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

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ABSTRACT

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

1. Introduction

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

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

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

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

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

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

2. The model

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

2.1. Purpose

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

2.2. State variables and scales

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

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

The combined total food stock assigned per grid-cell depended on the habitat type but not its cost (i.e. some high-cost habitats had higher food availability than some lower cost habitats, as described in Table 1). As the simulation progressed, the current food amount decreased in response to consumption by agents, and replenished with subsequent self-renewal of prey through production of new prey biomass. Table 1 details a reduction in prey resources by 30%