I developed B3GET and conducted simulations using NetLogo 6.1.1 (Wilensky, 1999), run on processors operated by the Minnesota Supercomputing Institute (MSI). I report the model and methods used following the Overview, Design concepts and Details (ODD) description protocol for agent-based models (Grimm et al., 2006, 2010).

Purpose

This model can test a broad range of hypotheses in biology, including those related to behavioral ecology and hominin evolution.

Entities, state variables, and scales

B3GET includes three types of entities: agents, groups and plants. Agents are virtual organisms who survive and reproduce with equivalent biological constraints to real world living organisms. All agents have a *group.identity* state variable to store their association with a single group. Groups are characterized by *group.color*, which facilitates visually distinguishing agents by their group membership. Plants follow similar rules to those in Conway's Game of Life (Gardner, 1970), and exist in the world in a gridlike fashion as in cellular automata. Similar to this model, plants are alive or dead based on criteria imposed by input parameters, which are related to their preferred minimum and maximum number of neighboring plants in the surrounding eight cells. Plants and agents have a state variable *energy.supply*, a value corresponding to the amount of energy that they have available. For living plants, *energy.supply* accumulates differentially based on input parameters for season and day length. For agents, *energy.supply* is obtained by either maternal nursing or eating plants and possibly eating each other.

Agents are characterized by several state variables, which are differentiated as (1) visible phenotype variables, (2) hidden phenotype variables, and (3) hidden tracking variables. Phenotype variables relate to the properties that an agent can see about itself and modify through actions (see Interactions), including *body.size*, current *life.history* stage, and *living.chance*. Tracking variables relate to those that do not influence the lives of agents in any way, but instead track their lives as a passive observer. For example, *ticks-at-weaning* and *ticks-at-sexual-maturity* record the time when an agent became a juvenile and an adult, respectively. Visible variables exist as part of the environment that all agents can see, such as another's *biological.sex* and current *life.history* state. Hidden variables are any variables that are not visible variables.

Upon conception, agents have several static variables that remain fixed for their lives, including *biological.sex*, *generation-number*, references to *mother.identity* and *father.identity*, and *chromosome* and *identity* chromosomes that contain the list of genes inherited from their parents. Agents also possess some dynamic variables pertaining to current status, such as *age*, *body.size*, *life.history*, and *female.fertility*, which change throughout the course of their lives. Furthermore, agents have spatial coordinates that change during the simulation. Agents also track the chance of certain events occurring, such as *juvenility.chance* and *weaning.chance*, which influence when an infant becomes a juvenile respectively through either her own or her mother's decision-making. Many of these variables, including *body.size, life.history, female.fertility, conception.chance*, and *living.chance*, encode a value between 0 and 1, which can be rescaled to match any value in nature. These values can be modified throughout an agent's lifetime depending on how much of their *energy.supply* they or another invests in actions to perform this modification. Agents pay a positive amount of their *energy.supply* to pay for all actions, and are not able to pay for actions if their *energy.supply* reaches zero. However agents can pass negative values to actions to produce the opposite effect. For example, paying negative energy toward the *sex-ratio* action increases the chance of conceiving a female, whereas paying positive energy toward this action increases the chance of conceiving a male. These modifications apply Equation 1, which can incrementally increase or decrease the original value while remaining within the 0 to 1 range: y_0 is the initial state variable value, x is an *energy.supply* value between $-\infty$ and ∞, and y is the weight's final value.

The agents inhabit the surface of a torus-shaped world (100 x 100 square cells). At each time step agents undergo a series of behavioral processes that are outlined in detail below (Submodels). There are no real-world equivalents to the space (square cell) and time (timestep) units in the model, which runs counter to many other agent-based models. However, this move was purposeful and important to fully recognize this model as a separate universe with its own physical laws.

Process overview and scheduling

The model is executed by the following processes: (1) environmental constraints, (2) agent actions, and (3) meta-analyses. Below, I refer to Ego as the hypothetical agent currently executing these processes and Target as a hypothetical agent that Ego can see in its environment and thus incorporate into its decision making.

Basic principles

B3GET combines principles of behavioral ecology (Alberts & Altmann, 1995; Hrdy, 1979; Isbell, 1991; Koenig, 2002; Mitani, Gros-Louis, & Richards, 1996; Nunn, 1999; Pusey, 1987; Sterck, Watts, & van Schaik, 1997; Terborgh & Janson, 1986; Trivers, 1972, 1974; Van Schaik, 1983; van Schaik & Kappeler, 1997; R. Wrangham, 1979; R. W. Wrangham, 1980), with concepts from virtual evolution (Dawkins, 1976; Holland, 1995; Neumann, 1966; Ray, 1991; Yaeger, 1993), and research in energy tradeoffs (Charnov, 1976; Mangel & Stamps, 2001; Rates et al., 2006), to simulate populations of virtual organisms evolving over generations, whose evolutionary outcomes reflect the selection pressures of their environment.

Emergence

Strategies emerge from a given ecological context over the course of generations of selection. The ecological context depends mainly on six parameter settings: *plant-annual-cycle* and *plant-daily-cycle* set the length of a year and a day, respectively, in timesteps; *plant-seasonality* sets the annual extremes in the *energy.supply* of plants; the *plant-minimum-neighbors* and *plant-maximum-neighbors* dictate each plant's preferred amount of surrounding plant neighbors, who spring to life if this context is met and die otherwise; and *plant-quality* sets the maximum *energy.supply* value of plants. Additionally, the ecological context is shaped by the phenotypes of the agents themselves, which may alter individual preferences for group composition or other interactive actions. Evolved strategies include the timing of life history events like gestation and weaning; the amount of energy allocated to body growth and maintenance; amount of time spent foraging; and others. Furthermore, agents move spatially in response to their environment and based on their genotypes, which include weighted preferences for moving relative to other agents. Population level spatial dynamics are not imposed by the model but emerge from individual interactions and movement preferences.

Adaptation

Agent populations can evolve through the inheritance of imperfectly-copied alleles during sexual reproduction. We represent inheritance using a set of diploid chromosomes that together form an agent's genotype. Each chromosome consists of a set of genes which encode rules for determining the targets and energy weights for actions. If Ego sees an environmental context that matches one of its genes, it performs that gene's corresponding action and invests an amount of energy to that action based on that gene's corresponding weight (see Submodels for more detail). Thus, each gene can have an indefinite number of possible alleles.

Agents reproduce sexually and so prior to conception, chromosomes undergo the genetic processes of recombination and mutation. During recombination, B3GET randomly selects one of two chromosomes from each agent's parent. Then, roughly 50% of alleles from the selected chromosome are randomly exchanged with alleles from the homologous chromosome. Finally, each parent provides this chromosome to produce a new homologous pair of chromosomes in the offspring. After this process, mutation at each locus occurs by chance based on the average *mutation.chance* of Ego's parents. Should a mutation event occur at a locus, one of the following processes is selected at random to occur: (1) deletion of allele, (2) duplication of allele, (3) creation of a new allele, (4) modification of numerical values, and (5) modification of non-numerical codons.

Thus as a population of agents evolves, behavioral traits change over time due to (1) variation in alleles resulting from mutation; (2) new combinations of alleles resulting from recombination and sexual reproduction; and (3) changes to the frequencies of alleles resulting from selection and drift.

Objectives

B3GET draws much inspiration from research on virtual evolution and genetic algorithms (Ray, 1991; Taylor, 2014). Accordingly, at each timestep, it imposes a fitness rule as follows: the environment checks each agent's *living.chance* against a randomly generated number between 0 and 1; if the number falls above the agent's *living.chance*, which is also constrained to values between 0 and 1, then B3GET sets the agent's *is.dead* state variable to TRUE. Thus an agent's survival depends solely on keeping its *living.chance* high enough to pass this check at every timestep, and its fitness depends solely on surviving long enough to differentially reproduce more than its competitors.

Learning

Future versions of B3GET will include agent memory and learning.

Prediction

B3GET is designed to model general patterns of evolution, and thus is expected to produce emergent patterns that should support fundamental predictions generated from biological theory. For example, B3GET explores whether agents will evolve to (1) differentially allocate more help towards kin (Axelrod & Hamilton, 1981), (2) primarily favor mothers who terminate care before their offspring stop demanding it (Trivers, 1974), and (3) forage optimally for their given environmental context (Charnov, 1976).

Sensing

Ego can sense its surroundings depending on its *day.perception.range* and *day.perception-angle*, or *night.perception.range* and *night.perception-angle*, which dictates the extent of its cone of perception, respectively for day or night. Ego can see all other agents and plants who fall within this cone of perception, and are able to assess any visible state variables they possess, such as their *biological.sex*, *life.history*, *body.size*, and *body.shade*. All visible state variables that Ego can perceive are summarized in the supplementary materials. This assessment includes relative measurements, such as: (1) the relative size of Target with respect to Ego, (2) whether Target is genetically similar to Ego, and (3) whether Target belongs to the same group as Ego.

Interaction

Ego performs actions in order to modify the phenotypic variables of itself or others. Ego can engage in any number of interactions per time step, depending on its current *energy.supply* available to use, and its decisions generated from the environmental context-dependent consideration of its genotype (this process is described in Submodels). Actions that modify the state variables of Ego are called "intra-actions," and those that modify the state variables of others are called "inter-actions". A full list of available agent actions are found in the supplementary materials.

Ego can perform intra-actions to invest in its own state variables, including grow-body and maintain-body. For example, agents invest in their *infancy.chance* to transition from a gestatee to an infant, their *juvenility.chance* to transition from infant to juvenile, and in their *adulthood.chance* to transition from a juvenile to an adult. Likewise, pregnant female agents invest in *birthing.chance* and lactating female agents invest in *weaning.chance* to restart their cycling. All agents must always invest in their *living.chance* high enough to avoid death, and in their *conception.chance* in order to conceive during mating. Agents can also leave their current group and travel alone until they join a new group.

Ego can perform inter-actions to invest in the state variables of others. Agents interact with other agents in the following ways: attack, help, mate, join group, pick up and put down Target. These interactions can only occur if both Ego and Target occupy any overlapping space. That is, the distance between the center-of-mass of Ego and Target is less than the sum of Ego and Target's *body.size* divided in half. Some of these interactions result in state variable modification for Target. For example, Ego can attack Target and reduce Target's *living.chance* by an amount corresponding to the energy that Ego invests in attacking. Likewise, Ego can invest in helping Target and increase Target's *living.chance* with every helping event. Mating may cause conception to occur, depending on the mean *conception.chance* of both potential parents, which results in the creation of a new agent. When Ego joins the group of Target, Ego's *group.identity* state variable updates to the *group.identity* of Target. Agents also indirectly interact through feeding competition by investing in foraging and thus limiting the amount of plant energy available to others.

Stochasticity

B3GET includes several stochastic processes to reflect analogous natural processes affecting living biological organisms. Computer processing limits the extent to which processes can happen simultaneously. To avoid emergent properties that are biases by computationally iterative rather than simultaneous processes, B3GET assigns agents to a random rank for each timestep, which determines the order in which that agent makes decisions and performs actions. Some agent actions result in statistically generated outcomes. The genetic processes of recombination and mutation, and checks to state variables like *living.chance* and *conception.chance*, are also stochastic. The likelihood of winning a fight during an attack is directly proportional to the ratio of Ego and Target's *body.size*: agents with a larger *body.size* have a proportionally greater chance of winning the fight, following Lanchester's linear law of battle (Wilson, Britton, & Franks, 2002). B3GET also randomly selects plants to check their surrounding neighbors against the *plant-minimum-neighbors* and *plant-maximum-neighbors* input parameters to determine if they should live or die.

Collectives

Each agent belongs to a group and often multiple agents belong to the same group and spatially aggregate based on group membership. However behavioral preferences related to group composition and affiliation are allowed to evolve in unexpected ways. In fact, agents may evolve to act without any consideration of its *group.identity*.

Observation

B3GET can produce several data files for use in biological experimentation. The two most apparent file types are population and genotype files, which are imported at the beginning of every simulation as the initial seed from which new virtual organisms will evolve. Likewise, users can save populations into a population file and an individual agent's genotype into a genotype file. B3GET also generates some behind-the-scenes files including the metadata file that contains mouse-click information and a simulations file that contains a list of all simulation runs performed. Most importantly, users are able to change *collect-data?* to ON and record information on the agents in the simulation. By default, B3GET keeps a complete record of all agents, whose major life history events are recorded into a census file upon death. More advanced users may directly modify the code for additional options including focal follows and scan sampling (Altmann, 1974).

Initialization

Upon initialization, B3GET populates the world with populations of agents and plants. Plants begin by populating every cell in the world, but once the simulation begins, they change into the ecological patterns expected from the selected input parameters. Agents are created from a population file and given an initial genotype copied from a genotype file.

Input data

B3GET requires an initial population and genotype file to begin any simulations. These files can be modified to create a range of initial conditions for this seed population.

Submodels

Each time step, B3GET activates the following processes (1) environmental constraints, (2) agent actions, and (3) meta-analyses.

1. Environmental constraints

First, B3GET performs a "reaper" check on all agents and kill any whose *living.chance* values are too low. Second, B3GET deteriorates all agents, living or dead, by reducing severall of their state variables by an incremental amount. Finally, B3GET updates the visible state of agents, such as updating their *color* based on their *group.identity* and *body.shade*.

2. Agent actions

B3GET selects agents in a random order and performs the following processes (Figure 2). Once these processes have been completed for one agent, B3GET continues to the next randomly chosen agent until all individuals have taken their turn. Ego evaluates its environment, which includes individuals within its cone-of-perception, including itself. Only mothers are able to perceive her gestatee offspring and gestatees are only able to perceive themselves and their mothers. B3GET combines each agent’s genotypes and current environmental context into a list of decision-vectors.

3. Meta-analyses

B3GET allows a user to select *collect-data?* and *selection-on?* to collect data on agents and apply artificial selection to their populations.

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