The Megafauna Hunting Pressure Model: An ODD Protocol

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# Purpose and Patterns

The Megafaunal Hunting Pressure Model (MHPM) is an interactive, agent-based model designed to conduct experiments to test megaherbivore extinction hypotheses. The MHPM is a model of large-bodied ungulate population dynamics with human predation in a simplified, but dynamic grassland environment. The overall purpose of the model is to understand how environmental dynamics and human predation preferences interact with ungulate life history characteristics to affect ungulate population dynamics over time. The model considers patterns in environmental change, human hunting behavior, prey profitability, herd demography, herd movement, and animal life history as relevant to this main purpose. The model is constructed in the NetLogo modeling platform (Version 6.3.0; Wilensky, 1999).

# Entities, state variables, and scales

Upon initializing the model, you first see a simplified grassland environment with randomly generated patches of grass, male and female ungulates, and human hunters. Ideally, experimental dynamics will demonstrate how environmental conditions, human hunting, and animal life history interact to either accelerate or buffer extinction or create equilibrium conditions which do not result in an extinction event. The temporal units used in NetLogo are “ticks,” which can be scaled to any temporal granularity through careful parameterization of input variables.

## Prey Animal Entities

The MHPM focuses on human hunting of a population of large-bodied (and potentially sexually dimorphic) prey animals, rather than between multiple prey species. Human forager agents evaluate whether to hunt (pursue, process, and eat) an encountered individual prey animal by balancing the current potential payoff of doing so compared to an estimate about the alternative possible payoff of continuing to search for a different individual within the prey animal population. This incorporates some assessment of potential future search costs in addition to prior “sunk” search costs. Forager agents move and search iteratively in a dynamic landscape inhabited by a population of mobile prey animal agents. The only prey choices are males, females, and females with calves of the same species, which can be individually parameterized in the model interface with distinct profitabilities, *P*, by balancing their raw food values, *E*, with their handling costs, *h*:

(1)

(2)

(3)

## Landscape Entities and Scales

The landscape consists of an abstract square universe that wraps at the edges. It exists on a 211x211 patch matrix and a relative spatial scale. Although these patches are unitless, it may be useful to image the landscape in km2 based on approximations of daily distance traveled by megaherbivores. Environmental dynamics are controlled by a set of parameters related to the spatial and temporal patterning of grass and regrowth following grazing. The basic spatial patterning of grass in the environment is determined by the grass proportion, *pgrass*, where the total number of grassed cells is determined by a random selection of *ngrass* cells from the total number of landscape cells, *ntotal*:

(4)

# Process overview and scheduling

## Foraging

In the MHPM, food value and handling costs are abstract values without intrinsic meaning other than to balance the prey choice equations to create a ranking of the three prey choices in the model. Forager energy is also set to an arbitrary scale of 0-100, which relates only to the energy gained from hunting prey animals (assumed to be top-ranked food items) as other dietary needs are outside the scope of the current model. Knowledge of the intrinsic pre-search-costs prey ranks and profitabilities are given to all forager agents, who employ a dynamic prey choice model upon any encounter. A forager agent is considered to have encountered a potential prey agent when both agents occupy the same or immediately adjacent landscape cells. At each encounter, the forager agents “scan” within a pre-set radius, *r*, to attain the current count of animals, *n*, within the local vicinity.

## Prey animal demography

When a male and female prey agent occupy the same or adjacent landscape cells, they can mate and produce offspring. The probability of a successful mating is linked to the energy status of the female animal, where the chance of producing an offspring decreases linearly from 100% at a full energy state to 0% at a zero energy state. Further, only females that have not recently calved are able to reproduce. This is controlled by a birth spacing interval variable, *Tbirth spacing*, that is set in the user interface. When a female reproduces, a counter, *Tr*, is set to zero and increases with each successive time tick. If *Tr* is less than or equal to *Tbirth spacing* then the female is considered to be pregnant, and eventually post-partum, with a calf:

*if:*

*then:* female is with calf (5)

Once*Tr* is greater than *Tbirth spacing*, the calf is considered to be full grown and will be weaned and live separately from its mother.

*if:*

*then:* calf is weaned (6)

Within the model, weaning spawns a new prey agent in the same landscape cell as the mother. The sex of the new prey agent is randomly determined with a 50% probability to be male or female, and it will be instantiated with the full adult food energy value and handling costs of the determined sex.

Births are balanced by a variety of causes of death. Any form of death for a postpartum female within the birth spacing window also includes the death of the calf. Firstly, any harvested prey animals are “killed.” Next, some prey animals may die from a variety of “natural” causes such as starvation, old age, disease, or non-human predation. They are instantiated with initial energy states, *E0*, a typical age of senescence, *Tsenescence*, a maximum possible lifespan, *Tmax*, and must graze grass to survive. Each movement step (see main text, Section 4.2.3) reduces an animal’s energy state by the animal movement cost, *manimal*, and each patch of grass encountered is grazed to replenish an animal’s energy by the energy gain value, *Egraze*.

(7)

If there is no grass on the current patch, then the energy state of the animal is determined as:

(8)

If an animal’s energy state drops to 0 it will die:

if:

then: animal dies (9)

In every time step, there is a random chance of death among the population of animals with energy below a starvation threshold, *Estarve*. The chance of death is controlled by an internal mortality variable, *pdeath*:

*for:*  *where:*

…a random selection of will die (10)

Likewise, animals that surpass the maximum lifespan, *Tmax*, will die:

*if:*

*then:* animal dies (11)

But, as animals surpass the age of senescence, there is an increasing probability of death from old age within that population of senescent animals, again controlled by the internal rate of mortality, *pinternal death*:

*for:*  *where:* &

…a random selection of will die (12)

There is also a stochastic external mortality probability, *pexternal death*, that can be adjusted to simulate a percentage of animals that die from disease, accidents, or non-human predation at each time-step:

*for:*

…a random selection of will die (13)

In each time step, animal ages are first increased by one. They then move to a new patch, and movement costs are deducted. They then graze grass if possible, and any energy gains are added. Then, deaths are assessed in the order of 1) human predation, 2) starvation risk, 3) old age risk, and finally, 4) external mortality risk. Next, mating occurs if conditions are correct. Finally, any female animals at the end of their birth spacing interval will wean their calves, which are spawned as new prey animal agents. Thus, at the end of each time step, the total new size of the population of prey animals is set for the next time step, and each animal has a newly updated set of energy and lifespan attributes.

## Environmental scheduling

If grass regrowth is turned off, then the spatial patterning of grass never changes throughout a simulation run, and grass will always be available to be grazed in a grassed patch. Turning on grass regrowth enables initially grass-covered patches to become depleted when grazed by prey animals. These patches will remain depleted of grass for a user-determined number of time-steps, *Tgrass regrowth*, before the grass is replenished. In this situation, the current number of grassed patches, *ngrass current*, is determined by the following equation:

(14)

Where:

…in time step (15)

If regrowth is turned on, a “keep-initial” option can also be turned on, which limits grass regrowth only to areas that were initially vegetated when the model was initialized. If this is turned off, but regrowth is on, then grass can regrow anywhere.

Finally, an optional seasonality slider can enable seasonal cycling in the growth of grass. The seasonality proportion *Ps* interacts with a year-length *Tyear* temporal variable to set up a growing season of Tgrowing ticks and dry season of Tdry ticks:

(16)

(17)

Note that values of *Ps* less than 0.5 indicate shorter growing seasons, values of *Ps* larger than 0.5 indicate longer growing seasons, and *Ps* = 1 indicates no seasonality. These seasons operate within a yearly cycle of Tyear ticks and overlay grazing regrowth such that grass grazed in the growing season will regrow within that season according the the regrowth time, *Tgrass regrowth*:

*if:*

*then:*  in time step (18)

However, grass that is grazed in the dry season will not regrow again until the start of the next growing season:

*if:*

*then:*  in time steps (19)

Thus, at the one extreme, the environmental components of the model can be set as completely static with continual grass coverage on every patch without the effect of grazing, or at the other, very patchy grass that is grazed and then regrows continually or seasonally.

* + A complete but concise model schedule that defines exactly what happens each time step.

# Design concepts

## Basic principles

The foraging decision engine in the model is inspired by, but does not exactly replicate, classical Optimal Foraging Theory (OFT) forging models. OFT has long been employed in archaeology as a baseline for understanding how human foraging behavior would play out under controlled circumstances with perfect knowledge of conditions and complete rationality (Codding and Bird, 2015; Gremillion, 2002). These restrictions have been fodder for many critiques (e.g., Keene, 1983), but we use the ABM formalism to mitigate the strict assumptions of classical OFT by embedding optimality decision logic in a changing, dynamic environment where foragers have limited knowledge about current conditions.

Following the best practices of the Open Science movement (Marwick et al., 2017), we reused and/or modified portions of the foraging logic code from Barton’s (2015) existing peer reviewed NetLogo ABM inspired by the well-known “Diet Breadth Model” (DBM) (Foley, 1985; Hames and Vickers, 1982; Smith, 1983). The classic DBM attempts to explain the diversity of human foraging diets under various biological and environmental constraints with the assumption that foragers will always make the most optimal foraging decision in terms of caloric (or other “currency”) payoff when presented. A detailed description of the classic DBM and the traditional OFT modeling approach is provided in the Supplemental Text, Section 2, but we briefly summarize it here. As with most traditional OFT models, the classic DBM is a “static” model that uses average values as input, and derives a list of prey species that should be included in the diet by comparing the profitability of all animals in units of energy gained per time, or in net energy recouped. To be included in the diet, the profitability of a food item must be higher than the average profitability of all other food items - including potential energetic costs from food search. of a food item must be higher than the profitability of all other higher-ranked food items when search costs are factored in. If a first-ranked item is encountered it is always pursued, processed, and eaten. If a lower-ranked item is encountered, it is only included in the diet if the densities of all higher-ranked items become low enough (and thereby increase their search costs) to offset the reduced payoff offered by the lower-ranked item. The diet breadth is then the set of top ranked resources for which this logic remains true.

Barton’s (2015) ABM implementation of the DBM differs from the classic DBM because the ongoing tabulation of diet breadth is determined dynamically through a temporal chain of individual prey choice foraging decisions made upon prey encounters. The outcome of each foraging choice has consequences for future choices as the ABM formalism incorporates dynamic feedback between foraging impacts and environmental conditions that play out over time. This important characteristic of the ABM approach liberates the model from the strict assumptions of perfect knowledge and rationality that burdens classic OFT models. The MHPM inherits this important distinction, but because so much prior work about foraging behavior in archaeology has employed OFT modeling, we have maintained the terminology of OFT in the MHPM to enhance continuity and comparability with previous approaches.

## Emergence

* 1. An emergent property of the movement algorithms (described in the next section) is that buffalo often self-organize into herds following the seasonal regrowth of grass patches. Herd demographic profiles (age, sex, number) are also emergent properties of the model, and will evolve depending on herd animal parameterizations, environmental dynamics, and foraging pressure.

## Adaptation

* 1. Prey animal agents will adapt behavior based on their current energy state and the state and configuration of other prey animal agents and landscape patches within their vicinity (denoted as a 5-cell radius). Animal agents are programmed to instinctively move as a herd with some feedback about local grazing conditions. At each time step, animals will first attempt to face the nearest patch of grass within a 3-cell radius and advance one cell in that direction. If there is no grass in this radius, they will instead align their heading towards the average heading of animals that are within a 5-cell radius and advance one cell in that direction. If there are also no nearby animals, then the animal will proceed in a true “random-walk” fashion by advancing one cell in a randomly chosen direction. As above, for each movement, a predetermined movement cost is incurred.
  2. Forager agents will adapt their foraging behavior based on the configuration of prey animals within their foraging radius and their own energy state. As in the classic Diet Breadth Model (Foley, 1985), a first-ranked prey animal will always be pursued, processed, and consumed on encounter. If a lower ranked animal is encountered, the foraging agent conducts a prey choice calculation by estimating an average search cost, *Sa*, to keep looking for a nearby first-ranked prey by dividing the area within the search radius by the current number of prey that are within it, and then multiplying that by the forager movement cost, *m*. In the model, the search radius is delineated as a discrete number of cells, *A*, that fall completely within a linear radius of *r* around (and including) the central cell occupied by the forager so that the scanning formula takes the form:
  3. (20)
  4. Where:
  5. (21)
  6. The estimated average pay-off, *Pa*, of the animals (*i* to *j*) within the foraging radius is then calculated as:
  7. (22)
  8. If the payoff of an encountered animal, *Pk*, is higher than the estimated return of searching for, encountering, and then processing the highest ranked prey animal within the search radius, then the currently encountered lower-ranked animal is processed and eaten:
  9. *if:*
  10. *then:* consume animal *k* (24)
  11. At each time step, the current energy states of the foragers, *Ecurrent*, are updated as a function of their previous energy state, *Eprevious*, the forager movement costs, *mforager*, and any new foraging payoffs, *P*:
  12. (24)
  13. Foragers are considered to be experiencing extreme food stress if their current energy state, *Ecurrent*, is less than the estimated average search costs, *Sa*. When in extreme food stress, foragers will process and eat any prey animal they encounter. This accounts for “sunk” search costs by allowing non-optimal foraging decisions when appropriate:
  14. *if:*
  15. *then:* consume any encountered animal (25)
  16. Finally, foragers can either only consume a hunted prey up to their maximum energy level, or can camp and consume the entire animal. If the former, foragers continue to move and hunt immediately after a successful kill, and any excess energy value from the kill is “wasted.” If the latter, they stay on the same patch (and do not move or hunt) until the full energy value of the harvested prey animal has been consumed. The rate of this consumption is the same as the movement cost per tick.
      1. We incorporate realistic movement algorithms for forager and animal agents. Forager agents are programmed to pursue high-ranked prey animals, and can update their trajectory as local conditions change. At each time step, forager agents will turn to face the closest, highest-ranked prey animal within their foraging radius, and then will advance one cell in that direction. If there are no nearby animals, then the forager proceeds in a true “random-walk” fashion by choosing a random heading and advancing to the nearest cell in that direction. For each movement, a predetermined movement cost is incurred.

## Objectives

At minimum, the model can be composed to study the impact of human foraging and/or environmental conditions on prey animal demographic dynamics over time. The specific objective of the model is to track the number and characteristics of the prey animal population as the model unfolds. A secondary objective is to also track the basic health (and perhaps number) of human foragers. A third objective is to track the impact of grazing on vegetation.

## Learning

Human foraging and prey animal grazing behaviors contain a component of learning, as outlined in the “Adaptation” section above. Agents only learn from direct experience, and do not copy pr learn foraging or grazing behavior from other agents. The only exception to this is that prey animal agents may align their orientation towards the most common direction of other prey animals in their vicinity as described in the “Adaptation” section.

## Prediction

The model simulates the collective behavior of herbivores and human foragers. To the extent that the model can be used to make predictions about these behaviors, it can do so only in abstract terms depending on the degree of realism intended by the model when compiling the relative values of the input variables. These values should be internally consistent, but the model specifically does not allow most variables to be input as “real world” values (e.g., kcal or kg), but instead are intentionally abstracted to showcase general behavioral dynamics over specific prediction or exact replication of specific case studies.

## Sensing

Forager and Prey agents can sense the presence of other prey agents that are within a radius of cells around them (see Adaptation section above). Forager agents can sense the size/payoff and handling values of prey within this radius. Prey agents can sense nearby/adjacent landscape patches with vegetation.

## Interaction

As described in the “Processes, overview, and scheduling” section, prey animals can mate and produce offspring. Offspring can be weaned from their mother. Prey animals can graze the vegetation on landscape patches. Forager agents can harvest and kill prey animals.

## Stochasticity

Stochasticity is used in the landscape generation and grass regrowth routines as described in the “Entities, state variables, and scales” section. As described in the “Processes, overview, and scheduling” section, the sex of offspring is randomly chosen with a 50% probability, and the algorithms controlling the number of “natural” deaths of prey animals incorporate stochasticity. Finally, as mentioned in the “Adaptation” section, sometimes forager and prey agents may opt to move according to a random walk function.

## Collectives

In the MHPM a forager agent represents a band of foragers rather than an individual hunter.

## Observation

Summary statistics are shown on the bottom left side in labeled output boxes and are formatted as continuous line graphs that reflect new data from each tick. They include:

1. Number of prey-items taken per 10 ticks. Three lines are generated to show how many males, females, or post-partum females are hunted over the past 10-tick cycle.
2. Proportion of grazed to ungrazed grass on a scale of 0-100.
3. Forager energy, which changes as hunters exploit prey and move in their environment.
4. Number of animals in the environment. Three lines are generated to show how many males, females, or post-partum females are in the environment over time.

# Initialization

This is an interactive manual model. The user can fully manipulate the variables to test a wide range of hypotheses related to extinction in a socio-natural system. To begin, first select the variables you would like to test in your extinction scenario (i.e., environmental patchiness or animal fecundity). We recommend keeping most variables constant, and only changing 1-3 variables per experiment. The user can also set the max ticks, which will stop the experiment after a designated number of ticks. Once the independent variables have been selected, use the interactive sliders to move them a few units at a time, avoiding large, drastic jumps in relative scale. When you are ready to run your experiment click the setup button. This will generate a landscape that matches the environment, herd demography, and hunting pressure reflected in the user’s parameterization. Then click the run button, and the experiment will begin.

Hunters are embedded with logic that approximates dynamic optimal foraging theory. In this model, hunter’s foraging decisions vary in response to environmental feedback. The decision to pursue a prey item is balanced between the current energy-status of the hunter, the food value of the prey, the relative density of prey in the landscape, and the cost of pursuing, hunting, and processing the animal. Hunters do not reproduce and lose a user-set amount of energy as they move in their environment. Hunters can die if they run out of energy, they can also store energy from food and create an energy surplus, which is consumed before hunting is resumed. Users can turn human mortality on or off.

Ungulate herds are sexually dimorphic, with distinct user-determined food value and processing costs for males and females. Animals are also capable of reproduction, and sex ratios and probability of reproduction can be controlled by the user. Additionally, females can become pregnant and spawn offspring. Once spawned, offspring nurse for a set amount of time determined by the user. A nursing offspring adds to the food value of the female. This allows the user to approximate animal life history with novel detail. Animals are programmed to move as a herd with feedback from environmental conditions. Animals age, and the probability of random death increases once the animal reaches senescence. There is also external morality probability which can be adjusted by the user to simulate a percentage of animals that die from non-human predation at each time-step. Maximum animal lifespan is also a slider set by the user.

The environment can be controlled by the user by changing the density of fodder in the landscape (grass-proportion) and the time it takes for grass to regrow once it has been grazed (grass-regrowth). Grass regrowth can be turned off which will create a static environment. Additionally, users can choose to the keep-initial option, which limits grass regrowth only to the areas that were initially vegetated. Users can also utilize a seasonality slider, which limits grass regrowth to a user-determined seasonal cycle.

The process of refining and experimenting with the relative value of independent and constant variables can be repeated until the experimental parameters appears to behave logically and work well to test the user’s hypotheses. When selecting values, it is useful to keep in mind that these values have relative, as opposed to absolute, value. For example, when picking a value for food-value-male and food-value-female (the energy hunter’s gain from eating male or female prey) do not think of the numbers in terms of kilogram or calories, but rather the relative size of males to females. In this case, a 2–5-unit difference may be sufficient to demonstrate how sexual dimorphism may impact human hunters operating under optimal foraging logic. The experiment will stop when: 1) human hunters die off, or 3) the experiment reaches the maximum number of ticks set by the user.

# Input data

* + - * 1. Depending on the hypotheses and/or data from a specific case study, you can manipulate the sliders in the NetLogo interface to establish the socio-natural dynamics of the experiment matrix. Broadly, the model allows you to change the following unitless categories that exist on a continuous scale: fodder availability, seasonality, relative animal food value, animal fecundity, lifespans of hunters and animals, relative hunting danger, as well as the energy required to move in the environment. While the MHPM specifically avoids “real world” measures, such as specific energy or weight units, real world data about specific case studies can be abstracted to fit the input parameters of the model. Further, the input variables feed into algorithms (described above in this document) that need reasonable values to calculate sensible outcomes. It is important, therefore, that input variables be parameterized to be in balance with real-world expectations, even if specific real-world values are not needed. We have constrained the input sliders for all variables to cover a reasonable range of expected values, but the modeler should carefully balance the specific values to ensure that model assumptions are not violated.

# Submodels

The model is coded in NetLogo with specific functions for prey animal movement, forager movement, prey animal mating and birth, prey animal death, weaning of prey animal offspring, human hunting of prey animals, prey animal grazing, and vegetation regrowth. These functions are described in detail earlier in the document, and the specific algorithms are provided.

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