between the intensity of the sampling regime and the duration of the study (Kolodzinski et al., 2010). As the time interval between fixes of locations - hereafter referred to as the “fix interval” – increases, the study misses more potential locations. This can lead to errors in calculations of metrics, such as step length and home range. Multiple studies have found that long fix intervals underestimate both step length and home range, because they miss out tortuous movement and extreme points (Otis and White, 1999; Mills et al., 2006; Kolodzinksi et al., 2010). As an example, Kolodzinski et al. (2010) found that calculations for MCP using telemetry with fix intervals of eight to twelve hours underestimated homes range by at least 50%. Furthermore, telemetry devices suffer from type II errors. In some cases, the success rate of fixes can be as low as 13% (Frair et al., 2004). This would change a sampling regime that takes location fixes every 2 hours to one that only samples locations every 16 hours, with implications for the accuracy of calculation of metrics.

The effectiveness of sampling methodologies, such as telemetry studies, can be investigated by way of virtual ecology. Virtual ecology concerns the replication of empirical studies in-silico using simulation models (Zurell et al., 2010). Studies incorporating virtual ecology not only expose the problem, they allow easy quantification of errors and effects of mitigation errors. Zurell et al. (2010) list the two main applications of virtual ecology as 1) testing and improving sampling schemes and methods, and 2) testing and comparing models. As experiments are conducted in a model with a known population, one can compare the result of such an in-silico study with the real-world data, thereby evaluating the effectiveness of this approach. Indeed, researchers have exploited virtual ecology for a number of purposes, such as evaluating the conceptualisation and implementation of species distribution models (Miller, 2014), assessing sampling designs (Albert et al., 2010; Ficetola et al., 2014; Lyashevska et al., 2016), and creating risk maps where species-specific data are scarce (Osawa et al., 2016).

Recent extensions of mechanistic, process-based models have incorporated a high level of complexity (Singer et al., 2016; Synes et al., 2016), reflecting a change in mind-set from the previously favoured simpler models (Evans et al., 2014). These mechanistic models aim for a realistic depiction of individual choices and interactions (Singer et al., 2016). More complex mechanistic models allow researchers to further explore virtual ecology questions using realistic simulations of animal behaviour, so as to investigate the interacting effects of animal behaviour and study methodology in greater detail. Hence, they have the potential to offer new and exciting insights into study design.

Numerous studies have investigated the effects of time between fixes and measurement error on the accuracy of telemetry data (Di Orio et al., 2003; Frair et al., 2004; D’Eon et al., 2005; Jerde and Visscher, 2005). However, none have attempted to provide a standard methodology for correcting estimates of metrics calculated from telemetry data. By using a mechanistic model with a known value for ‘step length’, we can identify percentage errors for fix intervals using different movement types in order to quantify the accuracy of the correction methodology. Given that the level of tortuosity in the movement path may affect the relationship between fix interval and the accuracy of metrics (Mills et al., 2006), we can additionally investigate how movement style affects accuracy. Models of different patterns tend to include only two varieties of movement style: short, torturous steps or long, straight steps (e.g. Beyer et al., 2013). True movement patterns, however, will have more complexity, with various levels of directional persistence (preference to move in the same direction as the previous step) and fine-scale habitat selection, such as avoidance or attraction to trails and rivers. Models that assume movement models based on ideal gas movement or Monte Carlo random walks (Rowcliffe et al., 2008; Howe et al., 2017; Nakashima et al., 2018) fail to account for fine-scale habitat selection. They may thus be less suited to organisms that inhabit dense forest and move principally along trails. To our knowledge, no studies have employed simulation models that are able to incorporate fine-scale habitat selection in analyses of telemetry data.

Our aim is to use an agent-based model (ABM) to develop a method for correcting estimates of movement metrics derived from telemetry data. The method defines the relationship between fix interval and estimates for six different movement types using nonlinear regression. In order to achieve this, we modified a spatially-explicit ABM of jaguar movements through Cockscomb Basin Wildlife Sanctuary in Belize, so as to simulate six movement types: a random walk, a least-cost walk using fine-scale features to calculate cost, and four models that used a least-cost walk with varying levels of directional persistence. We based the model on the ABM presented in Watkins et al. (2015), which includes interactions between agents and their environment. We constructed the model on similar mechanistic principles of pheromone-based movement to those described in Watkins et al. (2015), however restructured the model to accommodate responses to fine-scale terrain, and gender-specific responses to both pheromone and terrain. The fine-scale terrain features simulated in the model included trails and river systems, representing features that are known to affect the movement of large felids (Harmsen et al., 2009). Our model did not incorporate birth and death dynamics as the simulated period was short, hence we assumed that birth and death dynamics would have little effect on the outcome of the model. We ran in-silico telemetry studies with fix intervals ranging from 2 hours to 48 hours and from these studies we derived step length and MCP for multiple sampling regimes. We selected MCP as opposed to kernel in order to avoid potential bias from choice of the smoothing parameter *h* in kernel calculation (Calenge, 2015). We applied nonlinear regression in order to characterise the relationship between fix interval and accuracy of these metrics for the six movement types.

3.2 Methods

3.2.1 The model

Chapter 2 details the study site, study species and algorithm for the model (Parts 2.2.1, 2.2.2 and 2.2.4, respectively). We handled data and statistical analysis using a combination of Python and R. The simulation model in this study ran on a grid of cells, each representing

240 × 240 m. We used this coarser resolution due to the time taken to run the model for a large set of movement patterns. Moreover, a finer resolution was not required to answer the study question for this particular chapter. For each set of parameter values, the model ran for 17,520 time steps, simulating 2 years at 1 simulated hour per time step. Table 1 provides a list of parameters for the movement model using a least-cost path algorithm to select movement paths. All other movements include either wholly random movement, or a combination of directional persistence and least-cost path to define movement rules.

Table 1. Input parameters for the ABM using least-cost path choice-based movement algorithm.

Parameter	***Abbreviation***	***Value***
(a) Pheromone-related, determining interactions amongst individuals		
Population size	Po	50
Pheromone placed by agent each turn	Ph	77.00
Pheromone decay rate	PhD	0.92
Cost of females to males	CFM	-39.00
Cost of males to females	CMF	-1.00
(b) Parameters determining interactions with the abiotic environment		
Male distance to water multiplier	MDW	-0.18
Female distance to water multiplier	FDW	-0.06
Male distance to trail multiplier	MDT	0.39
Female distance to trail multiplier	FDT	0.05
Male trail square cost	MTr	-6.00
Female trail square cost	FTr	14.00
Male slope multiplier	MS	2.51
Female slope multiplier	FS	3.00
Male altitude multiplier	MA	0.47
Female altitude multiplier	FA	0.48

3.2.2 Raw data format

The model stored data in one text file, representing a virtual telemetry study. It wrote to this file at the end of each time step. The model wrote each agent's location and attributes to the telemetry file. The telemetry file also included information on the time step and replicate number.

3.2.3 Data analysis

We ran the simulation model 72 times for each of the six movement types using a combination of the Iridis supercomputer at the University of Southampton, 1 desktop computer and 1 laptop. One replicate of the simulation model took approximately 4 hours to run.

We calculated step length and MCP within the simulation model for each run using custom-built Python files for a fix interval of 1 hour, which represented our control (henceforth 'actual') value for each run, and for a test fix interval, which was between 2 and 48 hours. We scaled all step lengths down to a step length for 1 hour and found the difference between calculated values and control values for each run. We used the difference in metrics to calculate percentage errors at different fix intervals.

For all values, we tested three possible regression models for the relationship between error in metric between simulation runs and fix interval used for the simulation. We tested regression models by fitting parameters using the nonlinear least squares (*nls*) function in the R library *stats*. We then calculated the correlation between predicted y values from the regression model and actual y values from the difference between the simulation model at different fix intervals, which provided a rough estimate of goodness of fit. We used the correlation (*cor*) function in the R library *stats* to calculate the correlation. Although the correlation between the list of predicted y values and the list of actual y values is not a perfect measure of goodness of fit, it allowed comparison between the different nonlinear regression models in absence of the usual goodness-of-fit measures associated with linear regression models (for example, R^2). The dependent variable was defined as the difference between the estimated metrics, and the independent variable was defined as the fix-interval length. Once we had selected the equation that best characterised the relationship between fix interval and difference in metric for both step length and MCP, we used the *nlsList* package in the R library *nlme* (Pinheiro et al., 2017) to calculate the different parameter values for the equation corresponding to the regression model.

After defining the relationship between estimate and fix interval, we calculated a corrected estimate for the metrics by substituting $x = 0$ into the equation for the nonlinear regression. We repeated nonlinear regression for each movement type and calculated movement-specific corrected estimates.

3.3 Results

3.3.1 Step length

As the length of fix intervals increased, the difference between the estimated and actual step length increased (Table 2). Estimated step length decreased sharply at shorter fix intervals and then appeared to level out at longer fix intervals. A 2-hour fix interval had estimates for step length that were approximately 75% the size of the actual step length. Fix intervals of 10 hours and 30 hours resulted in estimates for step length that were respectively ~35% and 20% the size of the actual step length.

Table 2. Estimated values with percentage errors for different fix intervals. Actual value for step length is 240 m.

Fix interval (hrs)	*Estimated step length (m)*	*Percentage error (%)*	*Difference between actual and estimated step length (m)*
2	178	25.8	62
4	128	46.7	112
6	105	56.2	135
8	91	62.1	149
10	81	66.3	159
12	75	68.8	165
14	69	71.3	171
16	65	72.9	175
18	61	74.6	179
20	58	75.8	182
22	55	77.1	185
24	53	77.9	187
26	50	79.2	190
28	49	79.6	191
30	47	80.4	193

The regression model that best characterised the relationship between the estimated step length and fix interval had a goodness of fit of 0.891 (Table 3). We can estimate a corrected step length by inserting $x = 0$ into the equation, which represents a minimum fix interval. The resulting estimate for step length is 205 m. This estimate has a percentage error of 14.5%, which nearly halves the percentage error at a fix interval of 2 hours. Thus, we achieve close to double the accuracy of estimation by employing a combination of subsampling and non-linear regression.

Table 3. Models for the relationship between time-lag and estimated step-length with best-fit parameters and goodness of fit for the model.

Model	***Best-fit parameter values***	***Goodness of fit***
$y = \frac{a}{(b + x)}$	*a* = 1640, *b* = 8	0.891
$y = \frac{a}{(b + x^2)}$	*a* = 55100, *b* = 442	0.799
$y = a\sqrt[5]{x} + b$	*a* = -115, *b* = 274	0.862

Upon visual inspection of the data, it appears that the relationship between fix interval and the error in step length depends on movement type (Figure 1). The lines are in the roughly the same sequence as the proportion of directional persistence in the simulation model, whereby simulations incorporating random movement and 20% directional persistence reach a higher asymptote than simulations incorporating lower levels of directional persistence. It may therefore be possible to improve the fit of the regression model (Table 3) by tailoring parameter values to the movement type.

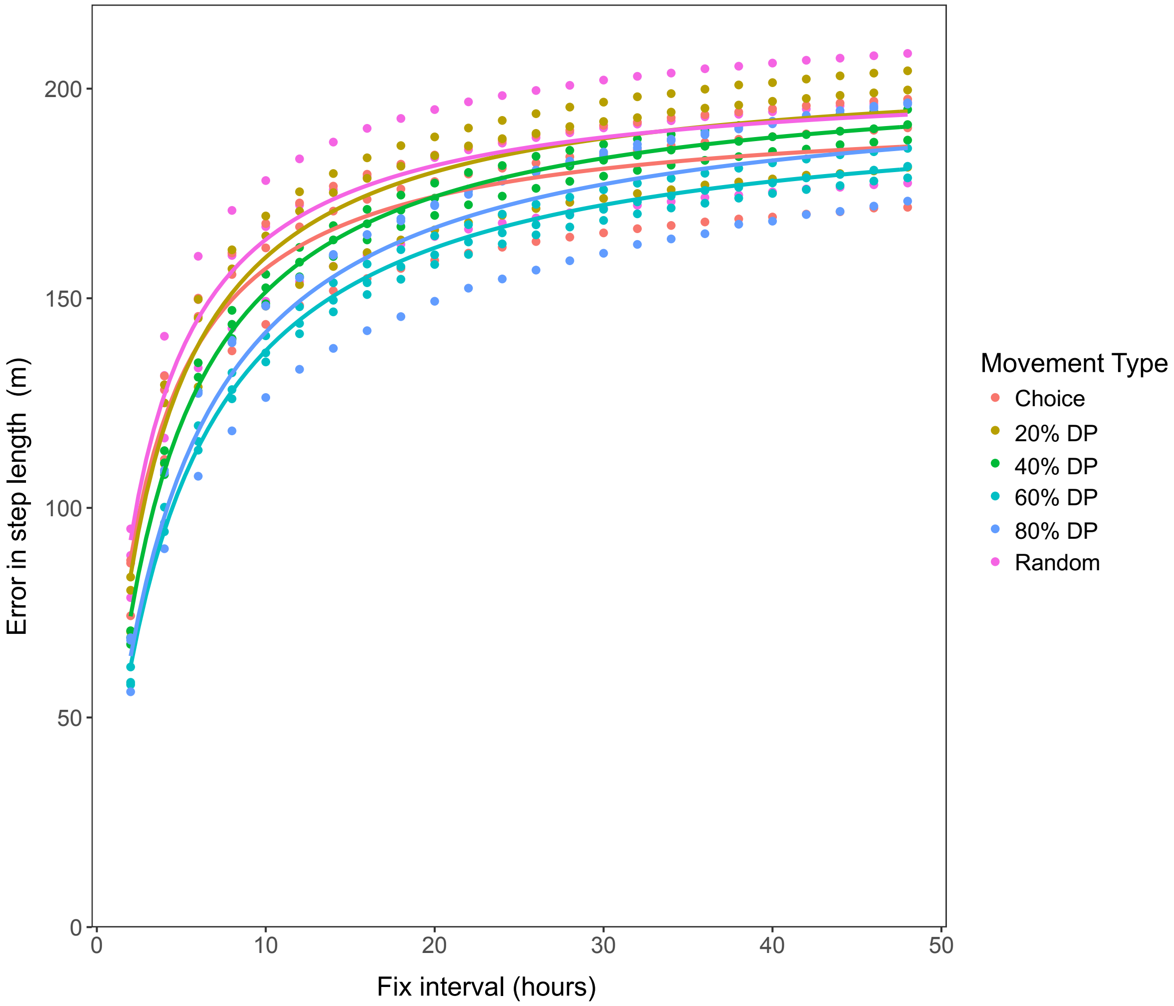

Figure 1. The relationship between time-lag and error (in metres) in step length for six movement algorithms. 'DP' stands for directional persistence. The error represents the difference between the actual step length and the estimated step length.

We calculated movement-specific values for *a* and *b* (Table 4). As directional persistence increased, the values of both *a* and *b* increased. The parameter *a* shifts the graph to the right, indicating that for simulations incorporating higher levels of directional persistence differences in estimated step length began to occur at longer fix intervals than when simulations incorporated low levels of directional persistence. Where fix interval was short, the low probability of tortuous movement in simulations with high directional persistence increased the accuracy of estimates for step length. The parameter *b* determines the steepness of the curve. The best-fit regression models of fix interval and estimated step length for simulations incorporating high levels of directional persistence therefore had steeper inclines than those incorporating lower levels of directional persistence.

Accounting for movement type increased the accuracy of estimate for most movement types. The exceptions to this were the least-cost walk algorithm, which had a similar corrected estimate, and the random movement algorithm, for which the corrected estimate was far lower. The maximum error from movement-specific regression models was 21%, which represents 80% of the error in estimated step length using 2-hour fix intervals. The minimum error was 11%, less than half the error of estimates using 2-hour fix intervals.

Table 4. Best-fit parameter values for different movement algorithms for a model representing the relationship between time-lag and estimated step length. 'DP' stands for directional persistence.

Movement type	***Best-fit value for a***	***Best-fit value for b***	***Goodness of fit***	***Corrected estimate (m)***	***Percentage error (%)***
Least-cost walk	1099	5.4	0.97	204	15
Random walk + 20% DP	1322	6.2	0.98	213	11
Random walk + 40% DP	1623	7.7	0.98	211	12
Random walk + 60% DP	2092	9.9	0.99	211	12
Random walk + 80% DP	2946	14.0	0.98	210	13
Random walk	1001	5.3	0.98	189	21

3.3.2 Minimum convex polygon (MCP)

As the length of fix intervals increased, the difference between the actual and estimated MCP increased (Table 5). As with step length, estimated MCP decreased sharply at shorter fix intervals and then appeared to level out at longer fix intervals. A 2-hour fix interval had estimates for MCP that were approximately 50% of actual MCP. Fix intervals of 12 hours and 30 hours resulted in estimates for MCP that were respectively ~10% and 6% the size of the actual step length.

Table 5. Estimated values with percentage errors for different fix intervals. Arithmetic mean for the actual value for MCP is 254 +/- 4.2 km^2.

Fix interval (hrs)	*Estimated MCP (km^2)*	*Percentage error (%)*	*Difference between actual and estimated MCP (km^2)*
2	131	48.4	123
4	69	72.8	185
6	48	81.1	206
8	38	85.0	216
10	31	87.8	223
12	27	89.4	227
14	25	90.2	229
16	23	90.9	231
18	21	91.7	233
20	20	92.1	234
22	18	92.9	236
24	17	93.3	237
26	17	93.3	237
28	16	93.7	238
30	15	94.1	239

The regression model that best characterised the relationship between fix interval and the difference between actual and estimated MCP had a goodness of fit of 0.767 (Table 6). The models for MCP generally had lower goodness of fit than models for step length, indicating a more complex relationship for the time-lag bias of MCP. We can estimate a corrected MCP by inserting $x = 0$ into the equation. The resulting estimate for MCP is 370 km^2. This estimate has a percentage error of 46%, which is similar to the percentage error at a fix interval of 2 hours. Hence, we were unable to correct our estimate using subsampling and nonlinear regression.

Table 6. Models for the relationship between time-lag and estimated MCP, with best-fit parameters and goodness of fit for the model.

Model	***Best-fit parameter values***	***Goodness of fit***
$y = \frac{a}{(b + x)}$	*a* = 370, *b* = 1	0.767
$y = a.ln(x) + b$	*a*= -28, *b* = 110	0.688
$y = \frac{a}{(b + x^2)}$	*a*=4294, *b* = 33	0.744

The inclusion of directional persistence in the simulations again appears to affect the relationship between fix interval and error in MCP, however the patterns are less clear than those for step length (Figure 2). Simulations employing a random movement algorithm or low levels of directional persistence are higher on the graph, indicating higher levels of error, than simulations employing high levels of directional persistence. The simulation utilising a least-cost choice algorithm has a different curve to the others, increasing rapidly at the start and reaching an asymptote at short fix intervals.

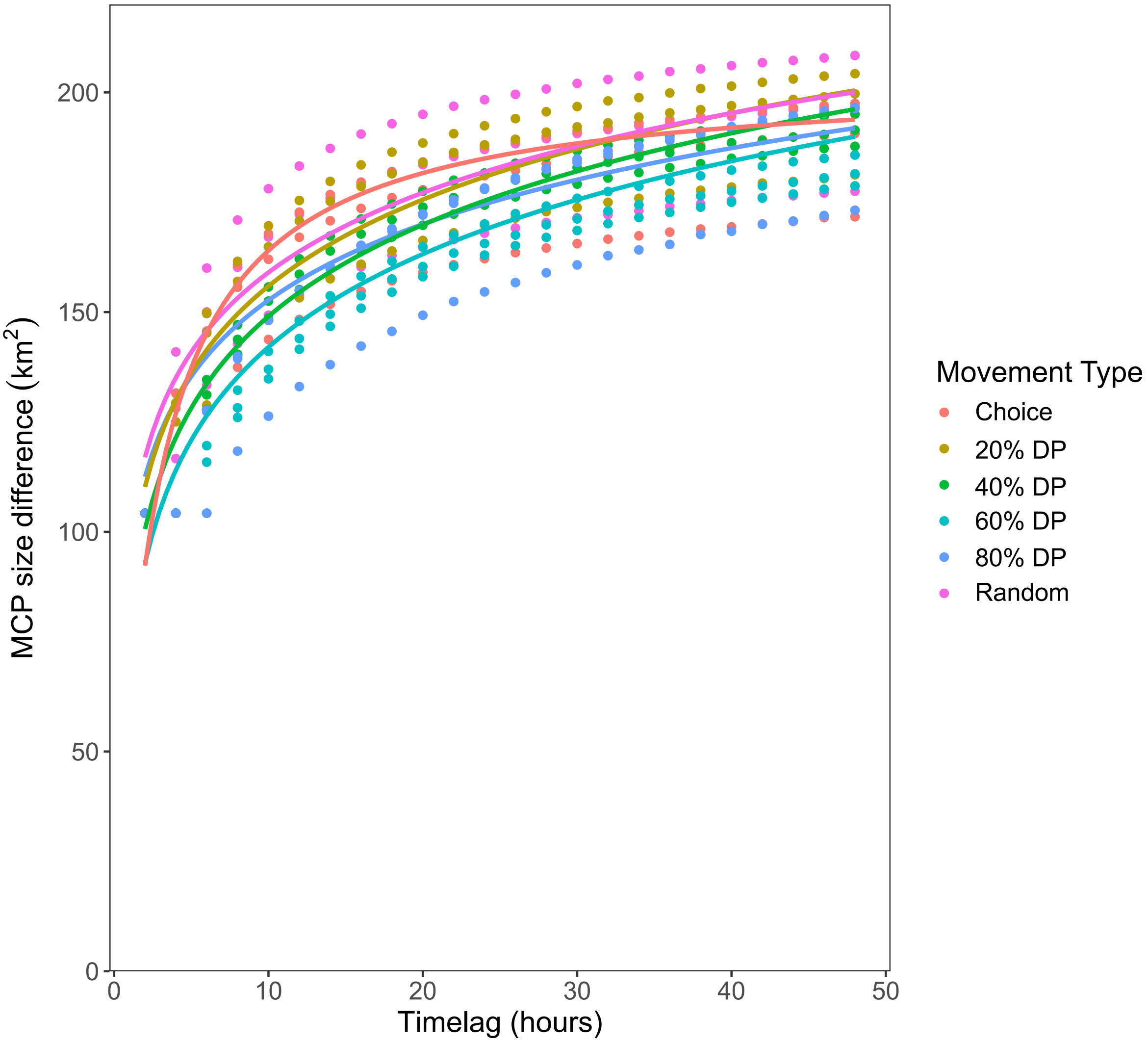

Figure 2. The relationship between time-lag and error (in metres) in MCP for six movement algorithms. 'DP' stands for directional persistence. The error represents the difference between the actual step length and the estimated step length.

We calculated movement-specific values for *a* and *b* (Table 7). There is no obvious pattern in values for *a* and *b* as directional persistence increases. Moreover, the corrected results are more mixed than those for step length. Overall, tailoring the results to movement type increased the accuracy of corrected estimates. Corrections for simulations that incorporated low levels of directional persistence decreased percentage error from estimates taken at 2-hour fix intervals by 80-90%. However, corrections for simulations that incorporated 60% directional persistence had a greater error than estimates taken at a 2-hour fix interval. There may be an equation that better explains the interaction between fix interval and MCP estimate for simulations employing 60% directional persistence. Fitting a more appropriate equation may go some way to solving the discrepancy between the results for these particular simulations and the other simulations.

Table 7. Best-fit parameter values for different movement algorithms for a model representing the relationship between time-lag and estimated MCP. 'DP' stands for directional persistence.

Movement type	***Best-fit value for a***	***Best-fit value for b***	***Goodness of fit***	***Corrected estimate (m)***	***Percentage error (%)***
Least-cost walk	357	1.1	0.82	324	28
Random walk + 20% DP	381	1.4	0.77	272	7
Random walk + 40% DP	364	1.5	0.84	243	4
Random walk + 60% DP	382	0.95	0.82	402	58
Random walk + 80% DP	478	2.4	0.82	199	22
Random walk	284	1.0	0.84	284	12

3.4 Discussion

In this study, we employed an agent-based model to investigate how fix interval increases the error between estimated and actual values for metrics derived from telemetry data. Agent-based models provide users with an in-silico environment where they can set known values for metrics of interest to allow their comparison with estimated values. We corrected estimates for two metrics by subsampling the data and defining an equation that best described the relationship between fix interval and estimate. By characterising the relationship, we can utilise percentage errors at certain fix intervals to identify a fix interval suitable for future studies, with a given threshold of acceptable error. The next stage in this process is to evaluate whether empirical studies can repeat this methodology for real ecosystems, and therefore whether the combination of subsampling and non-linear regression should become a standard method for correcting calculations from telemetry data. It is important that researchers account for bias in their calculation of home range and step length estimates so that models and strategies that include estimates for these metrics are as accurate and reliable as possible.

The final methodology, which we present to other authors for standard use in telemetry studies, is described below. To follow the method, researchers require data on the locations of a particular individual, and temporal metadata for the data points. Obtaining meaningful results from the method requires sampled fix intervals to be shorter than the fix interval at which the graph reaches its asymptote.

1. Subsample data to represent a range of fix intervals;
2. Calculate movement metrics at different fix intervals;
3. Use regression, non-linear or otherwise, to define the relationship between fix interval and the estimate for a metric;
4. Find a corrected estimate by inserting $x = 0$ into the equation.

We demonstrated how correcting the step length metric greatly reduced its error. The results for the MCP metric were more mixed, however accounting for the specific movement algorithm used greatly increased the accuracy of corrected estimates.

We showed that fix interval caused errors in step length up to 80% of actual values. Our findings agree with the findings of Mills et al. (2006) that long fix intervals result in underestimation of movement distance when individuals move in tortuous paths. The trend in increasing error with step length echoed that of Mills et al. (2006), who noted sharp increase in error of step length at initial fix interval increases followed by an asymptote. The authors referred to this as ‘logistic decay’ in the value of their metric. Logistic decay may arise due to the natural limit on amount of error. As the error can never be greater than the actual step length, the relationship between error and fix interval must therefore be asymptotic, characterised by a steep slope that becomes gradually less extreme.

Researchers may parameterise movement models with estimates for step length (Beyer et al., 2013). Applications for movement models include investigation of habitat selection (Turchin, 1998; Johnson et al., 2002; Morales and Ellner, 2002; Forester et al., 2007) and foraging behaviour (Weimerskirch et al., 2002). Findings from these models may then contribute to strategies for conservation management. If potential error of estimates is as much as 85% bias in step length, stakeholders utilising these models may develop inappropriate or insufficient plans for conservation action. Given the various uses of step length, and the potential consequences of using incorrect data where models inform conservation actions, it is imperative that researchers understand and highlight potential caveats in their calculations.

Error in estimates for MCP also increased as fix interval increased, however the pattern was more difficult to characterise than that for step length. This led to greater difficulty when applying correction factors for the MCP. There may have been an equation or pattern that was more appropriate for characterising the relationship between error in MCP and fix interval, which would have resulted in more appropriate correction factors. Furthermore, different movement models may have required wholly different equations. This would also have improved the accuracy of correction factors for particular movement models. The general pattern of increase in error with fix interval agrees with the pattern found by Kolodzinski et al. (2010), and by Mills et al. (2006), of significant biases from low-intensity sampling of location data. Home range calculations allow stakeholders to understand how animals select and utilise habitat, and thus may contribute to design of reserves and areas of conservation (Jenks et al., 2015). Here we selected MCP due to its practicality for a large sample size of replicates, however kernel analyses represent an alternate method for home range calculation (Girard et al., 2002; Mills et al., 2006). Although low-intensity sampling does affect estimates of home range from kernel analyses, the estimates are less sensitive to sampling rate than estimates of MCP (Boulanger and White, 1990; Kenward, 2001; Mills et al., 2006). We therefore recommend using kernel analyses rather than MCP to estimate home range, especially where the interval between fixes is large.

Our studies are consistent with the findings of previous authors (Mills et al., 2006. Kolodzinski et al., 2010) that fix interval affects the accuracy of metrics derived from location data. Our study expanded their findings by identifying a method for correcting metric estimation. We agree with their recommendations that the shortest fix interval possible should be chosen when conducting telemetry studies, especially where researchers suspect tortuous movement patterns indicative of foraging behaviour. However, there is a trade-off between length of fix interval and length of study, as sampling at short intervals reduces the lifetime of batteries in transmitters (Mills et al., 2006). Furthermore, even when intervals are set at relatively short periods of time, sampled fix intervals may be substantially longer. Fix intervals in conventional telemetry depend on weather conditions, accessibility of study sites and availability of personnel (Girard et al., 2002). GPS technology has increased both precision and accuracy of fixes, however the success of fixes still depends on terrain and cover (Frair et al., 2004). This may further bias results by disproportionately affecting fixes in areas of heavy canopy. It is in these scenarios that authors may use subsampling and non-linear regression to correct estimates.

One limitation of our study was that it didn't capture the trade-off between fix interval and study length. In this study, an increase in fix interval resulted in an increase in error of MCP estimation. However, an increase in fix interval would result in longer lengths of study, which was not incorporated in this chapter as the simulation runs were limited to a constant length of time. A greater study length would allow greater coverage of the study area, despite the increased fix intervals. Hence, this may remove the error associated with increased fix interval. Furthermore, a longer study length would better account for seasonal changes and annual changes. Therefore, an increase in fix interval may actually result in a more accurate calculation of MCP by enabling longer study periods. Nevertheless, shorter study lengths with shorter fix intervals may capture 'brief but long-distance forays' (Frair et al., 2010). The prioritisation of study length over fix interval, or vice versa, is linked to how authors define a home range in time and space: whether they discount short forays as outliers and whether they time-bound home ranges that may move from one season to the next. We recommend that authors consider the trade-off and its implications in detail before deciding on the methodology for their study.

Understanding the nature and underlying mechanisms of animal movement enables researchers to predict responses to anthropogenic change, identify metapopulation dynamics, and investigate the transmission of disease through a population (Bradshaw et al., 2007). It remains a key area of research in ecology (Beyer et al., 2013; DeMars et al., 2013). Many species of conservation concern are elusive and span large areas. Telemetry represents one of the most commonly utilised methods for sampling animal locations, providing large datasets that one can exploit to determine behaviour and parameterise predictive models (Jenks et al., 2015). Despite the biases we present here, telemetry will continue to augment knowledge and understanding of wildlife (Harbicht et al., 2017). By demonstrating how fix interval may increase the error associated with metrics derived from movement data, we hope to highlight caveats, provide a method to correct for error, and to corroborate the warnings of previous authors that fix intervals should be kept as short as possible in order to prevent large inaccuracies and bias.

We can use virtual ecology as a tool to help us understand the effectiveness of empirical methodologies (Zurell et al., 2010). Using mechanistic models in virtual ecology studies, we can highlight biases and caution against certain interpretations that researchers may draw from current methods. The limitations of virtual ecology depend on the model we select for a virtual ecology study. It is important that we capture the behaviour required to evaluate the methodology under study. Agent-based models are mechanistic rules-based models that allow behaviour patterns to emerge from the bottom upwards, making them well-suited to virtual ecology studies. Methods that do not work well in the model will likely not work in reality (Zurell et al., 2010). Thus, we caution against telemetry studies that trade shorter fixed intervals for a longer study duration, especially where these telemetry studies will inform conservation management or parameterise movement models.

Chapter 4.

Using a high-resolution mechanistic model to evaluate anthropogenic impacts on jaguar populations

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Chapter 4. Anthropogenic impacts

Abstract

Apex predators play a vital role in ecosystem maintenance and function, yet they have suffered disproportionately from human-induced rapid environment change (HIREC). Recent advances in computing have facilitated the creation of complex, mechanistic models that simulate movement, and can help predict animal behaviour in response to HIREC. We develop a mechanistic model of predator movement within a wildlife corridor to investigate the responses of agents, representing jaguars, to three anthropogenic effects: deforestation, wildmeat hunting, and persecution in response to livestock depredation. Probability of a depredation event, and resultant persecution, was a key factor in both the number of agent deaths and number of agents traversing the corridor. The estimated depredation probability rose almost eight-fold when depredation and deforestation had interacting effects. However, the interaction effect was less pronounced when forest thinning caused the deforestation as opposed to land conversion. The relationship between the simulated anthropogenic stressors and the number of agents crossing the corridor area was less obvious than the relationship between anthropogenic stressors and agent deaths. The best-fit model for number of agents crossing the corridor included both deforestation and probability of depredation. Neither the best-fit model for number of agent deaths nor the best-fit model for number of agents crossing the corridor included the probability of a wildmeat hunting event occurring. The number of agents crossing the corridor area depended on the number of agent deaths, indicating the emergence of an ecological sink within the model. The model has demonstrated the utility of complex, mechanistic models in conservation and has highlighted areas for future research.

Key words: agent-based model; bushmeat; human-wildlife conflict; landscape configuration

4.1 Introduction

Apex predators are important for ecosystem regulation and maintenance (Kelly, 2003; Watkins et al., 2015). However, human-induced rapid environmental change (HIREC) has led to a global decrease in range for the majority of large carnivores (Parmesan, 2006; Sih, 2013; Wolf and Ripple, 2017). Land-use change and human encroachment place humans and wildlife in close proximity, resulting in conflict as they compete for food and space (Urquiza-Haas et al., 2009). Advances in computing have allowed the development of complex mechanistic models that simulate animal behaviour, and attempts to predict how wild populations respond to HIREC (Singer et al., 2016; Synes et al., 2016). Here, we use a mechanistic model to investigate the dependencies of agents representing solitary carnivores on three interacting anthropogenic factors: deforestation, wildmeat hunting by humans, and livestock depredation that results in persecution by farmers.

Anthropogenic land-use change is one of the principal drivers of biodiversity loss (Sala et al., 2000). Humans have converted 40 - 50% of the global ice-free land surface into agricultural or urban terrain (Chapin et al., 2000). Activities associated with agriculture may be responsible for 70% of projected biodiversity loss in terrestrial taxa (Secretariat of the Convention on Biological Diversity, 2014). Land-use change is associated with massive deforestation. Anthropogenic land-use change or natural causes destroyed around 130,000 km^2 of forest between the years 2000 and 2010, with South America and Africa suffering the largest net loss of forest habitat (Secretariat of the Convention on Biological Diversity, 2010). Deforestation disproportionately impacts large-bodied predators as they require large home ranges (Urquiza-Haas et al., 2009). For example, de la Torre et al. (2017) suggested that female jaguars require patches of at least 180 km^2 of primary forest to meet their space requirements. Although some predators are able to inhabit unprotected areas (Boron et al., 2016), contact with agricultural regions increases the risk of livestock depredation and persecution as pests.

Unsustainable hunting of wildmeat significantly threatens many wild mammal species, including large predator species that hunters do not target (Ripple et al., 2016). Hunting has been responsible for the extinction of 12 species of vertebrate in Vietnam over the past five decades (Bennet and Rao, 2002). Most target species are large, K-selected mammals, whose low reproductive rates cause them to be more susceptible to hunting than smaller r-selected species (Mangel et al., 1996; Peres and Palacios, 2007). Hunting interacts with deforestation and fragmentation to further impact large-bodied animals, as larger species are often the first targets for wildmeat hunters (MacDonald et al., 2011; Ripple et al., 2014; Ripple et al., 2015). Population declines in large mammals can also impact on species at other trophic levels through trophic cascades, thereby disrupting entire communities (Peres, 2000; Osuri et al., 2016; Peres et al., 2016). Wildmeat hunting may result in competition between humans and large carnivores for food. In Belize, for example, 7% of protein-containing meals include meat from one of six wild species (Foster et al., 2016). These species are the nine-banded armadillo, paca, collared peccary, white-lipped peccary, red brocket deer and white-tailed deer: species that make up large proportions of jaguar and puma diets in Belize (Foster et al., 2016). Thus, humans in Belize put themselves in competition with large felids, with implications for predator abundance.

Livestock frequently appear in large-felid diets across the globe (Ghoddousi et al., 2016; Babrgir et al., 2017). Livestock losses due to large-felid depredation affect small economies and livelihoods (Inskip and Zimmermann, 2009). As a result, many stakeholders view large carnivores as pests (Babrgir et al., 2017), with local farmers potentially opting to poison or shoot large felids in order to protect their livestock (Treves et al., 2016; Trinkel et al., 2016). Lethal prevention is the main method of pest control for management of populations of large carnivores (Treves et al., 2009). For felids, direct persecution may represent a large proportion of mortalities in some areas. For example, Trinkel et al. (2016) found that within their study period, human-wildlife conflict caused almost 50% of lion mortalities on the border of Etosha National Park. Sub-adult males and adult females represented the majority of persecuted individuals, and this had second-order effects on the population structure of lion prides (Trinkel et al., 2016). However, non-lethal methods can present a more effective form of pest control than lethal methods (Treves et al., 2016). Moreover, wildmeat hunting and deforestation may augment the deleterious effects of direct persecution where deforestation places wildlife in closer proximity to humans and where hunting depletes the preferred prey of large predators (Ripple et al., 2014; Khorozyan et al., 2015; Ghoddousi et al., 2016).

Deforestation, direct persecution and wildmeat hunting have interacting effects. Land-use change (LUC), the construction of roads, commercialisation of hunting and the technological advance in hunting weapon technology have all led to the increase in wildmeat hunting (Peres, 2000; Wilkie et al., 2000; Milner-Gulland and Bennet, 2003; Wolfe et al., 2005). Inhabiting non-protected areas puts large carnivores into contact with livestock, increasing the risk of livestock depredation. Moreover, depletion of prey may cause jaguars to look for other prey sources, such as livestock. Previous studies have used mechanistic models to investigate the effects of manmade activities on carnivore populations (Kanagaraj et al., 2013; Watkins et al., 2015), but focus solely on the effect of landscape configuration. Direct persecution arising from livestock depredation and hunting may interact with landscape configuration, resulting in unintuitive effects undetectable in models that only account for deforestation. To implement suitable conservation policy, decision makers require an understanding of how multiple key threats interact to impact on the behaviour of large carnivores. Identifying how factors interact will help predict how large carnivores will respond to future HIREC. Identifying and quantifying interacting effects requires independently-replicated response measures across balanced combinations of levels often not available in the field. The difficulty in obtaining these conditions has meant that none have attempted to quantify the interacting effects of different anthropogenic threats on large felids. Virtual ecology provides an environment where modellers can explicitly control all variables, thereby facilitating the quantification of interactions that are otherwise unquantifiable without considerable bias.

Here, we use a high-resolution agent-based model of fine-scale felid movement decisions, developed in Ball et al. (Chapter 3), to evaluate the effects of interacting factors on agent movement across a corridor area in Belize. The model incorporates agent avoidance of hunted forest, persecution of agents in response to depredation events, and five deforestation scenarios. The deforestation scenarios represent differences in both forest loss and forest configuration (Fahrig, 2003). We evaluate interactions between the factors by investigating all three using one model. To our knowledge, there exists no other mechanistic model that evaluates the interacting effects of multiple anthropogenic impacts on large-bodied predators.

4.2 Methods

4.2.1 Study site

Belize covers a mainland area of 21,800 km^2 (Lands and Survey Department, 2015; United Nations Development Program, 2015). At 61%, it has the highest percentage of forest cover of any country in mainland Central America (FAO, 2010), with current or candidate protected areas taking up 43% of its mainland (Foster et al., 2016).

The Central Belize Corridor is a Darwin Initiative project that sought to secure a tract of land across the centre of Belize for use as a wildlife corridor, preserving a link along the

Mesoamerican corridor network at this particular latitude (Watkins et al., 2015). Other objectives included improving the monitoring of the jaguar populations in the area, increasing awareness and education, and encouraging sustainable harvesting of species. Threats to jaguars in this area are the central Belize highway, human hunting, fire and land conversion (Watkins et al., 2015). The result of this initiative has been the establishment of the first wildlife corridor in Belize, with support and recognition from the Belize government. It consists of 872 km^2 of forest, and connects the north and south forest blocks of Belize, forming part of the Mesoamerican corridor.

The study area consists of the 598 km^2 area comprising the full extent of the Central Belize Corridor. The corridor area consists mostly of broadleaf forest with some lowland savannah and agricultural areas. Although forest cover remains high in Belize, it has become partitioned into northern and southern blocks that converge to a single connecting strip of forest just 20 km wide and bisected by the Western Highway, the country's busiest trunk road. Without the corridor to protect this narrow strip from encroaching urbanisation and multinational agricultural ventures, Belize's southern and northern borders would no longer be linked by contiguous forest, and the isolated southern forest which currently supports up to 8 jaguars per 100 km^2 would not sustain viable populations of large cats (Foster et al., 2010). This would break the integrity of the Mesoamerican Biological Corridor, containing 106 critically endangered species, as no other connection exists between northerly and southerly forests at this latitude anywhere from the Atlantic to the Pacific.

Figueroa (2013) estimated the Belizean jaguar population at 446 – 754 individuals. However, the actual number probably lies towards the lower end of this range (Figueroa, 2013), with 276 – 531 of these inhabiting the networks of protected areas, 211 – 462 in the southern block, and 65 – 69 in the northern block (Figueroa, 2013). Half of all forest in Belize lies outside protected areas (Figueroa, 2013), and these areas contain the remaining 170 – 223 jaguars (Figueroa, 2013). The population of jaguars in the north-east of the country is unlikely to be viable in the long-term (Figueroa, 2013). The Western highway separates the two blocks of protected area networks (Figueroa, 2013). Although some mammals such as jaguars, pumas and tapirs cross highway barriers, white-lipped peccaries may no longer cross this road (Figueroa, 2013).

4.2.2 The base model

Here we use the agent-based model validated in Ball et al. (Chapter 2). Appendix I describes the model in full, with an Overview, Design Concepts, and Details document (Grimm et al., 2006). The model ran on a grid of 40 × 40 m squares, covering the entirety of the Central Belize Corridor. The Central Belize Corridor contains urban areas and bodies of water. Agents could not enter either of these areas in the model. Table 1 includes a list of parameters for the model.

The model contained an indefinite number of agents. Despite the reduction in realism associated with this assumption, the simplification allowed us to focus on the interacting effects without confounding the findings with complicated birth and death dynamics. The inclusion of realistic birth and death dynamics could have destabilised the model, and would have required more computing power to run. As a consequence, the number of deaths and number of crossings could increase indefinitely to unrealistic values, whereas in reality they would have reached an asymptote as the population of jaguars fell. We advise that readers consider this limitation when interpreting the results from the simulation model.

Table 1. Input parameter values for the ABM.

Parameter	**Abbreviation**	**Value**
(a) Pheromone-related, determining interactions amongst individuals		
Population size	*Po*	42
Pheromone placed by agent each turn	Ph	77.00
Pheromone decay rate	PhD	0.92
Cost of females to males	CFM	-39.00
Cost of males to females	CMF	-1.00
(b) Movement, determining type of algorithm for choosing next cell		
Probability of random movement	R	0.46
Male probability of directional persistence	MDP	0.62
Female probability of directional persistence	FDP	0.16
(c) Environmental parameters, determining interactions with the abiotic environment		
Male distance to water multiplier	*MDW*	*-0.18*
Female distance to water multiplier	FDW	-0.06
Male distance to trail multiplier	MDT	0.39
Female distance to trail multiplier	FDT	0.05
Male trail square cost	MTr	-6.00
Female trail square cost	FTr	14.00
Male slope multiplier	MS	2.51
Female slope multiplier	FS	3.00
Male altitude multiplier	MA	0.47
Female altitude multiplier	FA	0.48
Cost of woodland	W	1.00
Cost of lowland savannah	S	1.00
Cost of agricultural land	A	40.00

4.2.3 Anthropogenic impacts

4.2.3.1 Deforestation

We used the *Create Random Raster* function in GIS to create 4 deforestation scenarios for the study site (Figure 1a-d). 2 deforestation scenarios represented conversion of broadleaf forest to agriculture. For conversion, we removed multiple 1000 × 1000 m blocks of forest, amounting to a total of 33% (Figures 1a) and 66% (Figures 1c) of broadleaf forest in the region. The remaining 2 scenarios for each study site modelled forest thinning. We represented thinning by removing multiple smaller blocks (100 m × 100 m) of forest. The two thinning scenarios for each study site removed 33% (Figures 1b) and 66% (Figures 1d) of forest. Deforestation scenarios were static across replicates.

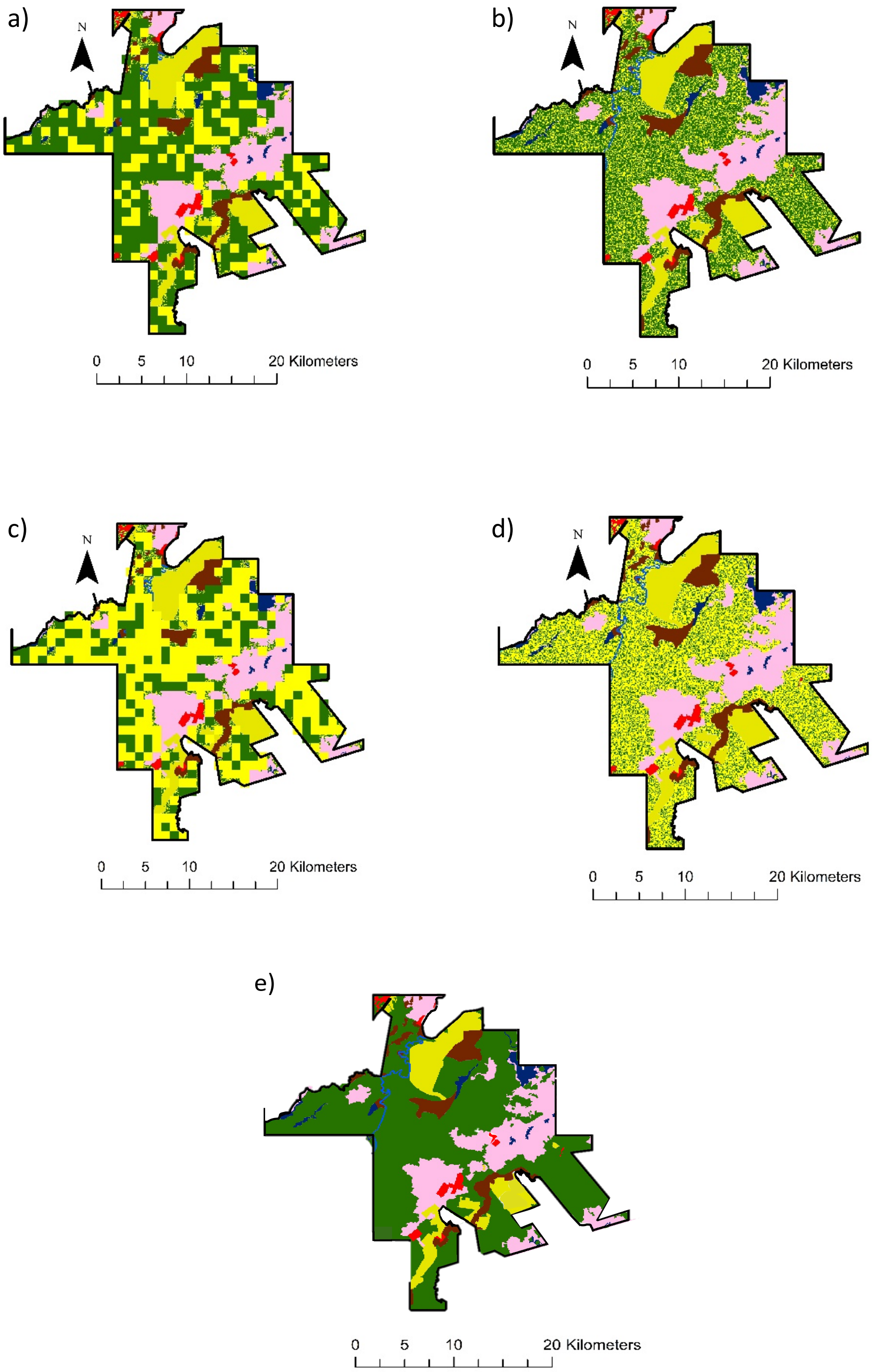

Figure 1. Deforestation scenarios for the model of the Central Belize Corridor. Colours represent habitat types, of forest (green), savannah (pink), agriculture (yellow), urban (red), open water (blue). Scenarios of land conversion in (a) and (c) and forest thinning in (b) and (d) involve 33% deforestation ((a) and (b)), or 67% deforestation ((c) and (d)), relative to the control scenario in (e) with no change from the current distribution of habitat.

4.2.3.2 Wildmeat hunting

A recent study by Soofi et al. (2018) provided evidence for the theory that wildmeat hunting in forests may lead to the depredation of livestock by large carnivores. We incorporated this into the simulation model by creating a sub-model of wildmeat hunting that included a cost associated with humans. The cost forces jaguar agents into the agriculture areas of the map, representing depredation of livestock in response to wildmeat hunting in areas of forest. The human hunting sub-model depended on three parameters: cost of hunting to jaguars, maximum time of cost effectiveness, and chance of a hunting event. We parameterised cost of hunting to jaguars to cause jaguars to choose agricultural areas over forested areas when the forested area was hunted and set the maximum time of cost effectiveness to one modelled day. Every cell had a *human cost* and *time since hunting* attribute. The *human cost* attribute was static and equated to the cost to jaguars of humans hunting their prey. The model created a random number for each forest cell every time step. If that number was less than or equal to the chance of a hunting event, the function set the *time since hunting* attribute to 0, with this *time since hunting* attribute increasing by an increment of one every time step. For any one instance, if the *time since hunting* attribute was above the maximum time of cost effectiveness, the individual would not include *human cost* in cost calculation. Otherwise, if the *time since hunting* was lower than the maximum time of cost effectiveness, the individual would use this cost in neighbouring cell cost calculations.

Table 2. Input parameter values for the wildmeat hunting sub-model.

Parameter	**Abbreviation**	**Value**
Human cost	H	50.00
Time since hunting	TSH	24.00

4.2.3.3 Persecution by farmers

The persecution sub-model ran on three parameters: the probability of the jaguars killing livestock, the probability of a jaguar dying on an agriculture cell, and the maximum time after an agriculture cell losing livestock that jaguars would die on agricultural cells. We ran sensitivity analysis on the probability of death and the maximum time of persecution following a depredation event to assess how these parameters affected the dependent variables.

4.2.4 Statistical analysis

We ran the full model for 1000 runs, consisting of 200 runs for each depredation scenario. We identified sets of parameter values for each run using Latin Hypercube Sampling (Carnell, 2018). Each simulation ran for 219,000 time steps, representing 5 years. We initialised the model with 6 individuals. We calculated number of individuals using figures from Figueroa (2013).

For each replicate, we calculated the number of agent deaths, and the number of agents leaving the corridor by a cell on the opposite side to that which they entered. The latter parameter represented an agent crossing the corridor area. When an agent died or left the corridor, another agent appeared at the edge of the model to replace the agent that had left the model.

We ran general linear models using a Poisson error to investigate whether agent deaths and number of individuals crossing the corridor depended on deforestation scenario, chance of a hunting event, and the probability of jaguars killing livestock. A lower probability of depredation event corresponded to farmers taking further measures to protect livestock. The dependent variables were counts: number of agent deaths and number of agents crossing the corridor area. The independent variables were deforestation scenario, probability of a human hunting event, and probability of a depredation event. We examined residual plots visually to test the assumptions of the general linear models. We employed the Akaike's information criterion (AIC) value of the statistical model to determine which statistical model best fit the data.

We ran sensitivity analyses on any parameters that we had not validated in previous studies (see Chapter 3) and could not determine from known empirical studies. The two parameters that met this criterion were the probability of death and the persecution period following a depredation event. We conducted sensitivity analyses so that we could quantify the potential bias of the selected parameter values.

4.3 Results

4.3.1 Anthropogenic effects on number of jaguar deaths

For the response of number of deaths, the best-fit regression model included deforestation scenario and probability of a depredation event (Table 3; Figure 2). The AIC for the best-fit regression model was 12466 (ΔAIC = 0). The model that included the probability of hunting to the model as an additive effect had a ΔAIC of 1. The model that included both probability of hunting and the interaction between probability of hunting and the other effects had a ΔAIC of 16. This indicated that including probability of hunting had no beneficial effect on the fit of the model. An additive regression model including deforestation scenario and probability of depredation, but no interaction, had the second lowest AIC for models that did not include the probability of hunting (ΔAIC = 535).

The result was 5 possible regression lines (Figure 2), one for each deforestation scenario. The generalised equation for the regression lines is given below in Equation 1. Y represents the number of deaths, α is the intercept where probability of depredation is equal to 0. The value of α is dependent on the deforestation scenario used. For example, if it is the control deforestation scenario then the value would be 11, or 47 (11 + 36) for deforestation scenario A. X is the probability of depredation. β is the slope associated with a particular deforestation scenario (see Table 3), be that deforestation scenarios A-D or the control scenario.

$$Y = \alpha + \beta X \tag{1}$$

Coefficient estimates for the slope of the regression line were relatively high (Table 3), however this was due to the independent variable for depredation ranging from 0 to 1. Therefore, an increase by 1 unit on the x-axis represented an extreme scenario, thus explaining the high estimates for slope. Standard errors associated with the coefficient estimates were generally high compared to the coefficient estimates for the regression slope, resulting in low F- and high p-values. The majority of statistically significant regression equations were associated with the probability of a depredation event, whether alone as a single variable or as part of the interaction with deforestation scenario.

Table 3. Estimates, *F*-values and *p*-values for coefficients from the best-fit regression model for number of agent deaths. Coefficient estimates represent the intercept of the linear regression line for the control deforestation scenario, estimate for the increment the number of deaths increases by for the categorical independent variables (deforestation scenario), and estimate of the slope of the regression line for the continuous independent variables. As depredation is assigned a value between 0 and 1, the value at $x = 1$ would be the highest possible number of deaths. *F*-values are calculated using the value of the estimate compared to its standard error (the higher the standard error in proportion to the estimate, the lower the *F*-value). *p*-values are determined from the *F*-value and sample size.

Coefficient	**Estimate**	***F*-value**	***p*-value**
Control intercept	11 +/- 17	0.65	0.51
Probability of a depredation event (Control deforestation scenario)	2196 +/- 600	3.66	< 0.001
Deforestation scenario A	36 +/- 25	1.46	0.14
Deforestation scenario B	3 +/- 25	0.13	0.90
Deforestation scenario C	45 +/- 25	1.82	0.07
Deforestation scenario D	14 +/- 25	0.58	0.56
Interaction: probability of depredation and deforestation scenario A	15862 +/ 848	18.7	< 0.001
Interaction: probability of depredation and deforestation scenario B	18 +/- 848	0.02	0.98
Interaction: probability of depredation and deforestation scenario C	15916 +/- 848	18.8	< 0.001
Interaction: probability of depredation and deforestation scenario D	10509 +/- 848	12.4	< 0.001

Overall, number of jaguar deaths rose with depredation rate but not with the probability of a hunting event, although the control scenario and deforestation scenario B (forest thinning) did not suffer as large a death rate as other scenarios. Deforestation scenarios A and C, which simulated a 33% and a 66% loss, respectively, with forest removed in 1000 m × 1000 m segments, had similar rates of increase in number of deaths with probability of depredation event (Figure 2). Deforestation scenario D, which represented 66% forest loss by thinning, did not have the same rate of increase as scenarios that modelled removal of forest for agriculture. Nevertheless, the relationship between probability of depredation and number of agent deaths was far more pronounced than the same relationship for deforestation scenario B. For thinning scenarios, there was a 570-fold increase in coefficients for the interaction of deforestation scenario and probability of depredation between the scenario with 33% forest loss and the scenario with 66% forest loss. Hence, although forest loss through thinning appeared to result in a lower number of deaths than forest removal through agriculture, effect sizes increased more rapidly with amount of forest loss. It is unclear from just these two thinning scenarios whether a similar increase in effect size would continue with greater forest loss, however it is interesting to note that forest loss through removal did not have a similar rate of increase.

Deforestation scenario A simulated deforestation through the removal of large blocks of forest, whereas deforestation scenario B simulated forest loss through the removal of smaller blocks of forest. At 33% forest loss, scenarios of forest thinning had a similar number of agent deaths to the control scenario. However, at 66% the results were similar to scenarios with larger segments. Deforestation using larger segments resulted in a more heterogeneous configuration on a landscape scale but a more homogeneous configuration locally. For a scenario with large segments, once an agent was in an area of agriculture, it is more likely that they would be stranded in that agricultural area. Agents in an agriculture cell in scenario B were more likely to be in close proximity to a forest cell, and therefore closer to refuge. As agents in the model preferentially chose forest cells, agents were hence less likely to spend as much time in agricultural cells, reducing the overall number of deaths.

Number of agent deaths depended less on the probability of a hunting event than the probability of a depredation scenario, and it did not appear in the best-fit regression model. The number of agent deaths did not depend on probability of human hunting event ($F_{1, 999} = -0.78$, $p = 0.44$). The model design predicated that incidents of human hunting only occurred in forest cells and increased the cost value of a cell to a level where it became preferable for agents to move to agricultural cells. By decreasing the amount of forest available to agents, deforestation scenarios prevented agents from locating forest cells free of human hunting pressure. Thus, one would expect deforestation to intensify the effect of human hunting on the number of agent deaths during the course of the model. However, this wasn't apparent in the model results. This could be due to the indirect relationship between hunting and deaths –

agents would have to depredate livestock and then move through agricultural squares for a short while after the event – or due to the stochastic nature of the movement model. It could also result from agents moving to neighbouring areas of woodblock rather than agricultural squares, or from agents quickly locating an area of undisturbed woodblock once on an agricultural square.

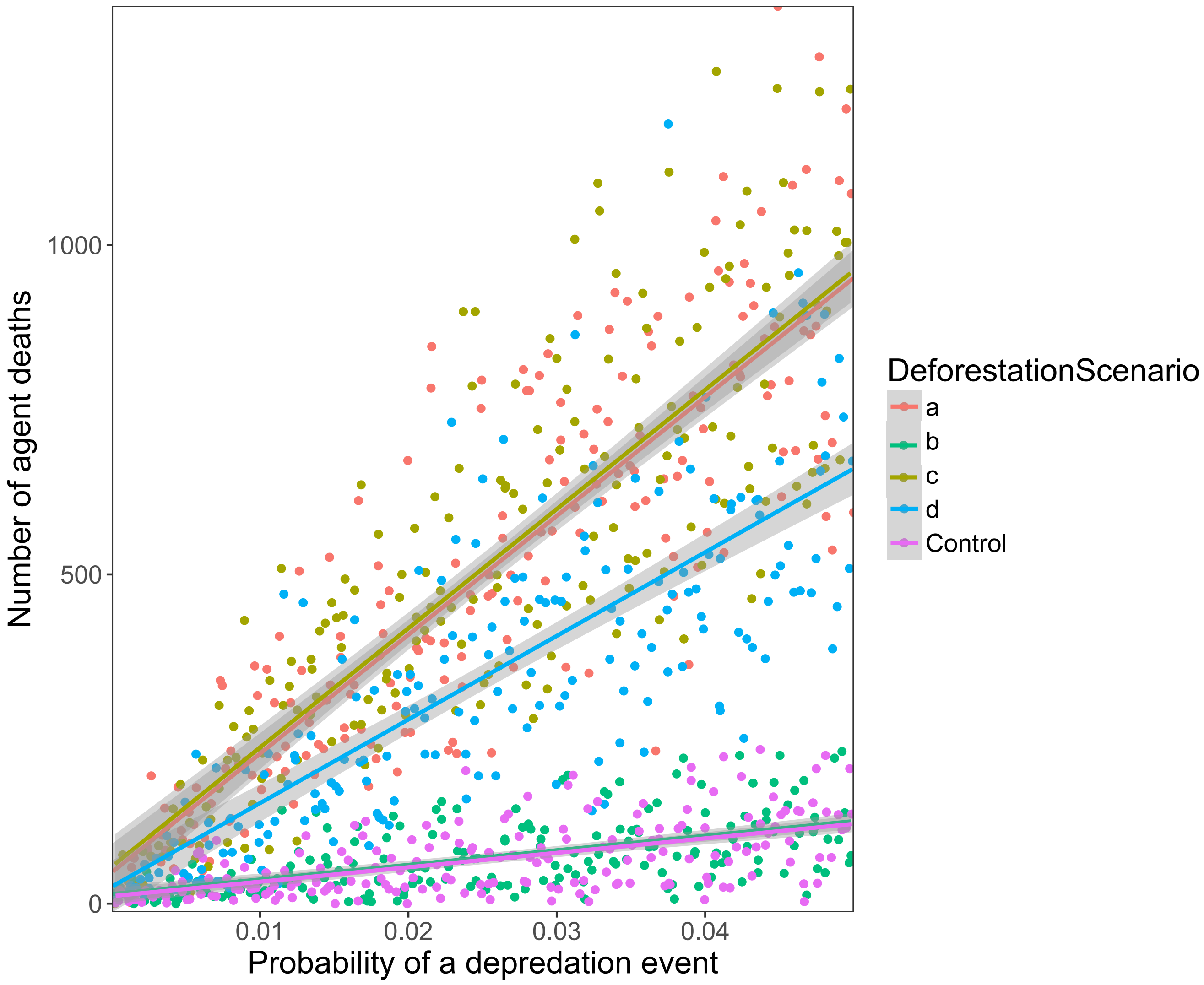

Figure 2. Number of agent deaths as a function of deforestation scenario and probability of a depredation event occurring.

We ran sensitivity analyses at an intermediate probability of depredation (0.25) on the probability of death given a previous depredation event and the period of time for which farmers persecute agents following a depredation event (Figure 3). The number of jaguar deaths during the simulation did not depend on the interaction between the probability of death and the length of a persecution period following a depredation event ($F_{2,96}$ = -0.3, p = 0.74; Figure 3). The number of jaguar deaths during the simulation depended on the probability of death when stepping on a square where they could be persecuted ($F_{1,97}$ = 14.9, $p < 0.001$). The dependency was strong and roughly linear, demonstrating that, despite the stochasticity and complexity in the model, the probability of death affected the number of deaths in an expected way. The number of jaguar deaths did not depend on the length of the persecution period following a depredation event ($F_{1,97}$ = 0.7, p = 0.46).

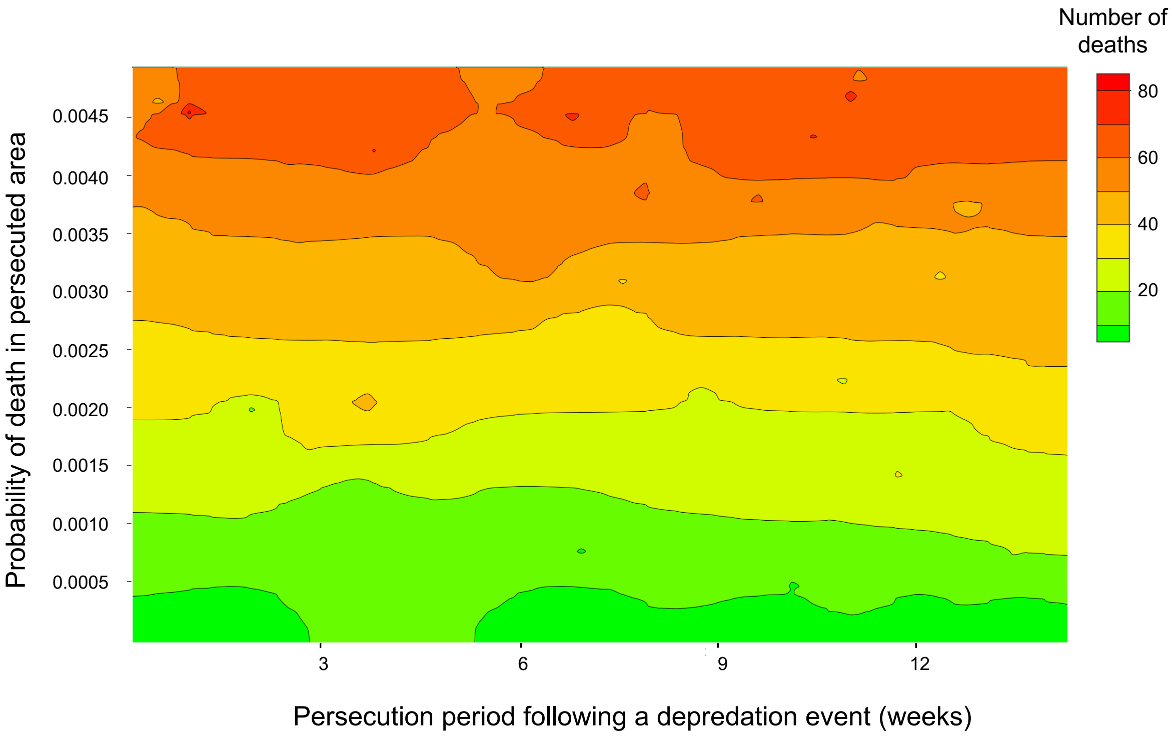

Figure 3. Sensitivity analysis: number of agent deaths as a function of probability of death and persecution period following a depredation event.

4.3.2 Anthropogenic effects on number of corridor crossings

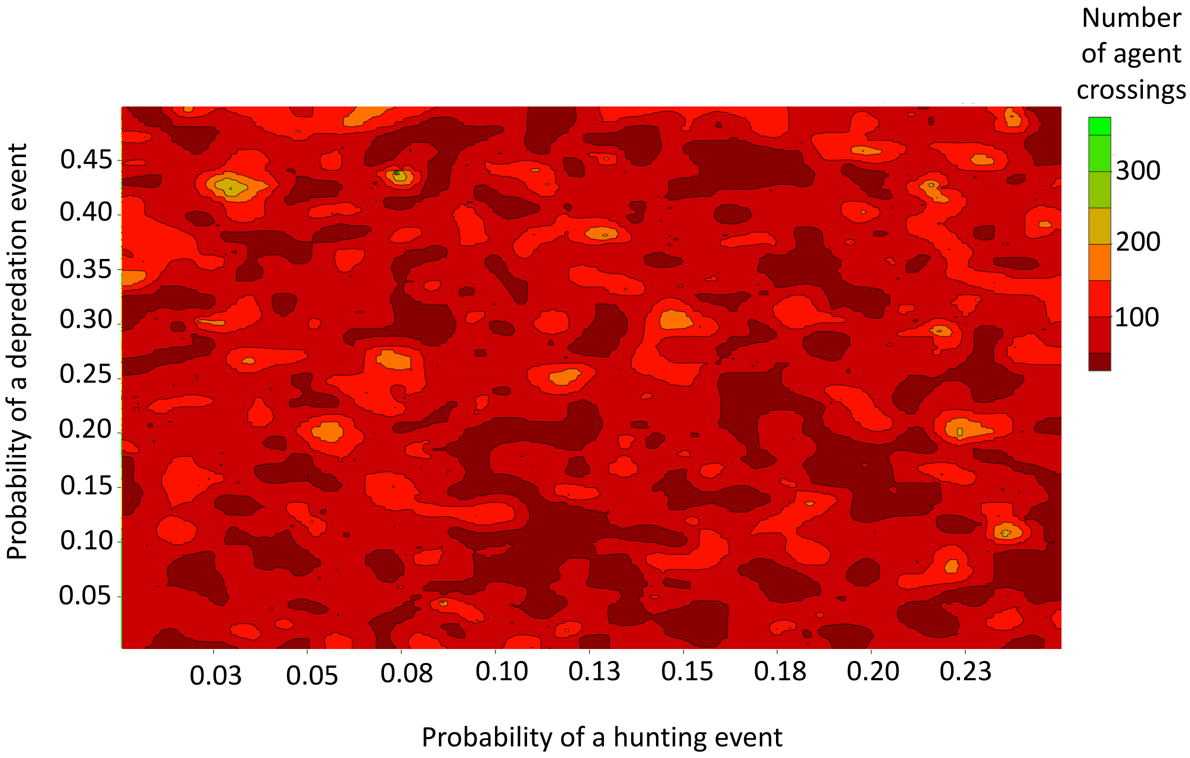

Figure 4. Number of agent crossings as a function of probability of depredation event occurring and probability of a human hunting event occurring.

The effect of anthropogenic activities on the number of corridor crossings made by agents is much less clear than their effect on number of agent deaths (Figure 4). No systematic pattern appears along either of the gradients. Moreover, there is no systematic pattern between deforestation scenarios (Table 4). This could perhaps point to other dependencies, or to the randomness of the movement model.

For the number of agents crossing the corridor, the model with the lowest AIC included probability of a depredation event, the deforestation scenario, and the interaction between depredation and deforestation scenario (Table 4). It did not include the probability of a human hunting event. The AIC for the best-fit regression model was 10579 (ΔAIC = 0). An additive regression model including deforestation scenario and probability of depredation, but no interaction, had the second lowest AIC (ΔAIC = 7). All other models had ΔAIC values greater than 21. As with the number of deaths (section 5.3.1), including the probability of hunting in the regression model had no beneficial effect on the fit of the model to the data.

The generalised equation for the regression lines is given below in Equation 2. Y represents the number of crossings. α is the intercept. α depends on the deforestation scenario. Hence, α is 66 for the control deforestation scenario and 68 for deforestation scenario B (calculated by adding the coefficient estimate for the deforestation scenarios to the intercept value for the control scenario). X is the probability of depredation. β is the slope associated with a particular deforestation scenario (see Table 4), be that deforestation scenarios A-D or the control scenario.

$$Y = \alpha + \beta X \tag{2}$$

Coefficient estimates for the slope of the regression line were generally lower than for the number of deaths (Table 4). Moreover, the standard errors associated with the coefficient estimates for the slopes were relatively high, resulting in generally low *F*-values and high *p*-values. The exceptions to this were the interaction between depredation and deforestation scenario A and the interaction between depredation and deforestation scenario D. Both had steep gradients, resulting in sharp rise in number of crossings with an increase in depredation probability given the deforestation scenario.

Table 4. Estimates, *F*-values and p-values for coefficients from the best-fit regression model for number of agent corridor crossings. Coefficient estimates represent the intercept of the linear regression line for the control deforestation scenario, estimate for the increment the number of deaths increases by for the categorical independent variables (deforestation scenario), and estimate of the slope of the regression line for the continuous independent variables. *F*-values are calculated using the value of the estimate compared to its standard error (the higher the standard error in proportion to the estimate, the lower the *F*-value). *p*-values are determined from the *F*-value and sample size.

Coefficient	**Estimate**	***F*-value**	***p*-value**
Control intercept	66 +/- 7	9.85	< 0.001
Probability of a depredation event (Control deforestation scenario)	-86 +/- 233	-0.37	0.71
Deforestation scenario A	-4 +/- 10	-0.44	0.66
Deforestation scenario B	2 +/- 10	0.19	0.85
Deforestation scenario C	6 +/- 10	0.68	0.50
Deforestation scenario D	-15 +/- 10	-1.56	0.12
Interaction: probability of depredation and deforestation scenario A	969 +/- 330	2.93	0.003
Interaction: probability of depredation and deforestation scenario B	75 +/- 331	0.23	0.82
Interaction: probability of depredation and deforestation scenario C	370 +/- 330	1.12	0.26
Interaction: probability of depredation and deforestation scenario D	871 +/- 330	2.64	0.009

Number of agents crossing the corridor depended on the interaction between deforestation scenario and the probability of a depredation event. The effect was most pronounced for deforestation scenarios A and D, but was also relatively strong for scenario C

(Table 4). The interaction between probability of depredation event and deforestation caused an approximately 15-fold increase in number of corridor crossings for deforestation scenario A.

The number of corridor crossings depended on the probability of death ($F_{1, 97} = -2.5$, $p = 0.02$; Figure 5) and the persecution period following a depredation event ($F_{1, 97} = -2.0$, $p = 0.05$) as additive effects, with no interaction between them ($F_{2,94} = 1.6$, $p = 0.12$)

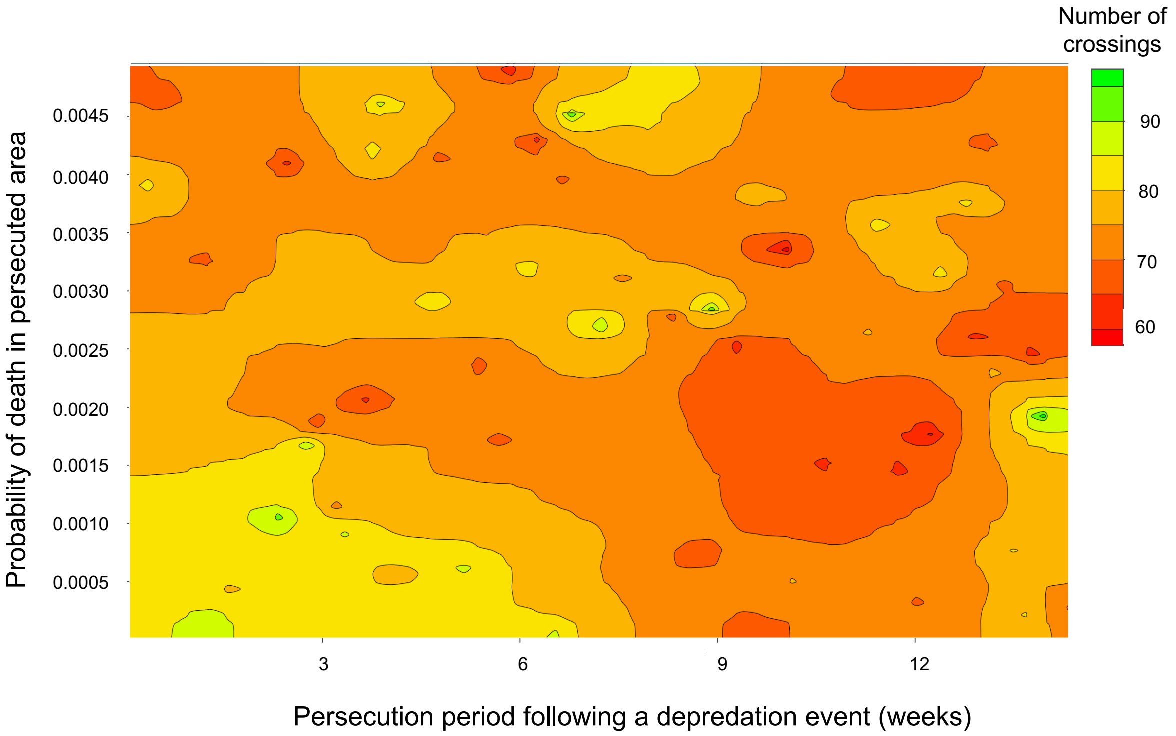

Figure 5. Sensitivity analysis: number of agent crossings as a function of probability of death and the length of a persecution period.

Best-fit models for number of crossings and number of agent deaths included the same independent variables. Number of crossings was highest when the probability of depredation was high. It was also highest for scenarios A, C and D, with B being the lowest. These three factors indicate that there may be a relationship between the number of agent deaths and the number of agent crossings. Number of crossings depended on number of agent deaths ($F_{1, 999} = 6.8$, $p < 0.001$). Number of crossings did not depend on the interaction between number of agent deaths and deforestation scenario (maximum $F_{1, 999} = 1.1$, $p = 0.29$). The relationship between number of deaths and number of crossings was stronger than that between the probability of a depredation event and the number of crossings. Thus, home ranges of other agents limited the number of crossings. As the number of agent deaths increased, the number of agents that could make their way through the corridor increased. Nevertheless, the number of agent deaths was far greater than the number of agent crossings. Hence, although agent deaths increased the mobility of agents throughout the corridor, given a finite population, the effects of depredation and deforestation would have a more negative than positive relationship on the agent population.

4.4 Discussion

In this study, we have shown that the number of agent deaths depends on the interacting effects of depredation and deforestation, with agent deaths responding more strongly to depredation where deforestation occurred as the removal of large blocks of woodland rather than as forest thinning (Figure 2). An agent-based model allowed us to model the reaction of individual agents as emergent behaviour from pre-defined behaviour rules. To extend the study, we should identify evidence of these patterns in real ecosystems by quantifying the number of large-felid deaths as a result of lethal control by livestock owners, and comparing over different configurations of deforestation. Identifying evidence of these patterns would allow us to validate the findings of the model. However, the challenge for replicating the findings in empirical studies comes from the inability to find study sites where the number of confounding variables is minimal. The inherent difficulty in ground-truthing the findings demonstrates the importance of models in ecology for identifying patterns in scenarios where confounding variables would bias otherwise results.

We reduced the complexity of the simulation in order to observe the interactions in absence of other population dynamics, which may have destabilised the model and overcomplicated the insights drawn from the model. Simplification of population dynamics means that the reader must not interpret these findings as patterns that would be reflected in the real world, as population dynamics would interact with anthropogenic effects to produce potentially converse results. Nevertheless, simplification of births, deaths, immigration and emigration of individuals prevented uncertainty arising as to whether the number of agents in the system could be attributed to the interactive effect of anthropogenic factors or to stochasticity in population dynamics. Our intention, therefore, was not to recreate the intricacies of reality, but to isolate anthropogenic effects and push them to extreme values in order to investigate how they interacted over a range of values, identifying a definite causal pattern in death rate arising from anthropogenic factors. Despite the simplifying assumptions made when creating the model, our study indicates that depredation may represent a key factor in large carnivore conservation, and that removal of large tracts of land may be more damaging than forest thinning, given the same amount of forest.

The number of corridor crossings depended on the number of agent deaths. This suggests that the modelled home ranges of other agents limited the mobility of agents. Our findings therefore support those of Watkins et al. (2015) from a much simpler model of habitat-dependent population dynamics in the Central Belize Corridor, who found that jaguar territories could block the passage of other jaguars through a corridor of sufficient width to contain a territory. Moreover, although connectivity of populations is important for processes such as gene flow (Coulon et al., 2004) and metapopulation dynamics (Hanksi, 1999), individuals immigrating into an area with a high probability of death constitutes an ecological sink (Chen et al., 2008; Heinrichs et al., 2016). Our findings not only support the idea that the Central Belize Corridor could become an ecological sink (Watkins et al., 2015), they refine previous conclusions by exploring and quantifying human-agent interactions, thereby identifying conditions that could enhance the sink effect.

Depredation had the most pronounced influence on the number of agent deaths, with agent deaths increasing as depredation rate increased. Moreover, the influence of depredation depended on the rate of deforestation. The effect of depredation on agent deaths is no surprise, given the direct link in the model between persecution and the probability of an agent dying. The simplified choice of immigration model allowed us to focus on the interactive effects of the anthropogenic parameters without including potentially destabilizing population dynamics. Furthermore, the simplifying assumption of an indefinite population of agents resulted in a constant increase in number of deaths, whereas in reality the number of deaths would reach an asymptote given a known population. Nevertheless, links do exist in the real world between depredation of livestock and the use of retaliatory force by stakeholders (Babrgir et al., 2017). The interaction between deforestation scenario and the influence of depredation on agent deaths is more surprising and warrants further study. Hence, the model indicates the importance of reducing the possibility of depredation and calls for a comparison of levels of lethal control across different forest configurations.

Our model included an indefinite number of agents in order to reduce the instability caused by adding birth and death dynamics to an already-complex model, and also to allow us to focus solely on the interacting effects, pushing the effects to extremes to investigate the interactions between the two independent variables. Given a finite population, the number of crossings would reduce over time with number of agent deaths as fewer animals would be available to immigrate into the area. In reality, the rate of depredation would decrease due to a reduction in individuals within an area, leading to a lower number of deaths. Moreover, a finite population would be unable to continuously fill voids left by dead individuals. Crossing corridors would thus remain open in some areas of the corridor. The lack of realism associated with this assumption must be considered when interpreting the results of our study.

The model did not capture precautionary lethal control of populations driven by public perception and the media (Fernández-Gil et al., 2016), or situations where stakeholders persecuted one species or individual for the actions of another (Knowlton et al., 1999). It is likely that inclusion of non-retaliatory lethal control would reduce the strength of relationship between depredation and agent deaths. It would also likely cause a sharp increase in agent deaths and, consequently, in number of agent crossings. Attitudes towards large carnivores may not be linked to depredation events, but to socio-economic factors (Rust et al., 2016; Mkonyi et al., 2017). We advise that future models investigate the interacting effects of public opinion, poverty, level of education, and number of depredation events on the number of agent deaths in a region.

The model demonstrated that scenarios of forest loss that removed larger segments suffered a higher number of agent deaths. Our study agrees with accepted knowledge that habitat loss can reduce species richness and has contributed to the reduction in the number of large carnivores worldwide (Fahrig, 2003; Urquiza-Haas et al., 2009). However, the effect of habitat fragmentation on ecosystems is an ongoing area of research (Villard and Metzger, 2014). Results from the model indicated that an environment that is more homogeneous on a local scale offered no refuge for agents in large expanses of agriculture, resulting in a high number of deaths. Large carnivores often have high mortality at the edge of reserves and national parks (Balme et al., 2010), however edges that create a locally heterogeneous configuration may offer refugia and cover for large carnivores. Regardless, our model indicates that at higher rates of forest loss, the benefits provided by the locally heterogeneous configuration disappear. Large mammals usually do not inhabit small fragments (Michalski and Peres, 2007) and at higher rates of forest loss, locally homogeneous configurations may prove more beneficial to the population than locally heterogeneous configurations.

Number of agent deaths did not depend on wildmeat hunting in the model. This could be due to the large effects of both depredation and deforestation distorting the effect of wildmeat hunting, or to the stochastic nature of the model. The world is suffering a wildmeat crisis

(Ripple et al., 2016) and this has led to multiple extinctions (Fa et al., 2002; Milner-Gulland and Bennett, 2003; Darimont et al., 2015) The extinctions in the literature, however, tend to concentrate on hunted species. Here, we have focused on competition between humans and large carnivores. We modelled avoidance of hunted areas, which represented both avoidance of humans in general (Packer et al., 2013) and avoidance of areas with fewer prey. The knockdown effect of wildmeat hunting of prey species is a complicated process, and likely could not be captured fully by the model. For instance, the model selected cells at random when selecting hunted cells. In reality, hunters would cover the entire area rather than one particular 40 x 40 m square, hence an element of spatial autocorrelation exists that the model did not include. We suggest that future studies attempt to isolate only wildmeat hunting in order to accurately evaluate its effect on large carnivores.

Our model has demonstrated the ability of spatially-explicit models to investigate interactive anthropogenic effects on simulated populations by isolating the effects, thereby simplifying the interpretation of results and identifying patterns that can directly be attributed to anthropogenic factors. Nevertheless, limitations of computing power necessitated the prioritisation of aspects of the system we wished to model, resulting in simplifying assumptions. The example here is the assumption of an indefinite population of agents. However, many agree that mechanistic modelling represents the future of ecological modelling, with the creation of fine-scale movement models that can capture species dispersal, genetics, demographics and anthropogenic activity to provide predictions on ecosystem response to HIREC (Sih et al., 2016). As computer speeds and capabilities grow, mechanistic models will be able to incorporate a greater level of realism. Our model has drawn attention to future areas of study: the incorporation of socio-economic drivers and public opinion in models of persecution for depredation; investigation of how the effects of configuration on large mammals change with overall forest loss; isolation of human hunting as a single independent variable. We must answer these questions. With computer power ever increasing, next-generation modelling (Grimm and Berger, 2016) may offer part of the solution to these questions and an increased understanding of how anthropogenic activities will continue to impact large carnivores.

4.5 Appendix I. Overview, Design concepts and Details

Appendix I follows the protocol of Overview, Design concepts and Details suggested by Grimm et al (2006).

4.5.1 Purpose

The model simulated small-scale movement decisions of jaguars in the Central Belize Corridor, Belize. Our purpose was to investigate the movements of jaguars in response to anthropogenic change.

4.5.2 State variables and scales

The model background consisted of 1000 × 900 grid cells. Each grid cell represented an area comprising 40 × 40 m. This grid includes "Null" cells that lay outside the park. The park consists of a modelled 598 km^2. GIS data (Meerman, 2011) informed data on static aspects of the cells: habitat type, distance to river, distance to trail, altitude, and slope. The agents occupied a single cell at a time. The model allocated each individual with a gender, transient/resident status, identity, location and graphics information. At the beginning of each timestep, the agent would deposit an amount of "pheromone". Pheromone represented the ability of agent to signal to each other. In reality, jaguars communicate using scrape markings, scent markings and vocal calls. The model stored pheromone levels as a feature of grid cells. Pheromone levels were gender-specific. Each replicate consisted of 219,000 timesteps that represented 5 years. Each timestep equated to 12 minutes.

4.5.3 Process overview and scheduling

At the beginning of each parameter set run, the model created the background grid and set static cell attributes: terrain type, distance to river, distance to trail, altitude, slope, coordinates and graphics information. The model then ran through replicates.

At the beginning of each replicate the model created output files and initialised a population of agents. The agents had an equal chance of being male and female. All agents created at the beginning of the simulation were “resident” agents. After initialisation, the model ran through a series of timesteps.

The model placed an amount of pheromone at the beginning of each timestep. It then looped through all individuals. If an individual was in the park area, the individual would undergo the move function. If an individual was a “resident” and outside the park the, it would undergo the re-entry function. After movement of “resident” individuals, the model went into an immigration function, which created new “transient” individuals. At the end of the timestep, the model would write to output files and decay pheromone levels. The model continuously updated all information on cell pheromone levels and jaguar locations.

4.5.4 Design concepts

4.5.4.1 Emergence

Individual home ranges emerged from the communication between agents via pheromone levels. The constant decay and placement of pheromone allowed home ranges to be dynamic.

4.5.4.2 Adaptation

Agents chose the least-cost neighbouring cell based on cell attributes. These attributes were both dynamic (for example, distance to river) and dynamic (pheromone levels). The parameter sets each had specific values for how an agent responded to each of the cell attributes.

4.5.4.3 Fitness

The model did not include mortality or fecundity, however this model represents a base model for future investigations of how movement decisions affect mortality and dispersal in a human-influenced environment.

4.5.4.4 Sensing

All agents could access information on neighbouring cell attributes. This information included environmental attributes (terrain type, distance to river, distance to trail, altitude and slope) and agent-related attributes (amount of male pheromone, amount of female pheromone, jaguar occupancy). The agent did not access camera-related cell data. Each cell had eight neighbours, representing north, north-east, east, south-east, south, south-west, west, north-west and north cells.

4.5.4.5 Interaction

Agents interacted using pheromone. Pheromone was gender-specific. Gender-specific parameters dictated how agents respond to same-gender, opposite-gender and own pheromone. Agents responded to pheromone levels by having an increased or reduced cost proportional to the amount of pheromone. Hence, pheromone resulted in avoidance or attraction to the same- and opposite genders, dependent on the parameter set.

4.5.4.6 Stochasticity

The model included parameters for probability of random movement, and probability of directional persistence. Hence, an agent could move in a random direction, in the same direction as previously or in a direction dictated by cost of neighbouring cells. The probability of these movement types depended on the parameter values and random number generation. The model allocated gender based on a 50% chance of being male or female.

4.5.4.7 Observation

The model used the Python package Tkinter for graphical representation during testing. The graphics provided information on environmental attributes and gender-specific pheromone levels in each cell, and individual movements around the grid.

4.5.5 Initialisation

The model reset all landscape and agent attributes at the beginning of a new parameter set. At the end of each replicate, the cell pheromone-related attributes reset. The model removed all individual and created a new population. The number of individuals in the new population depended on the value of the population parameter. Agents could then establish new home ranges.

4.5.6 Submodels

4.5.6.1 Pheromone placement

At the beginning of each timestep, each individual placed an amount of pheromone in its current cell equal to the pheromone placement parameter value. This allowed agents to communicate with each other.

4.5.6.2 Move

The function ran through each individual in the population, provided the individual was within the CBC area. It first created a random number. If this random number was less than or equal to the probability of random movement, the individual selected a random neighbouring cell as its next cell. There were eight neighbouring cells for each cell. This cell may be outside the park. If the individual did not undertake random movement, the model created another random number. If this random number was less than or equal to the probability of directional persistence (DP), the individual continued moving in the same direction it had moved previously. If an individual did not move randomly or in the same direction as previously, the model calculated the gender-specific cost values of all neighbouring cells. The individual chose the least cost neighbouring cell. Once the individual selected a cell, the model removed the individual from the cell occupancy list and changed the *x* and *y* coordinates of the individual. Graphics information also changed.

4.5.6.3 Re-entry

If an individual was a “resident” and outside park boundaries, the model entered a re-entry function. The program created a random number. If this number was less than or equal to the chance of re-entry, the model created a selection of cells consisting of the last non-null cell the individual stepped on and any “border cells” within 250 m of that last cell. The model selected one of these cells at random and moved the individual to this cell.

4.5.6.4 Immigration

If a model created a random number less than or equal to the probability of immigration, the program entered the immigration function. The immigration function created a new individual of class “transient”. The transient individual had an equal chance of being male or female. The model chose the initial location at random from all border cells.

4.5.6.5 Pheromone decay

At the end of each timestep, the model decayed pheromone levels in all cells by a multiplier equal to the pheromone decay parameter.

4.5.6.6 Wildmeat hunting

The human hunting sub-model depended on three parameters: cost of hunting to jaguars, maximum time of cost effectiveness, and chance of a hunting event. We parameterised cost of hunting to jaguars to cause jaguars to choose agricultural areas over forested areas when the forested area was hunted and set the maximum time of cost effectiveness to one modelled day. Every cell had a *human cost* and *time since hunting* attribute. The *human cost* attribute was static and equated to the cost of hunting to jaguars. The model created a random number for each forest cell every timestep. If that number was less than or equal to the chance of a hunting event, the function set the *time since hunting* attribute to 0, with this *time since hunting* attribute increasing by an increment of one every timestep. For any one instance, if the *time since hunting* attribute was above the maximum time of cost effectiveness, the individual would not include *human cost* in cost calculation. Otherwise, if the *time since hunting* was lower than the maximum time of cost effectiveness, the individual would use this cost in neighbouring cell cost calculations.

4.5.6.7 Persecution by farmers

The persecution sub-model ran on three parameters: the probability of the jaguars killing livestock, the probability of a jaguar dying on an agriculture cell, and the maximum time after an agriculture cell losing livestock that jaguars would die on agricultural cells. We ran sensitivity analysis on the probability of death and the maximum time of persecution following a depredation event to assess how these parameters affected the dependent variables.

Chapter 4. Anthropogenic impacts

Chapter 5.

Discussion

5.1. Introduction

Grimm and Berger (2016) coined the term ‘next-generation modelling’ to describe the complex, mechanistic models that they predict will become increasingly important in ecological research. They cite the three key features of ‘next-generation’ models, as structural realism, emergence, and predictions. High-powered computers, accompanied with methods such as cloud and distributed computing, offer the potential to create fine-scale models that incorporate high levels of complexity. Whether or not we now have enough computing power to capture the complexity involved in real ecological structures is up for debate. Nevertheless, it is likely that there will be further development of the kind of complex movement models seen in Watkins et al. (2015). They simulated large carnivore responses to anthropogenic effects. The model was spatially explicit, incorporated a least-cost path movement model, and included population dynamics. Despite its complexity, the model successfully produced results similar to empirical data, which allowed the authors to predict the consequences of increased deforestation in a corridor area.

With ever-increasing growth in computing capability, it is likely that the use of spatially-explicit ABMs will increase, especially those involved in the field of conservation. HIREC has left populations of carnivores worldwide in a highly degraded state, with populations dropping as much as 77% (Ripple et al., 2014). Some authors have referred to the current era as the sixth mass extinction (Monastersky, 2014). Given this gloomy outlook, researchers in conservation will seek to innovate and experiment with all tools available to them. Furthermore, ecological modellers may be increasingly aware of the struggles faced by conservation researchers, and may feel inspired to develop a model that can augment current research in this field.

It is therefore appropriate to evaluate certain aspects of mechanistic agent-based models at this point in time. What are the caveats of creating spatially-explicit ABMs? How does one parameterise an ABM using the metrics available from conservation studies? What sort of questions in conservation can ABMs be used to answer? This thesis aimed to explore these three research questions.

5.2 Parameterisation of spatial models

Chapter 2 explored the biases that arose from the parameterisation process of the ABM presented in this thesis. The movement model required parameterisation with spatial statistics, and in doing so, I found that the final values for parameters depended strongly on the initial choice of resolution.

Next-generation ecological models can incorporate high levels of realism, and may be able to predict the responses of organisms to environmental stressors (Grimm and Berger, 2016). An ability to predict and model behaviour could prove especially important in studies of rare, elusive, large-bodied species, especially where it is difficult – if not impossible – to get a full understanding of their patterns of behaviour by conducting empirical experiments in the wild (Hillborn and Mangel, 1997; Singer et al., 2016). However, despite the promise of models for conservation, the same limitations experienced by empirical studies of elusive species also plague modellers, due to the need for empirical data with which to parameterise models.

The parameterisation of models against empirical data is important as it increases the credibility of models, and permits the incorporation of added layers of complexity by providing a ground-truth in order to validate sub-models. Without the ability to ground-truth against empirical data, we are left with highly abstracted models, models that incorporate only what we feel to be intuitive or obvious behaviour. Although abstract models can provide mechanisms for processes in absence of stochasticity or noise, it is difficult to ascertain quite how predictive these models will be (Uchmanski and Grimm, 1996; Evans et al., 2013b). Thus, although abstract models are useful in some scenarios, more complex models are often better representations of ecological systems (Evans et al., 2013b).

However, we have demonstrated an issue with parameterising complex models of animal movement and choice. Namely, movement is inherently spatial, hence models that represent animal movement and habitat choice should be spatially explicit. How then should a modeller parameterise a movement model? It would be possible to use parameters such as step length or resource selection functions, which are calculated from spatial data, or to use the spatial data themselves. The latter includes data from camera-trap and telemetry studies. Our study showed that attempting to replicate either form of spatial data in the model resulted in parameterisation being sensitive to the resolution of the model. While it may be possible to mitigate this resolution issue by using simple descriptive statistics rather than attempting to quantify exact values (Jakoby et al., 2014), it may be difficult to justify this choice to members of an academic culture that are accustomed to making decisions based on levels of significance.

If the choice of parameter values depends on the choice of resolution, one cannot declare with certainty that a model replicates the behaviour of the organisms it attempts to simulate. If models cannot replicate behaviour, then they contradict Grimm and Berger's (2016) final feature of next-generation models: prediction. If the parameter values differ to the extent that mechanisms for movement vary depending on resolution, then which set of parameter values will truly capture the way organisms respond to environmental change? Modellers may be tempted to remove complexity by only including parameters that they know to be true, or for which they have a good idea of starting values for priors (for use in ABC, as per van der Vaart et al., 2015). Here again, researchers choose to abstract the model rather than find parameter values that tell them something they did not know beforehand. Indeed, without long-term data on how species do actually respond to environmental change, we cannot validate the predictive ability of our model.

The issues and limitations discussed in chapter 2 are important to note from the start. However, despite these, it may still be possible to develop a model that incorporates enough complexity to realistically replicate the movement of complex, large-bodied organisms. To achieve this aim and develop a model with predictive ability, we must overcome a range of challenges. First, we must continue to develop and improve empirical methodologies for sampling the spatial patterns in the movement of elusive, large-bodied species. Not only will this contribute to empirical literature on the species, it will also provide more data for parameterisation of complex models. Second, we must find a way to quantify the validity of spatially-explicit models that is not dependent on the resolution of the model. Third, we must continue to take advantage of modern advancements in computing, distributed computing in particular, in order to add the level of complexity required to study complex organisms.

5.3 Models for use in virtual ecology

Chapter 3 explored an application of the ABM in a virtual ecology study to evaluate methodologies frequently used to study rare and elusive species. We introduced a method for correcting metrics calculated from telemetry data and quantified its effectiveness by using a simulation model with a known 'actual' value for the metrics. Virtual ecology allows researchers to assess the effectiveness of the empirical methodology and quantify the effect of potential biases (Zurell et al., 2010). In-silico populations allow modellers to run virtual experiments with known values for parameters under investigation. ABMs are particularly useful in virtual ecology, as they simulate populations as a collection of agents that move according to certain rules and attributes. Hence, one avenue for the utilisation of ABMs in conservation is the virtual assessment of the effectiveness of methodologies used in conservation biology.

The study investigated the effect of fix intervals on the difference between estimated and actual values for two metrics derived from telemetry data: step length and MCP. The study showed that, for both metrics, error increased with fix intervals. At low fix intervals, the error rose steeply, reaching an asymptote at larger fix intervals. The steep increase in error was more pronounced for models that incorporated a lower rate of directional persistence, as larger fix intervals were unable to account for short, torturous movements. Finally, it was possible to correct the results of this model by using the known relationship between fix interval and error as a correction factor. If this pattern can be replicated in reality, then researchers could develop a metric for correcting statistics calculated using telemetry data, given a known fix interval. Moreover, they could sub-sample from their own data to find a model that explains increase in error with fix interval, and use this model to correct metrics, where necessary.

Strategies for conservation do not often use step length directly, but step lengths do often inform models of animal movement, which may then augment knowledge of species (Boyce et al., 2010; chapter 4). If researchers use metrics at different levels of abstraction, they must be corrected so that they align to the researcher's requirements. In contrast with step length, home range measurements - such as MCP - often directly inform conservation strategy by determining how much space a population requires, and hence how large reserves and corridors should be (Otis and White, 1999). Chapter 3 showed that it is possible to correct step length and MCP for certain movement models.

The ABM presented in chapter 3 was able to replicate findings of potential bias from previous studies, and extend that knowledge by incorporating varieties of movement patterns and environmental configurations. Both of these variables would be almost impossible to replicate in empirical studies. The findings presented in these chapters therefore provide insight into how sampling systems, movement type, and environmental factors affect common methodologies used in conservation biology. This chapter thus illustrated one route to employing ABMs to influence the field of conservation biology.

5.4 Simulation of responses to HIREC

Chapter 4 explored another use for ABMs in conservation biology. Here, we simulated the responses of agents to anthropogenic factors by varying the intensity of those factors, before investigating how the number of agent deaths and number of agent crossings depended on them. This model extended the work of Watkins et al. (2015) by incorporating multiple types of human activity in order to examine the potential for interactions between them. The results from this model demonstrated that depredation is a key predictor of agent death, that landscape configuration is important for the survival of agents, and that the number of crossings depended on number of deaths, indicating the replication of an ecological sink within the model.

This model cannot predict for certain how carnivores will react in the face of HIREC (Sih et al., 2016). Any model that wishes to predict this would require dynamic values for avoidance, and movement models that change as individuals learn how to move in a human-defined landscape. This model was therefore presented in more abstract terms, assessing how ‘agents’ responded to simulated effects. Within this model, it was possible to intensify anthropogenic factors to extreme values, and determine how each factor individually contributed to the responses of agents, as well as how they interacted. As the only factors that changed were the independent variables, it was not necessary to worry about noise or stochasticity from confounding effects, such as changes in level of poverty, the introduction of new conservation measures, or the effects of politics, the media and local economics. Hence, it was possible to create an experiment that isolated the distinct effects of HIREC, and in doing so, found some conclusions that warrant further study.

5.5 Limitations

The base model that underpinned the three results chapters was limited mostly by the availability of computing power and empirical data. The dearth of computing power only permitted parameterisation using a small sample of parameter values (~2000). Latin Hypercube Sampling mitigated for this constraint by selecting a representative set of parameter values, but the model was unlikely to converge precisely on its optimum parameter values. Nevertheless, the parameter values were able to replicate jaguar behaviour with enough accuracy to apply them to the research questions in the data chapters.

Chapter 5. Discussion

Despite the large amount of camera-trap data available from CBWS, the data from telemetry studies only included three individuals, all of which were male. This necessitated using a conversion factor to calculate the MCP size for female jaguars. The conversion factor was based on empirical data detailing MCPs of male and female jaguars, hence I have confidence that the conversion factor represented the ratio between male and female MCPs.

When transferring the model to a different area, a corridor area in this example, values for parameters that determined movement remained constant. Though we used this model as an abstract evaluation of anthropogenic factors, values for movement parameters in a corridor area may differ from those for a reserve. Although the values of movement parameters may change between areas, the effect on model results was likely to be minimal and the assumption of similar behaviour based on empirical data was easier than using a model that we had not validated against empirical data. Differences in behaviour between CBWS and the corridor area represents a future area of study, as an extension to our current work.

A further limitation was the re-entry function that allowed individuals to remain outside the study area for a short amount of time before re-entering at a nearby square. This assumes that all individuals were resident within study areas, rather than dispersing individuals that passed through. It also assumed that any areas occupied outside the study area were small compared to the section of the study area occupied by the individuals. Although this may be true for CBWS, it is likely to be less true for the corridor area. Despite these inaccuracies, incorporating a more complex model of re-entry and movement outside the study area would have taken up valuable computational resources and over-complicated an already complex model, for possibly very little benefit. Future extensions could consider the effect of both the re-entry function and areas outside the study area.

Finally, the model incorporated fine-scale habitat choice and interactions between individuals in detail, but did not include population dynamics, such as birth and mating, or attributes related to social dynamics, such as hierarchy and territoriality. The simulated period was short enough that it was reasonable to consider the simulation as a snapshot of a population of predators. Although the model incorporated males and females as separate entities, all males and females had equal status within the model, and similar levels of territoriality with members of the same gender. In reality, males may exhibit greater levels of territoriality than females, and social hierarchies may be important for utilisation of space within a given area. The addition of complex population dynamics and hierarchy would have necessitated more computing power. I elected to run more replicates at a finer resolution, rather than incorporating additional processes that could have destabilised the model and confounded the effects I wished to investigate.

5.6 Future work

Future work in the modelling domain will seek to innovate methods for quantifying the validity of spatially-explicit movement models without depending on the resolution of that model. In the meantime, researchers should aim to parameterise spatially-explicit movement models using only descriptive patterns (Jakoby et al., 2014). This is a large problem, and perhaps requires the use of a correction factor, similar to the one presented in chapter 3, in order to identify truer values for simulated spatial statistics.

A second challenge raised by chapter 2 is the requirement for larger amounts of empirical data in order to parameterise models. Modellers can contribute to this by using the virtual ecologist approach that I utilised in chapter 3 to improve and assess empirical techniques.

The final challenge raised by chapter 2 was the continued use of new and innovative technologies for use in modelling. These technologies include techniques often used for the analysis of big data, such as distributed and cloud-based technologies. Cloud-based technologies allow users to rent computing power without purchasing physical machines. Researchers pay for these machines only for as long as they need them. This would allow researchers to obtain greater amounts of computing power without spending money on expensive computers. Such a technique would have greatly reduced the limitation imposed on this project by lack of computing availability.

Chapter 3 introduced a potential method for correcting metrics calculated using telemetry data. Next steps for this project would include investigating real-world patterns to see if they aligned with the patterns we identified for step length and MCP, and creating a correction factor or method of calculating a correction factor. If the patterns do not align, we may advise investigating the ability of non-linear interpolation to correct these parameters instead. For this, researchers could sub-sample their telemetry data to identify the relationship between fix interval and error, then correct back to shorter fix intervals using that pattern.

Chapter 4 raised two important considerations that merit further investigation. Firstly, the effect of landscape configuration on agent deaths, and its interaction with depredation. Secondly, whether empirical or simulated, is how the number of deaths affected number of crossings. What would break this pattern? Under what conditions is this true?

Finally, one could extend the work presented in chapter 4 by including limited hunting seasons, where hunting effort was not constant throughout the entire year. We could also use dynamic scenarios for deforestation, comparing a scenario where deforestation occurs over time to one where deforestation is static. A more complex extension would include social, political, and economic dynamics that affect levels of depredation, rather than depredation resulting only from a depredation event.

5.7 Concluding statements

This thesis has explored applications of spatially-explicit ABMs and analysed caveats in the utility. It has concluded that before we can create truly predictive ABMs that stakeholders can use to reliably inform conservation strategy, a number of serious challenges must be met. Despite this, the work presented here has demonstrated the utility of a spatially-explicit ABM for three purposes, purposes that mostly focus on mechanisms behind processes rather than directly predicting effects. In doing so, this thesis has drawn interesting conclusions and highlighted areas for future work. Though the true utility of ABMs in conservation has yet to be fully demonstrated, the three examples presented here suggest potential pathways for models to inform and augment empirical studies.

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