ODD protocol for "Lethal Geometry"

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).

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.

Basic principles. For a macroscale model of intergroup aggression, we use simplified conditions. We assume that individuals move randomly, and thus intergroup interactions occur randomly. Additionally, we assume that individuals live in groups with fission-fusion dynamics (i.e., smaller subgroupings within a larger community), as in most mammals documented to have coalitionary killing. Within each territory, individuals thus travel in subgroups of varying size. We assume that intergroup killings occur when large subgroups happen to encounter isolated or greatly outnumbered members of neighboring groups, enabling the attackers to kill at low risk to themselves. Thus we assume intergroup killing is a stochastic process resulting from random encounters, with killings occurring whenever encounters happen to coincide with an extreme numerical asymmetry between subgroups. Since territory owners tend to avoid the periphery of their territory (e.g., chimpanzees), we assume that these intergroup encounters tend to occur in the border areas, along the periphery of each territory. The core consists of all territory that is not periphery and is the more central and safe location.

Assuming that the shape of the territory approximates a convex polygon, the length of the periphery should increase as a linear function of the reciprocal centroid distance, whereas the territory area should increase quadratically. We define the reciprocal centroid distance for convex polygon territories to be equivalent to a side for square territories, is equivalent to the periphery-area ratio (Figure 1). For very small territories, individuals are exposed to elevated mortality risk throughout their range. For very large territories, the rate of mortality declines asymptotically towards zero, such that increasing territory size eventually has negligible further impact on mortality risk (Figure 2a). We can also express this relationship as a positive correlation between the per capita mortality rate and reciprocal centroid distance (Figure 2a). In larger territories, individuals are less likely to die from lethal intergroup encounters, and therefore live longer, and as a result have more offspring in their lifespan. These demographic processes likely results in a virtuous cycle of benefits for larger territories: higher fertility leads to fighting ability advantages, which enables them to expand 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.

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 (see Table 2).

An agent enters into combat with each non-group member it senses within its cell. For each aggressive dyadic encounter, both individuals have an equal chance of winning and the loser incurs an energy cost equal to the *aggression-cost* initial 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, during each aggressive dyadic encounter, both combatants have a 50-50 chance of winning, which is determined stochastically.

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 (Figure 3).

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

Initialization. At the beginning of a simulation, Lethal Geometry builds the environmental food cells and agent groups according to the initial parameter settings (Table 2). Each cell receives a random initial *cell-energy* level, uniformly distributed from 0 to 100. A number of groups are created, totaling the *number-of-groups* parameter setting, and each containing a random initial population size uniformly between 1 and 500 agents. Each agent is given a random initial energy store ranging uniformly from 0 to 100. The simulation is run for a predetermined number of time steps, which is controlled by the *stop-at* parameter.

Submodels

(I) Agent deaths: During this procedure, any agents that have a subzero energy value 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 variable settings identical to their asexual parent, except in their *energy*: the parent and the clone each get half of the original *energy* stored by the parent. Additionally, the parent has its *energy* reduced by the *reproduction-cost* value (Table 2).

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

(IV) Agent movement: The agents are random-walking. For each simulation step and, an agent must move in a random 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. All fighting is dyadic for computational simplicity, with each aggressive pair of agents inflicting an equal energy cost, *aggression-cost* (Table 2) on each other. We thus 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. If more than two differently affiliated agents occupy the same cell, then a series of dyadic interactions will take place for a given simulation step, accounting for each agent fighting every other unaffiliated agent.

(VI) Agent reproduction: agents have a stored energy level and automatically reproduce if they reach some predetermined lower threshold energy, *reproduction-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.