

An agent-based model of jaguar movement through conservation corridors

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Abstract

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

Introduction

One of the most obvious effects of our own species on the planet has been the clearing of forests to make way for agriculture. In many parts of the world this means that the natural vegetation that remains tends to be divided into isolated patches (see figure 2 for an illustration) with disruptive consequences for the local wildlife. The establishment and maintenance of “corridors” connecting otherwise isolated areas of habitat have therefore been put forward as important tools in conservation biology (Bennett, 2000; Hilty et al., 2006). The idea of a corridor is to connect local sub-populations into a single meta-population and thereby reduce the risk of local extinctions due to human activity (hunting, land development, etc.) and, more importantly, to improve the species’ long-term survival chances by increasing the size of the gene pool.

Bennett (2000) shows that evidence for the effectiveness of habitat corridors is mixed: they have been more helpful for some species than others. Indeed, habitat fragmentation is itself a concept that depends on the details of the behavioural ecology of the species concerned (consider, for



Figure 1: A jaguar photographed using a stealth camera. Image courtesy of the Jaguar Corridor Initiative, Belize.

example, the difference between a bird and a snail in their ability to move between habitat patches). The current paper puts forward a simulation model to help assess the effectiveness of different corridor policies for the jaguar, *Panthera onca*.

The jaguar (figure 1) is an apex predator that stalks and ambushes its prey. It is the third-largest of the big cats and the largest big cat species in the Western hemisphere. Its range extends from the southern United States to northern Argentina. Jaguars are stealthy and elusive, and thus there is still much we do not know about their behaviour. However, one of the better-studied jaguar populations is in Belize, on the Caribbean coast of Central America. In particular, the Cockscomb Basin Wildlife Sanctuary (CBWS), a 425 square-km reserve in southern Belize, has been a productive jaguar fieldwork site for several decades (Rabinowitz and Nottingham, 1986a; Harmsen et al., 2010b). Biologists working there have been instrumental in setting up the Jaguar Corridor Initiative (Rabinowitz and Zeller, 2010), a cooperative effort between scientists, conservation groups, and regional governments to establish corridors connecting known jaguar populations.

Assessing the usefulness of a corridor initiative is diffi-

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

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

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

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

Least-cost modelling techniques are standard in many GIS (Geographical Information System) packages which offer built-in cost and distance functions that allow for rapid model construction (Rayfield et al., 2010). A raster-based grid of the landscape is generated with a cost assigned to each cell that represents the lowest cumulative cost from

that cell to the source cell. This cost is the inverse of the degree of functional connectivity of the landscape according to the species in question (Driezen et al., 2007) and thus the end product of the calculation can be seen as a probability distribution across the landscape describing the likelihood of the animal settling at any given position. Rabinowitz and Zeller (2010) developed an ambitious least-cost model of jaguar dispersal across their entire range in Central and South America.

Validating least-cost models is not easy, however. Driezen et al. (2007) produced one of the only studies to successfully compare the output of least-cost models with empirical data on animal movement. They used statistics on landscape-wide cost values and compared these to real hedgehog paths, constructing and presenting a novel approach to matching empirical movement trajectories with generated least-cost maps. Watkins (2010) demonstrated that this approach could be taken further through integration with agent-based modelling.

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

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

The model

The first step in constructing our model is devising a map layout that reflects the essentials of the problem. Figure 2 shows a typical Belizean landscape and illustrates the fragmentation of forest habitat that occurs due to road construction, tree-clearing for farming, urban development, etc. The key feature of our simulation will thus be two separated blocks of forest, surrounded by cleared farmland. Each forest section will hold an initial population of jaguars; the



Figure 2: An aerial view of a typical landscape in Belize. Note that regions of ideal jaguar habitat (i.e., forest) are separated by roads and cleared farmland. Image: Google Earth.

question is how easy or difficult it will be for them to travel from one forest zone to another.

Figure 3 shows the potential corridor designs that we will investigate. We begin with the basic two-forest layout in the top left corner. Note the blue edges where the forest meets farmland; we assume that these transitional zones are of intermediate appeal to the jaguars. The next design (top centre) features a corridor connecting the two forest sections. We also consider (top right) a layout with additional area added to the forest sections: this is equivalent to a control condition in which we spend the conservation budget on extending each forest rather than connecting them. Next we consider whether corridor width is more or less important than the number of corridors by looking at three- and five-corridor designs. In each case the same total area is devoted to the connecting corridors. These are followed by one- and three-island designs — alternatives to a direct corridor — and a design made up of many randomly placed islands. Again, the total area devoted to corridor is a constant. Finally we also look at a “contiguous forest” layout where the entire map is forested: this is another control condition in that it allows us to compare jaguar ecology in a modern fragmented habitat with what it might have been before human colonization.

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

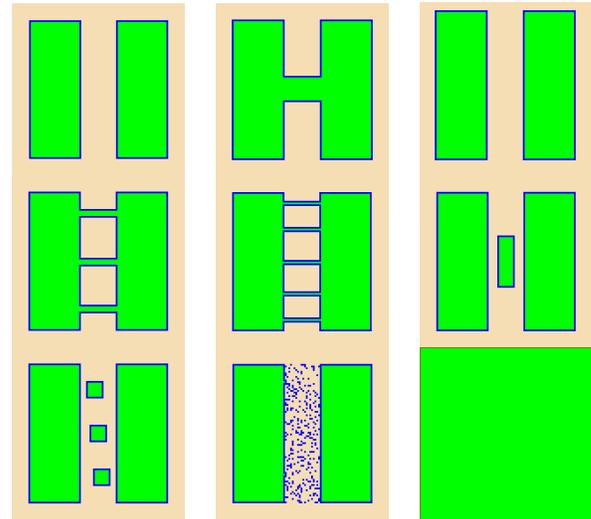


Figure 3: Map layouts investigated in the simulation. Core forest is in green, forest edges are blue, and farmland is khaki. First row: no corridor, one corridor, no corridor but equivalent area added to the forest. Second row: three corridors, five corridors, one island. Third row: three islands, random islands, contiguous forest.

the basic forest sections measuring 15×40 km and with a 10 km expanse of farmland between them. For comparison, the 2500 square km area of the map represents about 10% of the land area of Belize.

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

Edge effects are known to be important in landscape ecology, and so we added an edge-detecting routine to the initialization of our map. Any forest square that borders a farmland square (in any of 8 neighbouring positions) is labelled as an edge square. These are shown in blue in figure 3.

What about temporal scale? Schaller and Crawshaw (1980) recorded daily travel of between 1 km and 3 km straight-line distance for jaguars, with males travelling further than females. In our model male jaguars move one grid square every timestep; if all eight surrounding squares have equal cost, the movement will be in a random direction. In order to get plausible straight-line daily travel distances

we therefore set one timestep to be 4 hours. This gives 6 timesteps per day, and 2190 timesteps in a year — the standard length of one of our simulation runs.

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

At this point we need to start fleshing out the least-cost model with specific numbers describing the preference of the jaguar for the map's three habitat types: forest, forest edge, and farmland. We set the preferred forest habitat's cost value at 1.0 as a reference. Previous least-cost models (Driezen et al., 2007; Watkins, 2010) suggest that non-preferred habitat such as farmland will have values many times higher. The correct cost value for farmland for the jaguar is not yet known; we have chosen a value of 25.0. The forest edge is intermediate but still relatively low-cost at 5.0. At this stage these numbers are arbitrary as their rank order is more important than their specific values: the effect is that jaguars in the model will prefer forest to edge to farmland.

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

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

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

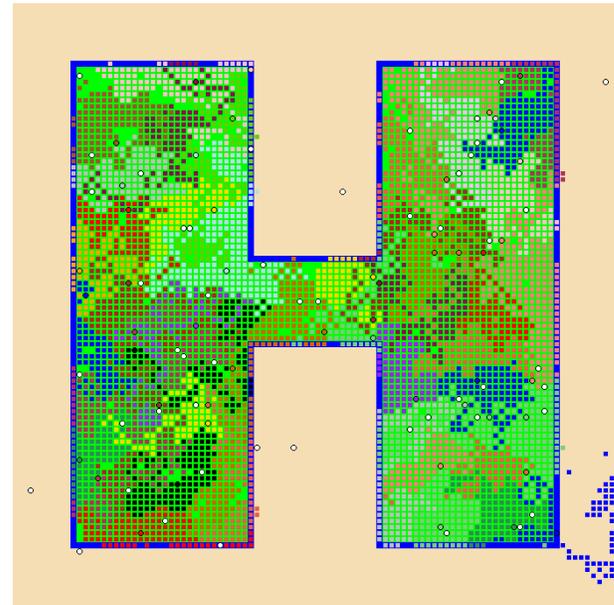


Figure 4: A representative screenshot of the simulation after 500 timesteps. Jaguar locations are represented as circles, with females in white and males in a random colour. Male and female pheromone trails (i.e., territories) overlap so, for clarity, only male territories are shown. Pheromone trails are in the same colour as the male that produced them. Note the variation in territory size, and the fact that a few animals have been “pushed out” into the less desirable farmland.

same-sex individuals are repellent: a pheromone deposited by another jaguar of the *same* sex adds to the cost value of the grid square in a 1:1 ratio, i.e., a freshly deposited same-sex pheromone trail in the forest will massively raise the cost of that square from the baseline 1.0 to 101.0.

All pheromone deposits decay over time at 2% per timestep. For computational simplicity, pheromone levels lower than 5.0 are reduced to zero. This decay rate means that a jaguar's pheromone trail has less and less effect until finally becoming undetectable around 150 timesteps (25 days) after it passed through a grid square. Thus we can imagine each jaguar trailing out behind it a “scent cloud” that dissipates over several weeks. Figure 4 is an example screenshot of the simulation in action and shows what this looks like in practice.

There is a finely tuned balancing act involved in deciding just how strong the repellent effect of other jaguar's territories should be. If we take the landscape cost value of 25.0 for pasture as a reference point, our parameters for pheromone cost and decay rate mean that a jaguar will be ambivalent between entering a farmland grid square and entering a forest grid square that had seen another same-sex jaguar pass by around 12 days earlier. Clearly there is some guesswork going on here: jaguars are not well-studied enough for us to

know the exact values that should be plugged in. The point is not to make a precise predictive model but to see whether it is possible to explain the basics of jaguar movement with some simple rules. In this regard, we do have circumstantial evidence: jaguars have occasionally been observed in pastures both in Belize and Brazil, and we know that jaguars are somewhat territorial. If we chose much higher values for the landscape cost of farmland, the jaguars would not leave the forest at all, even under extremely crowded local conditions. Conversely, if we make the cost of encountering another jaguar's pheromone too high, the animals will spill out into the farmland in great numbers in an effort not to encroach on each other's territory.

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

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

Unlike much ALife work, there is no genetic algorithm in our model: our central question is not evolutionary but ecological. In the same vein as Hemelrijk (1998) we are not asking about the evolution of the animals' strategies, but about the implications of how a hypothesized behavioural program would play out when followed by multiple animals in a simulated spatial world.

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

ues on the average-cost measure will therefore be associated with stress or over-crowding. If one corridor layout can reduce this value compared to another, this is evidence for its jaguar-conservation effectiveness.

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

Results

Figure 4 shows a typical screenshot from the simulation. We can see that the model has been successful in reproducing male territories of a plausible size of 10 to 20 square km, and that a minority of jaguars have resorted to hunting in farmland. When watching the animation over time it is very easy to interpret the jaguar movements as “patrolling” a territory and avoiding conflicts with each other; the forest edges are used as “pathways” around territories; established core territories shift only gradually; and the jaguars that are forced out into farmland eventually get back into the forest when they are lucky enough to find an undefended edge section. Figure 4 shows the “one corridor” layout, and we can see that the corridor is certainly occupied by jaguars and thus might be leading to genetic mixing between the two sub-populations.

However, we can also see a threat to this exchange: note that the brown and the yellow territories in the centre of the corridor act as barriers to the transit of any other (male) jaguars. Our qualitative impressions when watching the simulation run with different corridor layouts were that the geography of the corridor could certainly make a difference as some layouts, notably the five-corridor map, led to “channeled” movement back and forth across the corridor, whereas other layouts such as the one in figure 4 led to blockages.

Figure 5 shows the comparison of the average-cost values across all 9 conditions. The obvious pattern here was that the layout did not seem to make a great deal of difference to the average cost experienced by each animal, except in the “contiguous forest” case. It is obvious that the contiguous layout will lead to lower average costs, however, as the same number of jaguars are distributed across about twice as much forest, giving larger territory sizes and fewer encounters with the pheromones of others.

The “no corridor” and “random islands” conditions lead to slightly higher costs than in other conditions. In the former case this is simply because there is less forest territory available; in the “equal area” control condition this difference disappears. The “random islands” condition leads to

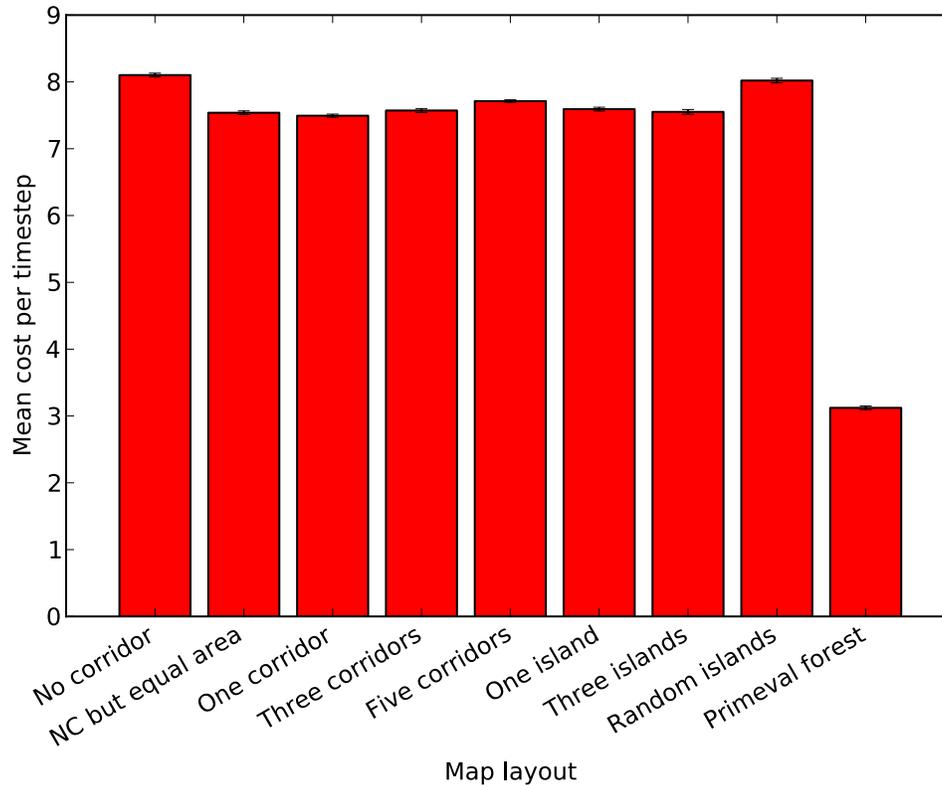


Figure 5: Mean cost figures per jaguar per timestep compared across the nine different map layouts. Standard errors are calculated across 25 replications of each condition with different random seed values.

most of the corridor squares being edge squares, and there is a concomitant increase in average cost. On this evidence it would seem that corridor design does not make much difference to jaguar welfare, and that the critical thing is simply to have as much favourable habitat available as possible.

What of the genetic mixing results? If we look at figure 6 we see the mean level of movement across the centre-line of the map, over the different conditions. The differences here are much more dramatic. The “contiguous forest” condition is again the most favourable for the jaguars, with 34% mixing (approaching the 50% level that you would get if the jaguar locations were shuffled at random). This contrasts with the “no corridor” conditions that support only 7 or 8% mixing. The island-based corridor designs perform very badly as well, although things are not quite so bad with the “random island” design. The striking finding from figure 6 is that corridor-based designs perform best, and that the more corridors and/or the thinner the corridor, the better. Observation of these runs suggests that the strong performance of the five-corridor design (26% swapping) is because the thin pathways promote rapid movement, often through the edge squares if another animal has recently

passed through the forest squares, and the very thin strip of core forest (just 500 metres wide) is not big enough to support a territory. Wider corridors (the three-corridor and the one-corridor cases) were better than island-based designs, and certainly better than no corridor at all, but did not match the mixing levels of the five-corridor case due to the tendency for the corridor to become blocked by an established territory.

Conclusions

We were pleased with the qualitative results of the model in that we managed to replicate plausible territorial behaviour in jaguars using the least-cost paradigm and only a few assumptions. The model has brought novel aspects of the corridor design problem to light, notably the possibility that some corridor layouts could be counter-productive due to being large enough to support internal territories that then acted as obstacles to travel by other animals. We feel that the agent-based modelling approach we have begun here has the potential to be extremely useful in drawing out the implications for different theories about jaguar behaviour and thereby helping to determine which of those theories is a

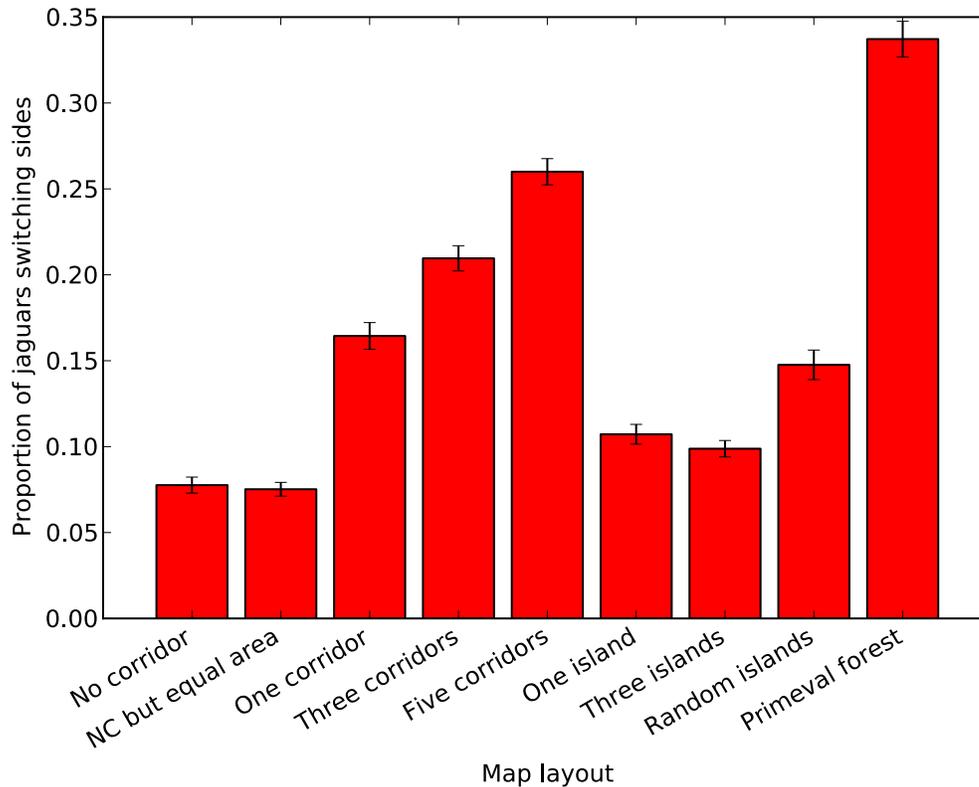


Figure 6: Proportion of jaguars that move from one side of the map’s centre-line to the other by the end of the simulated year, compared across the nine different map layouts. Standard errors are calculated across 25 replications of each condition with different random seed values.

better match for the multi-faceted and incomplete observational data we have on the real animals (see Di Paolo et al., 2000, for an account of how this process can work). There are many parameters in the model for which we have had to guess at an appropriate value, but the idea is to take these values as a starting point and use them in an iterative process of model refinement in future comparisons with empirical data from Belize.

We began our modelling with a hypothetical question about the best corridor design to choose if you had the resources to reforest a few tens of square km of Belizean farmland separating two forests. We can answer that question unequivocally: of the corridor layouts we explored, the five-corridor layout was the most effective. We had expected that we might see significant differences in the average landscape cost value experienced by the jaguars across the different corridor designs, but this turned out not to be the case. Average landscape cost, given a constant population of jaguars, seems to be explained almost entirely by the availability of core forest grid squares. This suggests, for example, that constructing a new conservation corridor in Belize would

not lead to a big boost in the landscape’s carrying capacity for jaguars. Instead, the key difference observed between our corridor designs was their capacity to promote migration from one side of the map to the other, and thus to promote genetic mixing at the whole-population level. The five-corridor case achieved levels of cross-map migration that were almost comparable to the “contiguous forest” condition, which is a great outcome from a conservation perspective.

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

In terms of the corridor design problem, a weakness of

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

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

Acknowledgements

AW was supported by the UK's Engineering and Physical Sciences Research Council via Southampton's Institute for Complex Systems Simulation and doctoral training centre. CPD was supported by Darwin Initiative grant 17-012 from the UK Department for Environment, Food and Rural Affairs. We also wish to acknowledge the assistance of the Jaguar Corridor Initiative.

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