

## **Purpose**

The purpose of the model is to examine the relationship between territory size and intergroup mortality risk under realistic assumptions. Furthermore, the model investigates how fertility is affected by this relationship.

## **Entities, state variables, and scales**

This model contains three types of entities: groups, individuals, and cells. Each group represents a collection of territorial individuals. Groups are characterized by a *group-color* variable, which is used to visually distinguish group members from non-group members. Individuals use the *my-group* variable to track their group membership, which is fixed from birth and assigned based on their mother’s group membership. Individuals also have a numerical *energy* state variable, which is used to complete certain actions, and a deficit results in death. Most state variables are used for data tracking: groups possess several state variables that collect information on the current state of their population and territory, and individuals have several state variables that track their current life and fertility status (Table 1).

The environment is composed of grid cells in lattice configuration, arranged into a 100 x 100 rectangle. It wraps both vertically and horizontally to avoid any boundary effects. These cells have two state variables: *cell-energy* represents the amount of energy available for individual consumption, and *cell-group* represents the current group affiliation, which is set as the group affiliation of the last individual to occupy that cell. The color of the cell is periodically updated to match the *group-color* of its currently affiliated group (Table 1).

# ODD protocol for “LethalGeometry”

a. Individual state variables	
<i>age</i>	The number of ticks or timesteps that an individual has been alive.
<i>energy</i>	The amount of energy an individual currently has.
<i>my-group</i>	The group to which an individual currently belongs.
<i>num-children</i>	The number of offspring an individual has produced.
<i>dying?</i>	This value is FALSE by default, but switched to TRUE if an individual’s energy value falls below 0.
<i>purple-heart?</i>	This value is FALSE by default, but temporarily switched to TRUE if an individual was attacked and therefore suffered an aggression-cost during the current timestep.
<i>birthing?</i>	This value is FALSE by default, but temporarily switched to TRUE during a timestep when an individual is reproducing.
b. Group state variables	
<i>territory-size</i>	Total count of all cells associated with a group.
<i>periphery-count</i>	Count of all territory cells that have
<i>population-size</i>	The total number of individuals who are members of a particular group.
<i>food-availability</i>	The total amount of energy currently available in patches within the territory of a group.
<i>total-death-count</i>	The total number of deaths recorded at the current timestep.
<i>war-death-count</i>	The total number of deaths due to warfare recorded at the current timestep.
<i>base-death-count</i>	The total number of deaths not due to warfare recorded at the current timestep.
<i>num-births</i>	The total number of births
<i>mean-age</i>	The average value for state variable age for individuals within the group.
<i>median-fertility</i>	The instantaneous median calculation of <i>num_children</i> for individuals within the group.
c. Cell state variables	
<i>cell-energy</i>	The amount of energy available for consumption.
<i>cell-group</i>	The group whose territory currently includes the given patch.

Table 1. LethalGeometry state variables for all (a) individual agents, (b) territorial agent groups, and (c) territory cells.

## Process overview and scheduling

During each time step, the following processes take place: (I) agent deaths, (II) agent births, (III) cell updates, (IV) agent movement, (V) agent fighting, (VI) agent reproduction, and (VII) agent foraging.

## Design concepts

**Basic principles.** In the conceptual model of intergroup aggression, we assume that territories are explicitly delineated as periphery or core and that lethal intergroup aggression only occurs in the periphery. For the agent-based model, we do not impose these restrictions but instead allow them to emerge from the simulation. Agents move randomly and their movements define the boundaries of their territory. Agents can also be aggressive towards other non-group agents at any point within their territory.

**Emergence.** We expect territory sizes to fluctuate over time in response to individual reproduction, random-walking, and lethal intergroup encounters. In turn, the individuals within these territories are expected to vary in their mortality and fertility rates according to food availability and frequency of aggression.

**Sensing.** Agents can assess their environment to determine (1) if there are non-group members within the same cell, and (2) if there is food within their cell.

**Interaction.** The agents are programmed to walk randomly about their environment, search for and eat food to obtain energy, reproduce if they can, and act aggressively toward individuals of other groups. During each simulation step, agents analyze their environment and internal state to determine which actions to take. The actions available to agents include moving, fighting, and giving birth (Submodels). Each action is associated with a predetermined energetic cost that is set by the user (Table 2). An agent enters into combat with one of the non-group members it senses within its cell and its victim incurs an energy cost equal to the *aggression-cost* parameter setting. An agent also eats any *cell-energy* that exists at its current location (Table 2).

**Stochasticity.** Individuals and cells are handled in a random order for each process described below (Submodels). Additionally, they move randomly as the simulation progresses.

**Collectives.** A group is represented by a collection of individuals and its territory is represented by a collection of cells. The territorial nature of these individuals often results in a spatial distinctiveness for both the individuals and cells of each group and territory.

**Observation.** The purpose of the model is to assess the relationship between territory size and per capita mortality and fertility rates. Thus, LethalGeometry collects data related to these factors at the end of each simulation run.

Parameter	Description of parameter
<i>initial-number-of-groups</i>	The number of groups initially placed in the environment.
<i>initial-group-size</i>	The number of individuals in each group during initialization.
<i>initial-individual-energy</i>	The energy first given to new agents who are initialized or born.
<i>cell-growth-rate</i>	The rate at which each cell or patch increases its resource energy.
<i>movement-cost</i>	The amount that an individual’s energy stores are reduced when it moves to an adjacent cell.
<i>birth-cost</i>	The amount that an individual’s energy stores are reduced when it reproduces.
<i>aggression-cost</i>	The amount that an individual’s energy stores are reduced when it is attacked by another individual.

Table 2. Initial parameter settings for LethalGeometry simulations.

## Initialization

At the beginning of a simulation, LethalGeometry builds the cells for the environment and agent groups according to the initial parameter settings (Table 2). A number of groups are created, totaling the *number-of-groups* parameter setting, and each containing a population size equal to *initial-group-size*. Each agent is given an initial energy equal to *initial-individual-energy*. Each cell receives a random initial *cell-energy* level, uniformly distributed from 0 to 100.

## Input

The model does not use input data to represent time-varying processes (Grimm et al., 2010).

## Submodels

(I) Agent deaths: During this procedure, any agents that have incurred a subzero energy value during the previous timestep are considered “dead” and are removed from the simulation.

(II) Agent births: During this procedure, any agents that are marked to give birth are cloned. These clones have settings identical to their asexual parent, except in their *energy*: the parent loses and the clone begins with energy equal to the *birth-cost* (Table 2).

(III) Update cells: The environmental cells each contain some variable amount of *cell-energy* (i.e. vegetation, fruit, prey), which is consumed by the agents and which regrows at a predetermined rate set by *cell-growth-rate* (Table 2). At any given time, each cell is associated with at most one specific group of affiliated agents, referenced as *cell-group*. This affiliation is determined by the agent who last occupied that cell. The full collection of cells associated with the same *cell-group* represents the territory for that group. During this procedure, the cell color is updated to match the current group territories.

(IV) Agent movement: The agents are random-walking. For each simulation step, an agent must move in a random cardinal direction one unit cell length and incur an associated energy cost, *movement-cost* (Table 2).

(V) Agent fighting: Fighting takes place when agents from different groups occupy the same cell. Each agent in a cell randomly selects another non-group agent to fight, and the victim incurs an energy cost equal to *aggression-cost* (Table 2). We do not make assumptions that killings occur only in cases of numerical asymmetry; but in practice, agents will be more likely to die when sharing cells with numerous rivals.

## ODD protocol for “LethalGeometry”

(VI) Agent reproduction: agents have a stored energy level and automatically reproduce if they exceed some predetermined lower threshold energy, *birth-cost* (Table 2). For simplicity, the species is modeled as monoecious: any individual can give birth. Giving birth can only occur if the agent can afford the associated energy cost. If an agent has enough energy to give birth, this action is obligatory.

(VII) Agent foraging: The grid contains a random distribution of food, which is used by the agents for energy. Stored energy is essential for allowing the agent to stay alive and deploy various actions. If an agent occupies a cell with some positive *cell-energy*, the agent “eats” the cell food, transferring that energy into the agent's own *energy* stores.