I developed BEGET and ran simulations using NetLogo 6.1.0 (Wilensky, 1999; 2007) and insert MSI supercomputer information here. 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).

2.2.1 Purpose

I developed this model to test hypotheses related to primate socioecology and hominin evolution.

2.2.2 Entities, state variables, and scales

The model included three types of entities: ***groups***, ***plants*** and ***agents***. All agents are associated with exactly one group a spatial association of agents. 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, and exist in the world in a gridlike fashion as in cellular automata. Two input parameters relate to this: *maximum-neighbors* and *minimum-neighbors*, which respectively define the preferred maximum or minimum number of other plants nearby (those in a Moore neighborhood), much like Conway's 'alive' cells only stay 'alive' if they have a maximum of three and a minimum of two neighbors. At each timestep, a set number of cells (see global parameters) either become alive or dead, or stay in the same state, depending on these rules and the settings for these input parameters. Plants have a state variable *penergy*, which accumulates in value as time goes on as long as the plant is alive. Agents are able to eat plants and take their *penergy* to use as *energy* for themselves.

Agents are characterized by several state variables, which can be split into three main parts: visible phenotype variables, hidden phenotype variables, and hidden tracking. Upon conception, agents have several static variables that remain fixed for their lives, including *sex*, *generation*, references to *mother* and *father* agents, and *chromosomes* that contain the list of genes inherited from these parents. Agents also possess some dynamic variables pertaining to current status, such as *age*, *body-size*, *life-history*, and *fertility*, which change throughout the course of their lives based on environment-agent interactions. Furthermore, agents have spatial coordinates that change during the simulation. Agents store energy in a number of ways and have state variables to this purpose: agents forage to obtain *stomach-energy*, and then transfer this energy to action-energy to perform actions, and energy is stored long-term in *reserve-energy*. Agents also track the chance of certain events occurring, such as *life-history-chance*, *fertility-chance*, *mortality-chance*, and *conception-chance*.

Many of these variables, including *body-size, life-history-chance, fertility-chance, mortality-chance*, and *conception-chance*, encode a value between 0 and 1, which can be rescaled to match any value in nature. These values can be modified throughout a agent's lifetime. Finally, agents have a few state variables that do not influence their behaviors but instead are used to facilitate record keeping and data analysis, such as count-conceptions and count-group-transfers, which track the reproductive success and number of lifetime transfers between groups, respectively.

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). Some text needed here about how there are no real-world equivalents to the space and time units in the model, which runs counter to many other agent-based models. Not defining a specific scaling unit here because I want it to be more abstract.

2.2.3 Process overview and scheduling

The model is executed by the following processes: (I) environmental constraints, (II) agent actions, and (III) 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' and thus incorporate into its decision making.

2.2.4 Basic principles

This agent-based model combines principles of behavioral ecology (Trivers, 1972; 1974; Hrdy, 1979; Wrangham, 1980; van Schaik, 1983; Terborgh and Janson, 1986; Pusey, 1987; Isbell, 1991; Stearns, 1992; Andersson, 1994; Alberts and Altmann, 1995; Mitani et al., 1996; Sterck et al., 1997; Nunn, 1999; van Schaik and Kappeler, 1997; Koenig, 2002) with concepts from virtual evolution (von Neumann, 1966; Dawkins, 1986; Ray, 1991; Yaeger 1994; Holland, 1995) and in the same vein as others who appreciate the need to model energy tradeoffs (citations) to allow agents flexibility in behavior, but also a finite range of possible evolved strategies.

2.2.5 Emergence

Strategies emerge from a given ecological context over the course of generations of selection. The ecological context depends mainly on six parameter settings: the parameter. Additionally, the ecological context is shaped by the phenotypes of the agents themselves, which may alter individual preferences for group composition. 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.

2.2.6 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 action. 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, BEGET randomly selects one of two chromosomes from each agent 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 Ego's mutation-rate.

During mutation, modifications to gene weights are calculated using Equation 1, which can incrementally increase or decrease the original gene weight while remaining within the 0 to 1 range: y_0 is the weight's initial value, x is a randomly generated number between -1 and 1, and y is the weight's final value. 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. More text needed here about the types of possible mutations at a locus.

2.2.7 Objectives

While B3GET draws much inspiration from the fields of virtual evolution and genetic algorithms, it does not center around a fitness function that defines which strategies are selected. However, there is a fitness rule that all agents must follow: have as high as possible value for living chance, which is only allowed to vary between 0 and 1. At each timestep, the environment rolls the dice for each agent and those with lower living-chance values have a higher chance of dying through this process.

2.2.8 Learning

Text needed here about agent memory and how that works.

2.2.9 Prediction

Since B3GET is designed to model general patterns of evolution, it is expected to produce emergent patterns that either confirm previous predictions or generate new ones. Chapter 3 discusses how B3GET tests three current predictions in behavioral ecology: (1) the degree of help towards another correlates with degree of relatedness to that individual, (2) mothers generally terminate care before offspring, and (3) organisms evolve to forage more optimally over time.

2.2.10 Sensing

Agents can sense the surrounding agents and plants with their *perception-range* and *perception-angle*, in a collection which can include Ego itself. From this, Ego can see the following state variables. Agents can sense all of their phenotype state variables and can check what their exact values are at any timestep.

All information that Ego can 'see' when perceiving another agents are its visual phenotype state variables. These include factors such as its *sex*, *life history* stage, and *fertility* state. This status also includes factors determined using information from both individuals, such as the relative size of Target with respect to Ego, whether Target is genetically similar to Ego, and whether Target belongs to the same group as Ego, and the on-off status of the ABC signals, the color and shade of another individual.

2.2.11 Interaction

Agents perform actions in order to modify the state variables of themselves or others. Agents can engage in any number of interactions per time step, depending on their current action-energy available to use, surrounding environment, and their own genotype. 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. Agents can engage in any number of actions per time step, depending on their current action-energy available to use, surrounding environment, and their own genotype. A full list of available agent actions are found in Table X.

Agents interact with themselves to change their own state variables: agents can invest energy into their infancy-chance,..., state variable, which affects the probability of transitioning to the next life history stage (for example, from "juvenile" to "adult"); maintenance decreases living-chance; growth increases body-size; conception investment increases conception-chance; agents can increase their maternal-stores, the energy stores used by their dependent offspring; and investing in fertility increases fertility-chance, or the chance of transitioning to the next fertility stage (for example, from "pregnant" to "lactating"). These state variable modifications are calculated from Equation 1: y_0 is the variable's initial value, x is the amount of invested energy, y is the variable's final value, and the sign of x is negative if the effect is to decrease the state variable and positive otherwise. Agents can also "leave" their own group and travel alone until they join a new group. When this occurs, BEGET creates a new group agent whose only member is the agent leaving its current group, and that agent updates its group state variable to refer to this newly made group.

Furthermore, agents must undergo the obligatory action of make-decisions, which allows the agent to assess the current environment and make decisions for the upcoming timestep.

Agents directly interact with other agents in the following ways: fight, mate, groom and join another individual's group. These interactions can only occur if both Ego and Target occupy the same cell, and in some cases both agree to do the action (such as mating). Some of these interactions may alter agent state variables: the mortality-chance variable is increased for the loser of a fight, and decreased for the receiver of a grooming event. Mating may cause conception to occur, which results in the creation of a new agent agent. Agents can also decide to "join" another agent's group and in effect transfer to that group. When this occurs, their group state variable updates to their new group designation.

Agents also indirectly interact through feeding competition by investing in foraging. If agents attempt to forage when no energy is available they will not receive energy.

2.2.12 Stochasticity

The order in which agents act is randomly generated each timestep, to avoid any emergent properties to be based on the 'rank' of the individuals in the action order. The genetic processes of recombination and mutation are stochastic. Several agent status updates are also based on chance, such as conception-chance. For example, a agent's living-chance is its chance of not dying each time step. The model calculates the chance of events occurring by (1) generating a number between 0 and 1, (2) comparing that number to the chance state variable, and (3) activating the associated event if the number falls below the variable's value. For example, if mortality-chance is activated, then the agent dies. Some agent actions are also stochastic. The likelihood of winning a fight during an attack is directly proportional to the ratio of the opponents' body-size: agents with a larger body-size have a proportionally greater chance of winning the fight, following Lanchester's linear law of battle (Lanchester, 1916; Wilson et al., 2002). Also plants are randomly selected to grow...

2.2.13 Collectives

Each agent belongs to a group. Often, multiple agents belong to the same group and spatially aggregate based on group membership. But beyond that, I did not specify any emergent pattern for collectives.

2.2.14 Observation

Data can be collected in the following ways: genotype files, population files, verification files, scan and focal data collection, metadata, and file data. Must include more text on these files here.

2.2.15 Initialization

Upon initialization, BEGET populates the world with a population of agents. The plants begin with settings based on the global parameter settings (Table X). Each agent either comes with or receives a genotype file, which is used to populate its chromosomes. Both of these are based on input files (see Input data). Thus, B3GET strives to divorce itself from the messiness of initial conditions by preserving populations and retrieving them as such.

2.2.16 Input data

At the start of each simulation, we selected a series of genotype files used to seed the initial population files of agents. These genotype files contain all information necessary to create a population of 'clones' based on the individual or individuals originally used to create each genotype file. More text here on genotype and population files.

2.2.17 Submodels

Each time step, BEGET activates each agent in random order. Each agent then undertakes a series of processes. Once these processes have been completed, BEGET continues to the next randomly chosen agent until all individuals have had their turn.

(I) Evaluate Environment. Ego evaluates its environment, which includes individuals within its global-perception-range, including itself. As noted above, during each time step, Ego can focus its attention only on 10% of individuals within this observable range. Ego identifies the status of all Targets being considered and, in conjunction with its own known status, uses them to create a list of Ego-Target status combinations (see Sensing).

(III) Make Decisions. From the previous step, Ego has gathered a list of Ego-Target status combinations based on its current environment. We can consider each combination a 'key' that can be used to 'unlock' one of Ego's genes. As described above (see Adaptation), each gene contains an environmental context, which includes a hypothetical Ego-Target status combination. We can consider this environmental context the 'lock' that can be unlocked from a matching 'key.' During this process step, Ego checks all of its keys against each of its genes' locks. A key matches a lock if each element in the lock can be found in the key. If Ego finds a matching gene, then it puts the gene's corresponding action and weight into a queue. The weights in the queue are further modified to account for the distance from the target. In analogy with physical forces, these weighted values follow an inverse-square rule, decreasing in value with the squared distance to the target.

(IV) Execute Actions. Ego executes all actions in its queue, allocating a portion of its action-energy as calculated from the associated weights for each action. Mult iple actions can be executed within the same time step. Many actions result in state variable changes (see Table 2-5).

(V) Move. Some actions are movement-based: "Mate," "Move Toward," "Join Group," "Fight," and "Groom" trigger Ego to move toward Target, and "Move Away" and "Leave Group" trigger Ego to move away from Target. Ego calculates the direction to move based on the summation of all decision vectors based on these actions. Once this calculation is made, Ego moves in the calculated direction, the distance moved is based upon body-size and energy from action-energy allocated for movement.
(VI) Status. Finally, Ego changes its status based upon a series of calculations. First, Ego increases age and mortality-chance by one unit, and decreases conception-chance by one unit, simulating the normal aging process (deterioration). Second, based upon the current values of its life-history-chance, fertility-chance, and mortality-chance, Ego has a chance to update those respective status factors (see Stochasticity). If life-history-chance is activated, Ego upgrades its life-history to the next available stage ("gestatee" => "infant," "infant" => "juvenile," "juvenile" => "adult," "adult" => "senescent," or "senescent" => "dead"). If fertility-chance is activated, Ego upgrades its fertility to the next available stage ("pregnant" => "lactating," or "lactating" => "cycling"). If mortality-chance is activated, or life-history reaches "dead," it is removed from the simulation. (moved here because now energy is taken care of with other updates) (I) Update Energy. Agents have two pathways to gaining usable action-energy, depending on their current life-history status. If Ego has a life-history status of "gestatee," "infant," or "juvenile," it transfers any available energy from the maternal-energy of its mother, if she is alive, to its own stomach-energy. While the model allows juveniles to continue to take energy from their mother, it is likely that the mother no longer invests in her maternal-energy at this stage since she is now cycling and thus ready to conceive and invest in a new offspring. The age at which mothers end investment in maternal-energy for each offspring is a life history trait that can evolve in this model. If Ego has a life-history status of "juvenile," "adult," or "senescent," it forages to obtain energy, which it stores in its stomach-energy. Then, Ego updates its action-energy, which is the difference between its stomach-energy and its basal metabolic energy cost, which is calculated based on the formula: BMC = body-size $^{(0.762)}$ (Nagy, 1994).