An Agent-Based Model for the Formation of Butterfly Corridors through Hilltopping Behavior

Jake McClure

Sept 23, 2024

Introduction

The individuals of many species are not equally present throughout a large region that may be traditionally called their spatial extent. Rather, they move along *corridors*, relatively narrow stretches of land connecting various habitats of interest. Identifying corridors is important for effectively surveying and protecting wildlife species. Though corridors have been studied and observed in many species, the exact mechanisms behind their formation have not been fully identified. In this project, I use an agent-based model of butterfly movement to show that the simple behavior of *hilltopping* found in butterflies – their tendency to move uphill to find mates – is sufficient to generate corridors. I also examine the influence of movement stochasticity on the width of corridors, as well as the success in mate-finding. I predict that greater movement stochasticity will increase the width of corridors and lead to butterflies finding fewer mates on average.

Methods

The agents in my model are butterflies, which are randomly distributed throughout a landscape of varying elevation captured from real topographical data (Railsback and Grimm 2019). At each timestep, the agents pick one of two movement strategies – either to a random neighboring patch (with probability $1-q$) or to the neighboring patch with highest elevation (with probability q). The parameter q is the only parameter for this model. Agents move according to this rule for 1000 timesteps, at which point the simulation ends. Some important assumptions in this model are that butterflies are always on the move, and that their motion is completely independent of the presence of conspecifics. These assumptions are not realistic, but the fact that corridors can form without their consideration is reason enough to leave them out for this model.

The three things I measure from these experiments are corridor formation, corridor width, and mate accessibility. To identify corridors, I have the agents leave a trail as they move around. Corridors should appear as bundles of agents' trails (Figure 1). A more quantitative assessment of corridor formation can be found by measuring their width. In this study, the corridor width is defined as the number of patches visited by any agent (an area) divided by the average distance between all agents' current location and their starting point (a length). The corridor width will vary with time; I record the time-series history of corridor width for various values of q to assess how stochasticity influences the transient dynamics and steady-state values of corridor width. Finally, the number of mates accessible to an individual at the end of an experiment can be measured by asking each agent how many other agents are within a specified radius (here, 10 patches) and taking the average. This value is also expected to vary with q.

A complete description of this model according to the ODD format can be found in the appendix.

Results

The simulations show agents' trails following the same paths, and the variance between these trails appears to decrease as movement becomes more deterministic (as *q* increases; see Figure 1). This visual impression is quantitatively supported by corridor width measurements, which peak earlier on and ultimately settle on lower steady-state values as *q* increases (Figure 2). Finally, the number of mates accessible to each agent initially increases as *q* increases from 0 to 0.2, but does not appear to change with further increases in *q* (Figure 3).

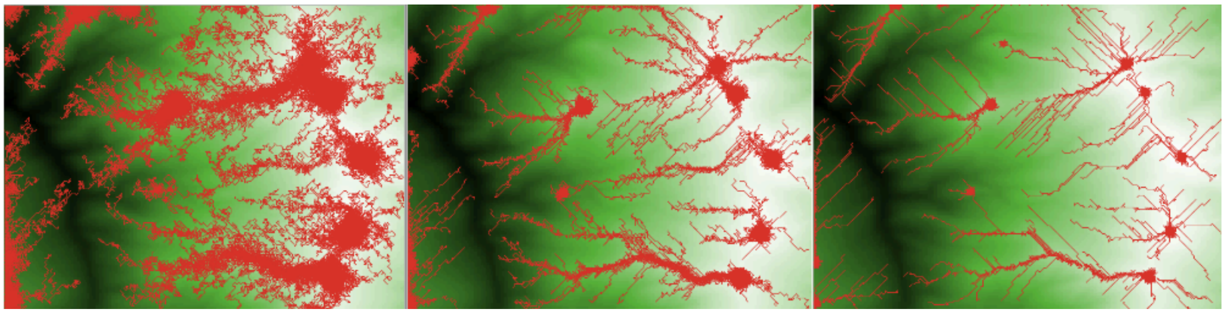

Figure 1. Three different simulations of butterfly hilltopping. The green background is the landscape with brightness varying by elevation (darkest is lowest, brightest is highest). The red trails are left by agents as they move. Each simulation has a different probability to move uphill, *q*. Left: *q* = 0.2, middle: *q* = 0.5, right: *q* = 0.8.

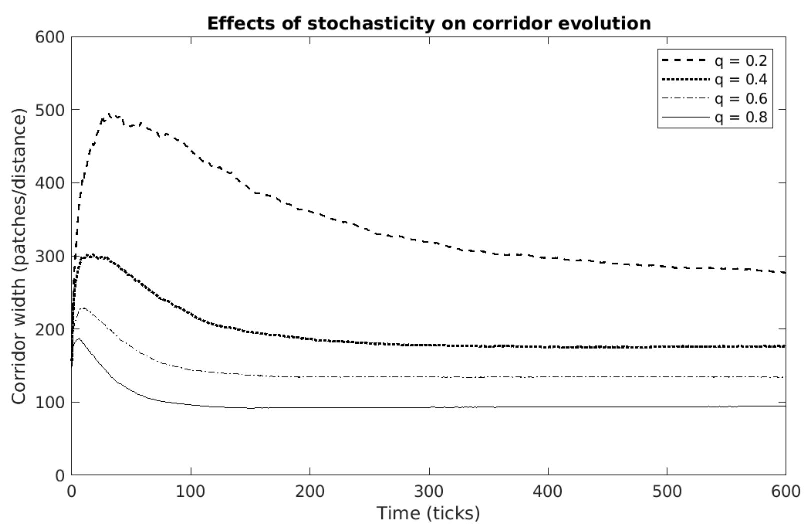

Figure 2. Evolution of corridor width over time for four different values of *q* (the probability of moving uphill at any timestep).

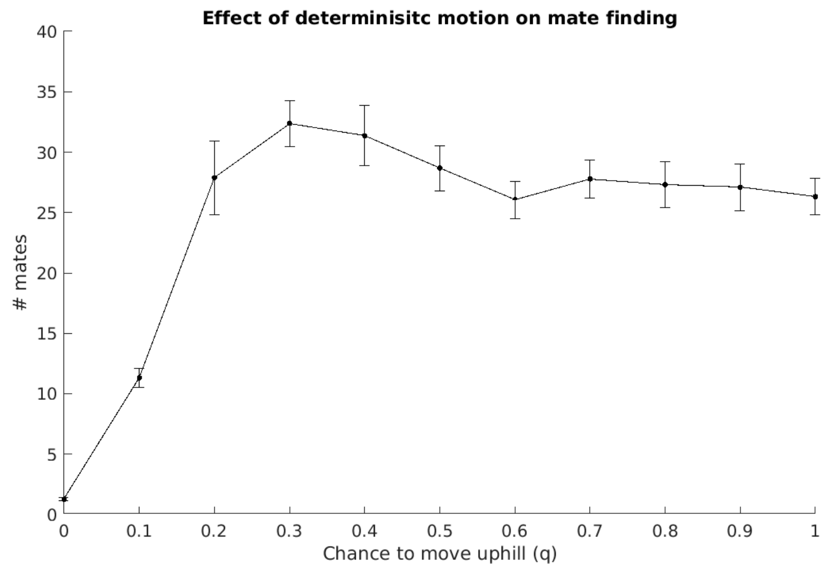

Figure 3. The average number of mates accessible to each agent at the end of a simulation with varying *q*. Ten simulations were performed for each value of *q*: the error bars show the standard deviation of accessible mates in each batch.

Discussion

These simulations show that movement along corridors can arise from the simple behavior of hilltopping in butterflies. When $q = 1$, this is just movement along the gradient of elevation – any butterflies in the vicinity of a ridge will all move to the top of this ridge, and then follow that ridge until it meets a summit. Any lower value of q will introduce randomness that deviates from these deterministic paths, in turn widening corridors. This is exactly what we see in Figures 1 and 2. However, butterflies are not optimizing for corridor width in the wild, but instead for the number of mates they can find. The success of mate-finding does not seem to increase past $q = 0.3$, indicating that even a small tendency to move uphill is sufficient to ensure reproduction. Still, definite corridors emerge from this small tendency.

Future work in this area of study may include a mechanism of butterfly interaction on the way uphill. If butterflies are attracted or repulsed by conspecifics, this would probably alter the shape of corridors. Additionally, this model assumed all butterflies began at randomly-distributed points in the landscape. This is probably unrealistic, as butterflies likely exhibit some kind of pattern in the locations they choose to lay eggs after mating. Adding these considerations to this agent-based model would help researchers understand how corridors emerge across multiple life cycles in a butterfly population.

Appendix: ODD

Butterfly Model ODD Description

This model is originally from Pe'er et al. (2005). The description is taken from Section 3.4 of Railsback and Grimm (2019), with some additions by me in 2024. The model is implemented in NetLogo.

1. Purpose and patterns

   The model was designed to explore questions about virtual corridors. Under what conditions do the interactions of butterfly hilltopping behavior and landscape topography lead to the emergence of virtual corridors, that is, relatively narrow paths along which many butterflies move? How does variability in the butterflies' tendency to move uphill affect the emergence of virtual corridors? This model does not represent a specific place or species of butterfly, so only general patterns are used as criteria for its usefulness for answering these questions: that butterflies can reach hilltops, and that their movement has a strong stochastic element representing the effects of factors other than elevation.

2. Entities, State Variables, and Scales

   The model has two kinds of entities: butterflies and square patches of land. The patches make up a square grid landscape of 201 × 153 patches, and each patch has one state variable: its elevation. Butterflies are characterized only by their location, described as the patch they are on. Therefore, butterfly locations are in discrete units, the x- and y-coordinates of the center of their patch. A patch corresponds to 25 × 25 square meters. Simulations last for 1000 time steps; the length of one time step is not specified but should be about the time it takes a butterfly to move 25–35 m (the distance from one cell to one of its neighbor cells).

3. Process Overview and Scheduling

   There is only one process in the model: movement of the butterflies. On each time step, each butterfly moves once. The order in which the butterflies execute this action is unimportant because there are no interactions among the butterflies.

4. Design Concepts

   The *basic principle* addressed by this model is the concept of virtual corridors—pathways used by many individuals when there is nothing particularly beneficial about the habitat in them. This concept is addressed by seeing when corridors *emerge* from two parts of the model: the adaptive movement behavior of butterflies and the landscape they move through. This *adaptive behavior* is modeled via a simple empirical rule that reproduces the behavior observed in real butterflies: moving uphill. This behavior is based on the understanding (not included in the model) that moving uphill leads to mating, which conveys fitness (success at passing on genes, the presumed ultimate objective of organisms). Because the hilltopping behavior is assumed a priori to be the objective of the butterflies, the concepts of *Objectives* and *Prediction* are not explicitly considered. There is no *learning* in the model.

Sensing is important in this model: butterflies are assumed able to identify which of the surrounding patches has the highest elevation, but to use no information about elevation at further distances. (The field studies of Pe'er 2003 addressed this question of how far butterflies sense elevation differences.)

The model does not include *interaction* among butterflies; in field studies, Pe'er (2003) found that real butterflies do interact (they sometimes stop to visit each other on the way uphill) but decided it is not important to include interaction in a model of virtual corridors.

Stochasticity is used to represent two sources of variability in movement that are too complex to represent mechanistically. Real butterflies do not always move directly uphill, likely because of (1) limits in the ability of the butterflies to sense the highest area in their neighborhood, and (2) factors other than topography (e.g., flowers that need investigation along the way) that influence movement direction. This variability is represented by assuming butterflies do not move uphill every time step; sometimes they move randomly instead. Whether a butterfly moves directly uphill or randomly at any time step is modeled stochastically, using a parameter q that is the probability of an individual moving directly uphill instead of randomly.

Collectives are not represented in this model.

To allow *observation* of the two patterns used to define the model's usefulness, we use graphical display of topography and butterfly locations. Observing virtual corridors requires a specific "corridor width" measure that characterizes the width of butterfly paths from their starting patches to hilltops. Additionally, we count the number of mates accessible to each individual (i.e. within a certain radius) at the end of each simulation.

5. Initialization

The topography of the landscape (the elevation of each patch) is initialized when the model starts. This topography is taken from a real study site, imported from a file containing elevation values for each patch. The butterflies are initialized by creating five hundred of them and dispersing them throughout the landscape: each butterfly's initial location is set to a patch selected randomly from among all patches.

6. Input Data

The environment is assumed to be constant, so the model has no input data.

7. Submodels

The movement submodel defines exactly how butterflies decide whether to move uphill or randomly. First, to “move uphill” is defined specifically as moving to the neighbor patch that has the highest elevation; if two patches have the same elevation, one is chosen randomly. “Move randomly” is defined as moving to one of the neighboring patches, with equal probability of choosing any patch. “Neighbor patches” are the eight patches surrounding the butterfly’s current patch. The decision of whether to move uphill or randomly is controlled by the parameter q, which ranges from 0.0 to 1.0 (q is a global variable: all butterflies use the same value). On each time step, each butterfly draws a random number from a uniform distribution between 0.0 and 1.0. If this random number is less than q, the butterfly moves uphill; otherwise, the butterfly moves randomly.

CREDITS AND REFERENCES

Pe’er, G., Saltz, D. & Frank, K. 2005. Virtual corridors for conservation management. *Conservation Biology*, 19, 1997–2003.

Pe’er, G. 2003. Spatial and behavioral determinants of butterfly movement patterns in topographically complex landscapes. Ph.D. thesis, Ben-Gurion University of the Negev.

Railsback, S. & Grimm, V. 2018. *Agent-based and individual-based modeling: A practical introduction, Second edition.* Princeton University Press, Princeton, NJ.