Model 2: Basic Hunter-Gatherer

Narrative

Two million years ago, there were humans somewhat like us. There were not very many of them, and while they had primitive tools, their tools did not change significantly over many millennia. They were similar, in some ways, to the hunter-gatherer tribes still in existence in the jungles of the Amazon, Central Africa, and a few other remote locations. We can apply the rabbit and fox model to them, except humans take the places of the foxes and perhaps somewhat larger game replaces the rabbits. In fact, we can generalize the "game" to include not only various kinds of game, but other foods as well.

This model starts with the same families stepping off the same raft onto the same lush, deserted island as those in the Population Growth model. This time, however, they have to hunt for a living and their prey is not unlimited. The human population grows as they hunt down the prey, but the human population can then crash if hunting drives the prey near extinction.

This model and the following three models are all based on Lotka-Volterra (LV) system of linked differential equations. They were developed by Charles Efferson and Peter Richerson based on the widely used LV framework for studying multiple populations linked together in a common ecology. It is a useful approach with potential applications in fields quite far from ecology as we will see in Model 7 (economics).

Ecologists are interested in how species interact with one another—predators and prey, competitors, and mutualists. The basic model we construct in this section is the foundation for the more complex models to follow. The core of the LV system is the logistic model of population regulation that lets a population grow to a carrying capacity. In the case of two interacting populations, population growth rates are affected not only by competition with others of the same kind, but also by the second population. In the case of predators and prey, the prey population has a positive impact on the predator population, but the predators have a negative impact on the prey. In fact, we assume that the human predators in our model eat nothing but the prey, so there is no carrying capacity for the human predators. Their population growth rate is regulated only by a maximum possible growth fraction and by the availability of prey.

The LV framework is very flexible and has been endlessly elaborated to explore all sorts of dynamic interactions. An important applied use of the LV framework includes modeling economies as species-like industries that "consume" the output of other industries and produce outputs that are consumed by others. The auto industry consumes steel, rubber, textiles and so forth to produce cars that are purchased by consumers.

Another important application is epidemiological models. Bacteria and viruses are like predators that partially consume the "prey" they infect. But, typically, immune systems mount a defense, large numbers of victims survive and are immune to reinfection for some period of time, sometimes for life. This sets up a cat-and-mouse game between diseases and immune systems that we are all aware of in the age of Covid-19.

It is also easy to build LV models with more than two species. For example, humans now harvest krill, small shrimp-like herbivores abundant near Antarctica. But krill are also exploited by whales, fish, and seabirds. Southern Ocean ecologists would like to know how much impact krill fishing will have on the rest of the krill eating community. As you can imagine, such models rapidly begin to violate the KISS rule.

However, given complex applied problems like ecosystem management and weather forecasting, mathematicians and computational modelers work hard to develop the tools to study complex systems of coupled differential equations. We are introducing you to the tip of an iceberg; but you should be aware of the vast part of the modeling enterprise that is below the KISS waterline. Violating the KISS rule does have its costs, however. You can never build a model that completely captures the behavior of complex systems. Complex models, well short of being truly realistic, become hard to understand, are computationally time consuming, and become hard to discipline with data.

Further Reading

Bettinger, R. L., R. Garvey and S. Tushingham (2015). *Hunter-Gatherers: Archaeological and Evolutionary Theory.* Springer.

Hill, K., M. Barton and A. M. Hurtado (2009). *"*The emergence of human uniqueness: Characters underlying behavioral modernity.*" Evolutionary Anthropology* 18: 174-187.

Kelly, R. L. (1995). *The Foraging Spectrum: Diversity in Hunter-Gatherer Lifeways.* Washington, Smithsonian Institution Press.

Lee, R. B. (2018). "Hunter-gatherers and human evolution: New light on old debates." *Annual Review of Anthropology* 47(1): 513-531.

Richerson, P. J. and R. Boyd (1987). *Simple models of complex phenomena: The case of cultural evolution. The Latest on the Best: Essays on Evolution and Optimality. J. Dupré. Cambridge, MIT Press: 27-52.*

https://en.wikipedia.org/wiki/Lotka-Volterra_equations
https://en.wikipedia.org/wiki/Competitive_Lotka-Volterra_equations
https://en.wikipedia.org/wiki/Mathematical_modelling_of_infectious_disease
https://en.wikipedia.org/wiki/Hunter-gatherer

White Box Graphical Model

The White Box under-the-hood model description below can be skipped and you can proceed directly to the Black Box Simulations if you just want to operate the simulator and skip the model diagram and equations. You can always come back to this section if you would like to explore the model further.

The graphic Stella model, shown in Figure 2-1 is broken into two major sections, the prey and the humans who hunt them. Each major section of the model is discussed below.

Model 2: Basic Hunter Gatherer

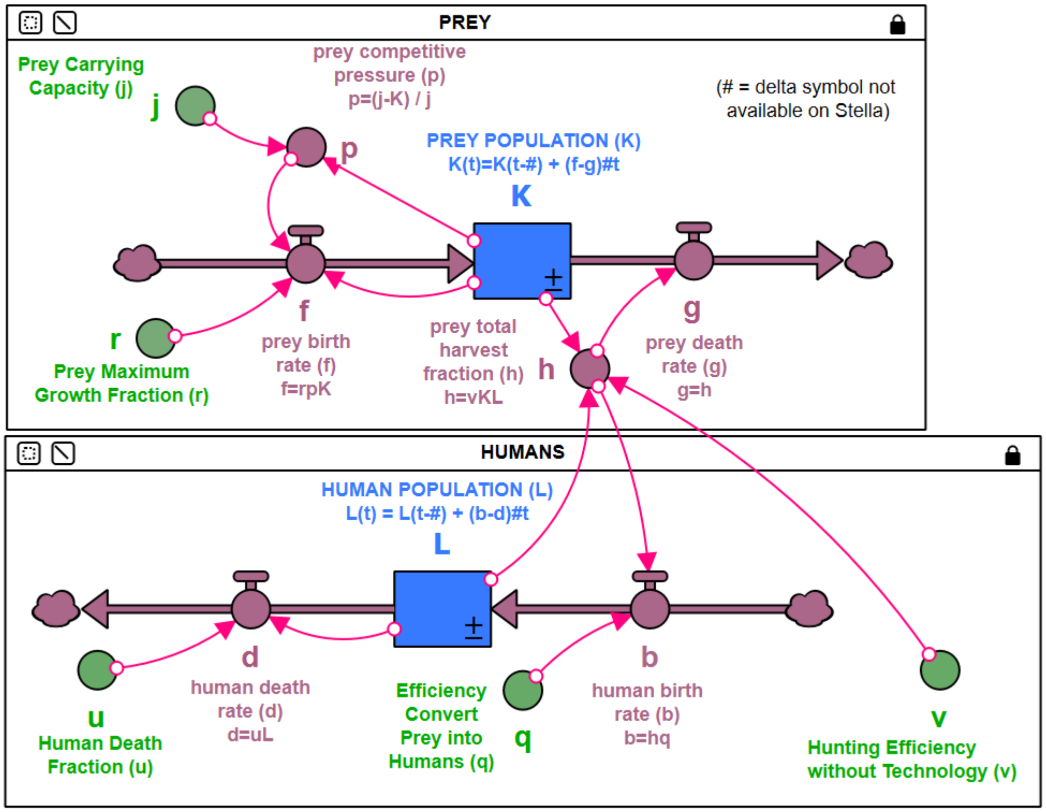

Figure 2-1: Stella Basic Hunter-Gatherer model.

For the PREY section of the model, the PREY POPULATION (K) is a state variable (i.e., a “tank”) whose value can change during the simulation for each small step in time. The amount of change is the rate of input, the prey birth rate (f) minus the prey death rate (g) times the small increment of time, Δt (shown as #t in the model diagram because Stella does not have the Δ symbol). Thus, for each step in time, the simulation makes the calculation:

$K(t) = K(t-\Delta) + (f-g)\Delta t$

The prey birth rate (f) is the product of the Prey Maximum Growth Fraction (r), the prey competitive pressure (p), and the PREY POPULATION (K), i.e.

$f = rpK$

The Prey Maximum Growth Fraction (r) is the per individual growth rate of the prey population in the absence of any competition from other members of the population. It represents the per-capita birth rates in the absence of competition and hunting. Mathematically, r is the population growth rate when K is very near but not quite 0.

The prey competitive pressure (p), is, in essence, the prey competing against itself for a limited supply of what the prey eats to stay alive and reproduce. When K is small relative to j, p is approximately 1 and the prey population is free to grow exponentially. As K approaches j, p approaches 0 and competition alone stops the prey population from growing. For antelopes, for instance, it would be the grass in the meadows, knee deep when K << j, grazed tight to the ground as $K \rightarrow j$. This competition for a fixed resource is calculated, for each simulation step as

$p = (j - K) / j$

From this equation it can be seen that when K is zero or very small, then p is essentially equal to 1.0. This is the green light (excuse the pun) to the antelope that all the meadows are green with grass. However, as K gets larger, i.e. the number of antelope increase, there is less uneaten grass in the meadows. As K gets larger and larger, p approaches 0.0 and the number of antelope is limited by the Prey Carrying Capacity (j). If there weren't any humans hunting antelope, the PREY POPULATION (K) would, over time, asymptotically approach the Prey Carrying Capacity (j) and then stay at the number forever.

$g = h$

The prey total harvest fraction (h) is the fraction of the antelope that humans kill.

$h = vKL$

This equation simply suggests that the more antelope there are, the more humans there are to hunt them, and the greater the efficiency of the humans, the more antelope that will be killed.

Hunting Efficiency without Technology (v) represents the predatory efficiency of an imaginary australopith-like ancestor who, like living chimpanzees, hunted small game by using their hands and teeth to catch and kill the game. Note that in the next model, Hunter-Gatherers *with* Technology, we will introduce evolving technology. Hunting technology has evolved from simple spears and clubs, to stone tipped spears, then bows and arrows, and eventually guns. A realistic value for v for our australopith ancestors would be so low that they could not live by predation alone. Their competitors—specialized predators like leopards—would have had v values large enough to live by predation alone, as did our more recent technology-aided ancestors and, currently, the living hunters of the High Arctic, for example, with their very sophisticated hunting toolkit. One could model a more realistic approximation of actual australopiths by introducing a plant resource. This could look just like the existing submodel of K except that we would assign v a substantially larger value for the plant resource. Even if our ultimate objective is to build a more complex, more realistic model, applying the KISS rule at this point focuses our attention on building it submodel by submodel.

For the HUMANS section of the model, HUMAN POPULATION (L) is a state variable (i.e., a "tank") whose value can change, during the simulation, for each tiny iteration of the Stella model, each small step in time. The amount of change is the rate of input, the human birth rate (b) minus the human death rate (d) times the amount of time, Δt (shown as #t in the model because Stella does not have the Δ symbol). Thus, for each step in time, the simulation makes the calculation:

$L(t) = L(t\text{-}\Delta) + (b\text{-}d)\Delta t$

The human birth rate (b) is the product of the prey total harvest fraction (h) and the Efficiency Convert Prey into Humans (q). The more antelope the hunters can kill, and the more efficiently they use this food (cooking all the parts and breaking the bones open for the marrow) to produce more humans, the more baby humans will be born.

$b = hq$

The human death rate (d) is the product of the Human Death Fraction (d) and the HUMAN POPULATION (L).

d = uL

human death rate (d) is the *number* of humans that die of old age, diseases, accidents, etc., each year.

Human Death Fraction (u) is the *fraction* of humans that die each year.

Model Variables and Equations

The visual flow diagram “white box” model, described above, can be reduced to a set of initial conditions and independent (and intermediate) variables which, through mathematical relationships (equations), provide the results (the independent variables). These, without the graphical flow diagram, are given in the table below:

Key: STOCKS**,** Parameters, intermediate variables

PREY	Units	Stella Equations
PREY POPULATION (K)	Prey unit	K(t) = K(t-Δ) + (f-g)Δt
Prey Carrying Capacity (j)	Prey unit	
Prey Maximum Growth Fraction (r)	1/year	
prey birth rate (f)	Prey unit/year	f = rpK
prey competitive pressure (p)	Unitless	p =(j – K) / j
prey death rate (g)	Prey units/year	g = h
prey total harvest fraction (h)	Prey unit/year	h = vKL
HUMANS		
HUMAN POPULATION (L)	People	L(t) = L(t-Δ) + (b-d)Δt
Human Death Fraction (u)	1/year	
Efficiency Convert Prey into Humans (q)	People/prey unit	
Hunting Efficiency without Technology (v)	1/(people*year)	
human death rate (d)	People/year	d = uL
human birth rate (b)	People/year	b = hq

Table 2-1: Model variables and equations.

Equations without Intermediate Variables

The intermediate variables can be eliminated by substitution, leaving just the dependent variables as a function of the independent variables. Shown below are the equations in a simulation, one-step-at-a-time form. Given the values of the state variables in the previous step, this provides the rule on how to calculate their value in the next increment of time.

K(t) = K(t-Δ) + [rK(j-K/j) – vKL]Δt
L(t) = L(t-Δ) + (vqKL – uL)Δt

If Δt is made smaller, we reach, in the limit, the differential equations where the prime, as in K', indicates the first derivative with respect to time, i.e., dK/dt.

$K' = rK(j-K/j) - vKL$
$L' = vqKL - uL$

Black Box Model

As suggested in the course Introduction, when using a black box model, one is just concerned with the model's inputs, not its internal workings which can be extraordinarily complex. To run the Basic Hunter-Gatherer model from this black box perspective, bring it up at:

https://exchange.iseesystems.com/public/cherylgenet/basic-hunter-gatherer

This is what you should get:

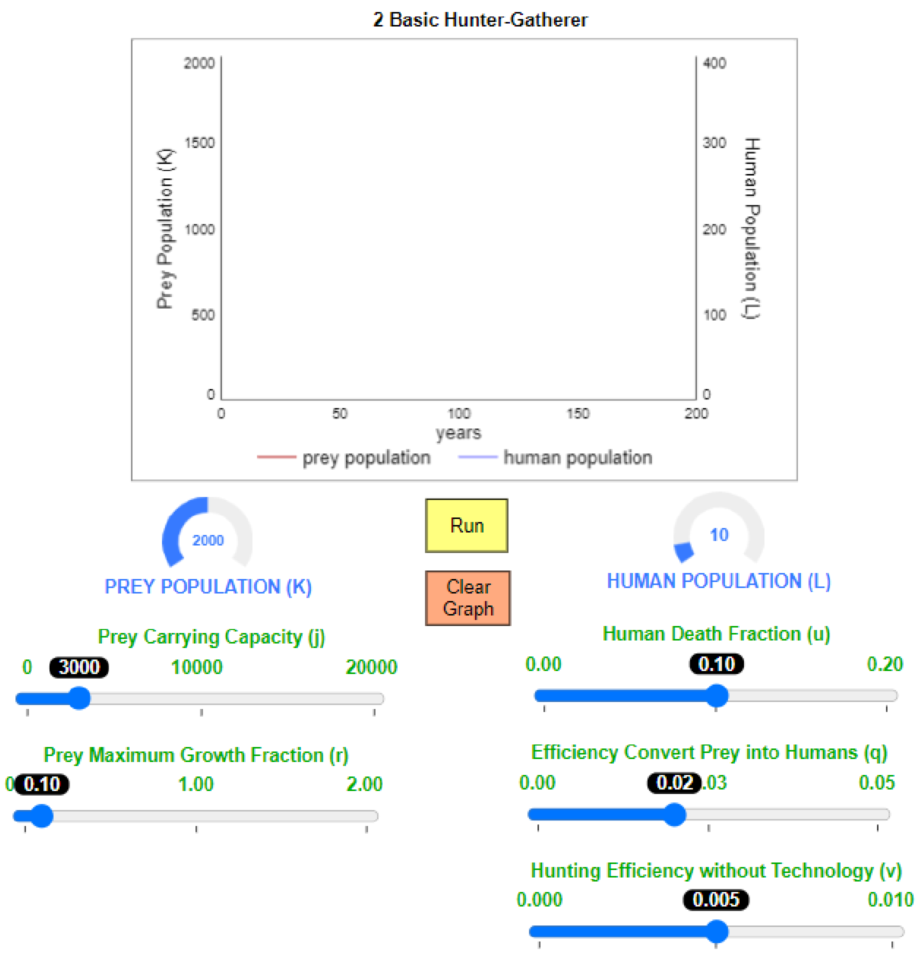

Figure 2-2: Simulation controls for Basic Hunter-Gatherer.

The simulation model has two initial condition Population Control knobs:

- PREY POPULATION (K)
- HUMAN POPULATION (L)

And five independent variable parameter adjustment sliders:

- Prey Carrying Capacity (j)
- Prey Maximum Growth Fraction (r)
- Human Death Fraction (u)
- Efficiency Convert Prey into Humans (q)
- Hunting Efficiency Without Technology (v)

The initial condition knobs and independent parameter sliders require minimum, maximum, increment (resolution), and reset values. These are provided in the table below.

Key: STOCKS; Parameters

	Min	Max	Increment	Reset
PREY POPULATION				
PREY POPULATION (K)	0	42000	100	2000
Prey Carrying Capacity (j)	0	20000	100	3000
Prey Maximum Growth Fraction (r)	0	2.0	0.01	0.10
HUMAN POPULATION				
HUMAN POPULATION (L)	0	100	1	10
Human Death Fraction (u)	0	0.2	0.01	0.10
Efficiency Convert Prey into Humans (q)	0	0.05	0.01	0.02
Hunting Efficiency Without Technology (v)	0	0.01	0.001	0.005
OUTPUT GRAPHS				
prey population	0	2000		
human population	0	400		
years (t)	0	200		

Table 2-2: Simulator interface values.

Each simulator control has a minimum and maximum value. Each control also has an increment (resolution) and default reset values that will be in place if you press Clear Graph. These values cannot be changed by the model user and have been set by the model designers to allow the model to be exercised over a useful range of values while avoiding extreme values that would be confusing. While they are “fixed” values in the simulation program, the table is provided not only as background information, but as a starting point for those who would like, on their own, to modify the Stella model.

Prey Arrive on the Deserted Island

In our first scenario, we start with a small, lush, deserted island in the South Pacific. Click Clear Graph to make sure all the knobs and sliders are at their default reset values.

We start by making the island small by reducing its Prey Carrying Capacity (j) from the default value of 3000 down to 1800. Most terrestrial prey that humans target are herbivores. Successive levels of the food chain dissipate about 90% of the energy they extract, so the predators of herbivores are only 10% as abundant as the herbivores they eat. Thus, the prey carrying capacity is highest for low trophic (position on food chain) level animals. Targeting terrestrial predators seldom makes sense. Aquatic food chains are quite different because the planktonic "grass" of the sea and lakes is mostly microscopic. The herbivores that eat them are correspondingly tiny and the animals of a size worth human attention are typically trophic level 3 or 4 out of 5 (5 being the highest top predator in a long food chain).

Now we want to introduce just a few animals to the Island. Perhaps they floated to the island on a pile of driftwood. Turn the PREY POPULATION(K) down from its default value of 2000 to 100, the smallest number we can get with this knob.

To start with, we would like to have slowly maturing animals, such as deer or pigs, and not like rabbits or rats, so turn down the Prey Maximum Growth Fraction (r) from its default value of 0.1 to 0.05. People can and do eat rats and rabbits, but small animals have three drawbacks as prey. First, they are time-consuming to harvest and process. Second, they require fairly high-quality plant resources and so their biomass isn't particularly high in most circumstances. The prey growth fraction is highest for efficient medium sized and large herbivores and these are the animals hunters tend to target. Third, small animals have low body fat. Human physiology is not adapted to using large amounts of protein for energy. Using protein for 35% or more of caloric needs generates toxic nitrogen wastes. Hence, human hunters target large game with respectable amounts of fat. The Plains Indian winter staple was pemmican, a mixture of dried pulverized meat, fat rendered from broken up bones of bison, or other large mammals, with some dried berries for flavor.

Finally, we do not want any humans hunting our animals as this is supposed to be a *deserted* island. So, turn down the HUMAN POPULATION (L) from its default value of 10 all the way down to 0. Even one human will hunt animals and multiply because the model is not smart enough to know that it takes at least two humans to start multiplying.

Press Run. Here is what you should get:

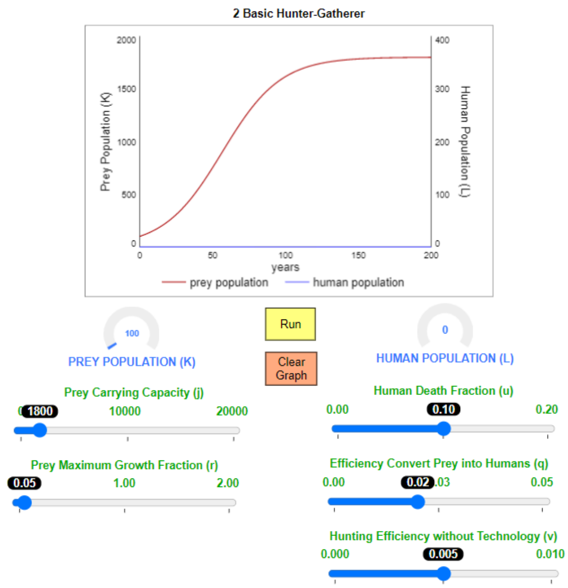

Figure 2-3: Prey populate the deserted island.

We can see from this graph that it took the prey population almost 150 years to reach its steady state value of 1800 animals, the Prey Carrying Capacity (j). How many years did it take to reach half of the carrying capacity, i.e., 900 animals? To answer this question, place your cursor anywhere on the graph and hold down the left mouse button. A vertical line will appear. You can move the cursor left and right and the values of prey and humans will appear under the graph's caption. Make sure no humans snuck onto the island; Humans must = 0. Your answer should be ~57 years (give or take a year or so).

These are slow reproducing animals—even elephants would not take so long to double their population. So, let's speed up their reproduction by moving the Prey Maximum Growth Fraction (r) from 0.05 up to 1.00. Do *not* press Clear Graph as we want to leave all the other values alone. Press Run and this is what you should get:

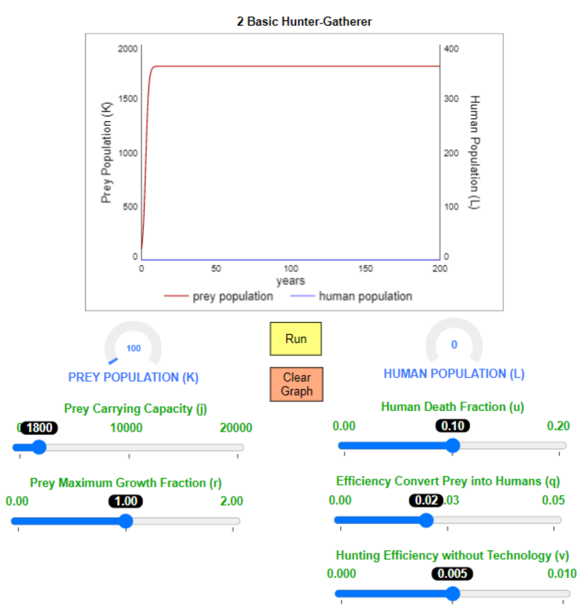

Figure 2-4: Rabbits populate faster than elephants.

Now how many years does it take to reach the carrying capacity of 1800 animals?

Explore with this model. What happens if you reduce the Prey Carrying Capacity (j) from 1800 to 900?

Humans Arrive on a Prey-Rich Island

Clear Graph for a fresh start. Our first island was too small to support many humans, so we will up the size of the island and thus the Prey Carrying Capacity (j) from 1800 to 12000. We want our prey to reproduce fairly rapidly so we'll up the Prey Maximum Growth Fraction (r) to 1.0. Finally, we want there to be plenty of food for our newly arrived humans to eat, so we will up our Initial Prey Population (K) to its maximum value, 4000.

When we cleared the graph, we got the default (reset) values for the humans. The HUMAN POPULATION (L) is 10. We could have gone for 1 human and that would not have changed the model results significantly (try it), but we know 1 human is not realistic. We could have gone for two, but we wanted to avoid incest. So, we went for a raft full of 10 adventurous humans looking for New Paradise, the default (reset) value.

Leave the Human Death Fraction (u) is at its default value of 0.01. Think of this as related to the average age when people die. If our happy natives brought diseases with them, this number would be lower. If they are disease free and watch their diet so they do not become overweight, this number would be higher, and more humans would be hanging around to hunt animals. In fact, small groups of people who voyage long distances to settle remote islands often arrive rather free of disease. Sick voyagers have either died or recovered before they landed. Hunters and gatherers also get plenty of exercise feeding themselves, so obesity and other diseases caused by sedentary lifestyles are not a problem. In this model, even when game is in short supply people do not starve to death (perhaps they eat roots).

However, if game is scarce or their hunting is inefficient, then fewer babies are born. Efficiency Converting Prey into Humans (q) is directly related to hunting efficiency. Of course, if game is scarce then even efficient hunting will not provide the food necessary to produce babies. q is also a matter of physiology. Humans grow slowly and require a lot of food investment to live long enough to become competent hunters. Hence, compared to faster growing carnivores, humans are not very efficient at converting prey into humans.

Humans appear to have become highly carnivorous in the Pleistocene to get the nutrients to support our large brain, but we don't seem to have been very numerous until nearly the end of the Pleistocene, perhaps because our **q** is unimpressive. Cold blooded predators are more efficient in this regard than warm blooded ones. Snakes, for example, need eat only at long intervals because they do not waste energy maintaining a high body temperature. On the other hand, humans cook their food and that makes digestion more efficient. Leave **q** at its default value of 0.02.

Finally, we have Hunting Efficiency without Technology (v). We will also leave this at its default (reset) value of 0.005. This value is for stone-age humans whose technology did not change significantly for over a hundred thousand years. Over the long haul, technology did change of course, and late in our history it began to change rather rapidly. We will introduce this wrinkle in the next model. The objective here is to introduce a baseline. What difference does it make when we add in the human specialty of toolmaking? The change, as we will see in our next model, is pretty dramatic!

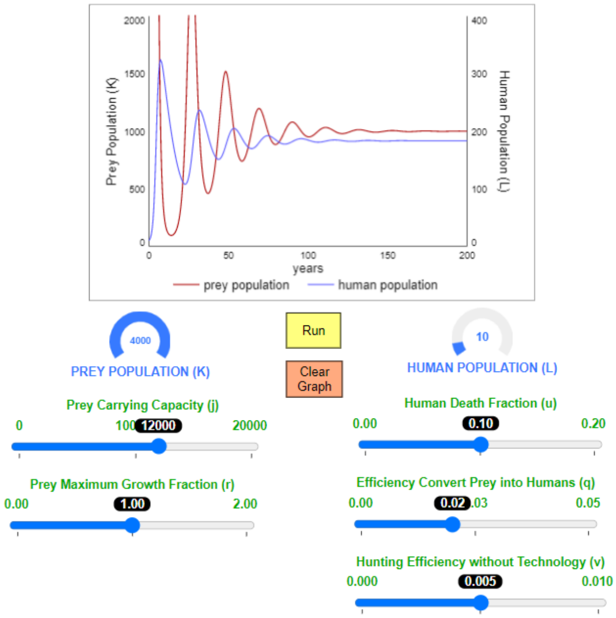

Figure 2-5: Run with settings as shown.

All set now. Some 4000 fast reproducing prey on a large island that would support 12,000 prey and would rapidly reach that number if it wasn't for the 10 humans who stepped ashore on Day 1.
Press Run.

Wow! What is going on here? All over the map at first.

To see what is happening, place your cursor on the graph and hold down the left mouse button and move all the way to the left of the graph. As expected, there are 4000 prey (off the chart) and 10 humans. Now move the mouse to the right. How long does it take for the prey to reach its maximum (off chart) number, and what is that number? (About 3 years and almost 9000 prey.) Why didn't the prey reach the carrying capacity of 12,000? (Because humans were hunting them.) How many human hunters were there when the prey was at its maximum value? (About 65.)

The human population kept growing. When did it reach its peak, and with how many humans? (7.4 years and 324 humans.) How many prey were left at this point in time? (Down to 890.) When did the prey reach its low point, and how many prey and humans were there? (13.5 years, 95 prey, and 208 humans.)

As the human population continued to fall (less babies while, at the same time, the oldsters continued to die at a steady rate), there were less hunters, and the prey began to recover, reaching a peak population of 2555 in year 27, followed by a decline of prey as the number of humans recovered.

These oscillations mainly died out by Year 100, and a steady value of about 183 humans and 1000 prey continued onward, presumably forever, or until the sun turned into a red giant or the volcano on the island stirred back to life, whichever came first.

If Human Dearth Fraction (u) is cut in half to 0.5 (left below), the prey nearly gets wiped out on the first swing and never gets back to any high values, nor do the humans. Sort of everyone suffers (although the humans live longer).

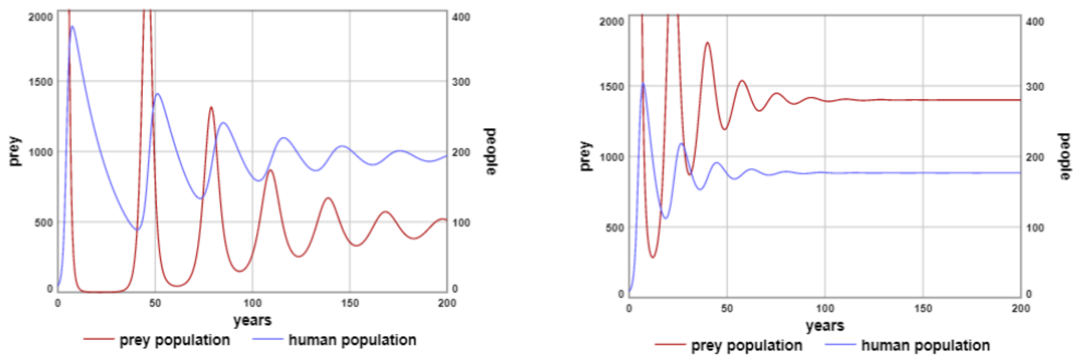

Figure 2-6: The virtues of not overhunting; everybody wins!

On the other hand, if the Human Death Fraction (u) is made half again as large (to 1.5 as shown above right), then everyone does better, although the humans do not live as long. If our human residents ate more roots and less prey, there could be more humans and more prey. The moral of the story: do not overhunt prey, especially when you first arrive at a new location, because you might drive it to extinction.

You can also see what sort of strategy will lead to a comfortable and secure hunting and gathering life. Suppose you choose to exploit populations that cannot be over-exploited. The natives of the West Coast of North America harvested acorns on land and fish from the sea. Harvesting acorns does no damage to the oak trees, and acorn harvesting has the effect of spreading acorns around. All the acorn harvesters leave a few behind and drop a few as they move them to caches. Oaks live a long time, and all it takes is a few lost acorns to keep the population healthy. California's coast is on the edge of a huge and highly productive upwelling system. People patrolling the shore and operating offshore in frail boats can only glean scraps from a huge table. Humans can't generate enough pressure on the oaks or most marine populations to significantly deplete these resources. Nature handed them a nice steady carrying capacity as in the logistic model. Ecologists call this situation "donor-controlled dynamics."

If we decrease the Efficiency Convert Prey into Humans (q) down to 0.01, the prey does well, quickly rising to ~ 3000, well off the graph. Everything settles out quickly to a steady state. On the other hand, if we increase q to 0.04, the prey almost goes extinct on the first level and when things finally settle out after 100 years, although the level of humans is slightly higher, the prey, instead of being around 3000 is well under 1000. You can already see, from a management perspective, that managing hunting is a delicate and tricky business unless you are lucky enough to live under a donor-controlled regime. It seems as if you might need a quite sophisticated fisheries and game management department to do the job. Anthropologists know that hunter-gatherers tend to live in cooperative groups but there is much debate about whether, and under what circumstances, they are good fish and game managers.

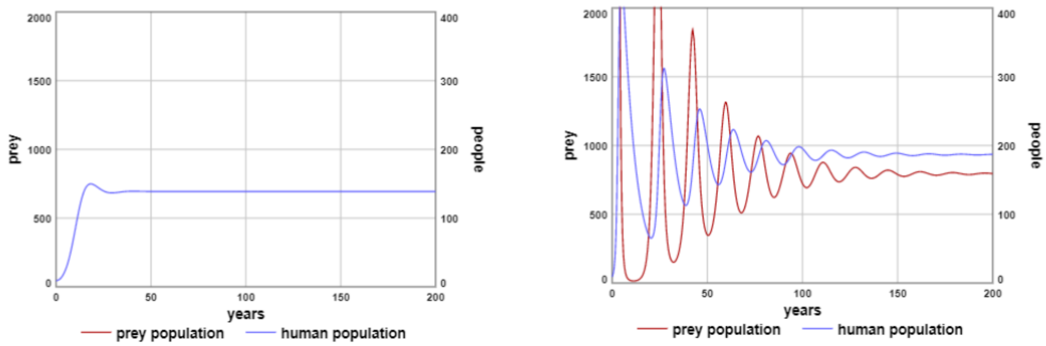

Figure 2-7: *Graph (left) with q = 0.01 and (right) u = 0.04, all other settings as in Figure 2-5.*

Conclusions

Compared with the simple population growth model, the growth of the prey in this model, even without any humans, is limited by the carrying capacity. This still-pretty-simple logistic carrying capacity model brings a vital element of realism. And it is well behaved.

As soon as we bring in humans and have two linked differential equations in the model, things get complicated, and all sorts of things that are very different can happen just by changing the model's initial conditions or parameters by small amounts. Mathematical biologists speak of "complex dynamics." The tendency of predator-prey models to cycle is our introductory example of complex dynamics.

If we had not severely restricted the range of the knobs and sliders, then for most settings the model would have shown strange, wild results. One of the big lessons from mathematical biology is that most models have rather large regions of parameter space where the model behaves in ways that bear no relationship to reality. Math theorists depend on ecologists and evolutionists to tell them what part of parameter space is real. Otherwise the modelers are simply studying questions like how many angels can dance on the head of pin. (Fun math though!)

We saw what happened when we increased the Efficiency Convert Prey into Humans (q): The Prey almost got wiped out on the first big swing. Now imagine inventive hunter-gatherers who constantly increase their hunting efficiency over time. What do you think will happen? Let's find out in our next model, Hunter-Gatherers with (dynamic and normally continually increasing) Technology.

Appendix / Stella Top-Level Model Code

Stella's top-level code for the Basic Hunter-Gatherer Model is given below. It is useful for determining what the model is actually doing (and hence for trouble shooting the model). It could also be useful for those who want to understand the model in more detail or to use this model as a starting point for their own Stella model.

```
Top-Level Model:
K(t) = K(t - dt) + (f - g) * dt
  INIT K = 2000
  UNITS: prey unit
  INFLOWS:
    f = r*p*K {UNIFLOW}
      UNITS: prey unit/years
```

```
   OUTFLOWS:
      g = h {UNIFLOW}
         UNITS: prey unit/years
L(t) = L(t - dt) + (b - d) * dt
   INIT L = 10
   UNITS: people
   INFLOWS:
      b = h*q {UNIFLOW}
         UNITS: people/years
   OUTFLOWS:
      d = u*L {UNIFLOW}
         UNITS: people/years
h = v*K*L
   UNITS: prey unit/year
j = 3000
   UNITS: prey unit
p = (j-K)/j
   UNITS: unitless
q = 0.02
   UNITS: people/prey unit
r = 0.1
   UNITS: 1/year
u = 0.1
   UNITS: 1/year
v = 0.005
   UNITS: 1/(people*year)
{ The model has 13 (13) variables (array expansion in parens).
  In root model and 0 additional modules with 2 sectors.
  Stocks: 2 (2) Flows: 4 (4) Converters: 7 (7)
  Constants: 5 (5) Equations: 6 (6) Graphicals: 0 (0)
  }
```