

Population Dynamics Models

We will start by examining the dynamics of a single species. Populations do not, generally, only grow by colonization or die to extinction. Instead, they tend to oscillate somewhere above levels which risk extinction and that at which their habitat would be destroyed.

In general, the goals of population ecology are:

- 1) Quantify the rates of birth, death immigration, and emigration.
- 2) Use this information to explain what is influencing the timing and magnitude of these fluctuations.
- 3) Alter the mean level of these fluctuations.
- 4) Prevent over exploitation and extinction.

Most information of this nature is about pest insect populations because of monetary and lifespan reasons. There is also limited harvesting information. We will concentrate on theoretical (laboratory) growth rates. Population dynamics models are usually created by starting with a very simple model and adding additional features, as necessary.

Two classes of basic growth models are used depending on the ecology:

- 1) Organisms with overlapping generations
Examples: Humans, Bacteria, Protozoans, Birds, Mammals, Trees, and Some Insects.
- 2) Organisms having discrete generations.
Examples: Moths & Butterflies in temperate regions in which eggs are laid by females in phase, Caterpillars hatch. . . Eggs are laid only by new generation.

Exponential Growth

One can combine the birth and death rates into a single value. This is the effective growth rate of the population. Under these conditions the equation for the population growth is:

$$\frac{dN}{dt} = r \cdot N$$

Where: N = the number of individuals in the population
 t = time
 r = intrinsic rate of natural increase
 = birth rate - death rate under fixed conditions

The coefficient “r” is a function of:

- 1) Reproductive delay
- 2) Distribution of progeny during the organism’s lifespan
- 3) Length of life

etc.

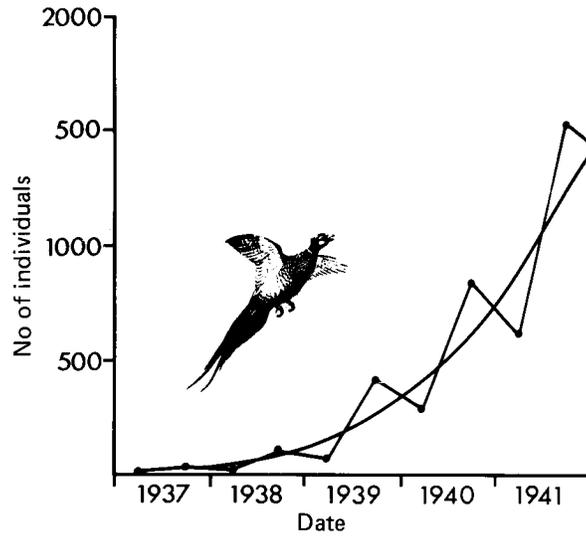


Figure 6.1: Exponential Growth of Pheasant (*Phasianus colchicus*) Populations on Protection Island, Washington. Smoothed curve connects average numbers at the end of each year. Source: After Einarsen, 1945.

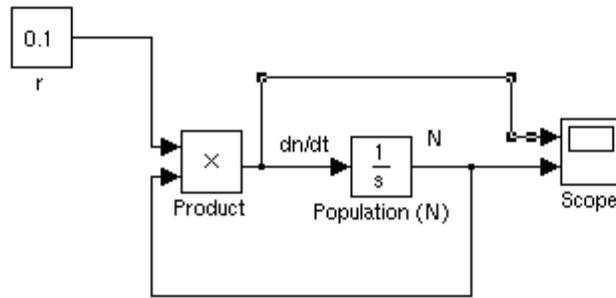
[1]

Increased values of r give a reproductive advantage and can be used to rank plant and pest species. For example, an examination of the reproduction of three species of aphids on 20 relatives of the broad bean (*Vicia*) yielded r ranging from 0 to 0.30, suggesting directions for breeding resistance.

If N_0 occurs at t_0 , this equation can be integrated to yield

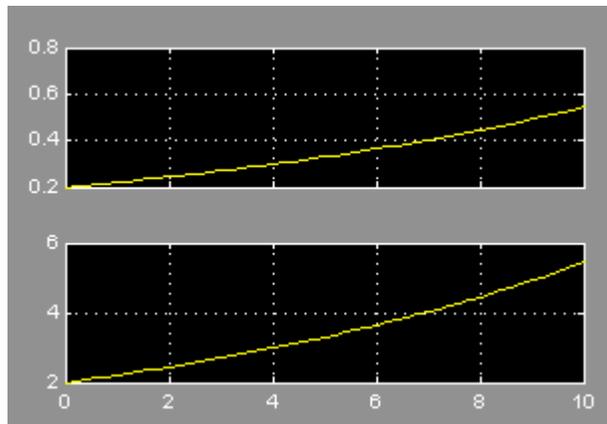
$$N_t = N_0 e^{rt}$$

This exponential growth is known as “Malthusian Growth” after Thomas Malthus (b. 1766; d. 1834). His “Essay on the Principle of Population” predicted disaster noting that, unless offset by war or disease, the world population grows at an exponential rate (doubling every 25 years) while food supply grows linearly. The Simulink model is shown below [2].



Where: $N = 2$ (initially)
 $r = 0.1$

Note the presence of the positive feedback loop. A system containing this type of feedback is almost always unstable. The model was built from the equation by assembling dN/dt graphically. Note the presence of the feedback loop. Running the model results in the following plots from the scope.



Note that the upper input, and hence the upper plot, is the growth rate of the population. The lower plot is the actual population size.

The results of this equation can be linearized by taking the natural log of both sides to yield

$$\ln N_t = \ln N_0 + r t$$

Therefore, if one has raw data of population versus time, one can plot the log of the population number versus time and use linear regression to obtain a value for “r”.

Logistic Growth

As you know, populations do not expand exponentially forever. There is a limit to the number of individuals that a space can support. In population dynamics this limit is known as “k”, the

carrying capacity. In logistic growth, the rate of growth is reduced based on the space available for individuals. This is performed by including the following term in the growth rate:

$$\left(1 - \frac{N}{k}\right)$$

Where: k = the carrying capacity of the ecosystem

Note that for the case $N \ll k$, this term is essentially 1, yielding an exponential growth rate. However, when $N = k$, this term becomes 0, eliminating any further population growth. When this term is included in the population equation, it becomes

$$\frac{dN}{dt} = r \cdot N \cdot \left(1 - \frac{N}{k}\right)$$

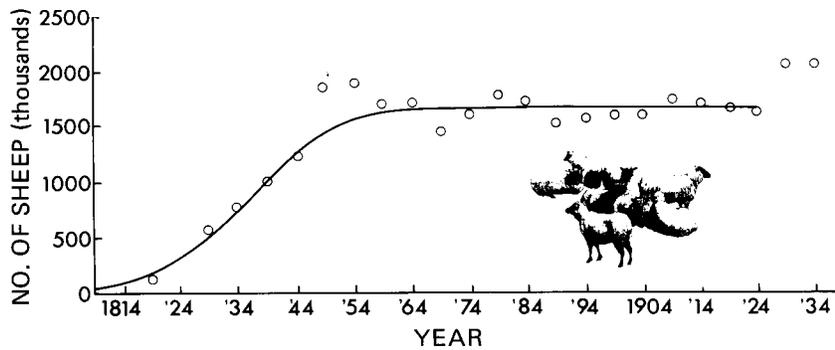


Figure 6.2: Typical Sigmoid Curve for Population Growth. The graph plots the development of sheep populations in Tasmania. Source: From Davidson, 1938 after Odum, 1959.

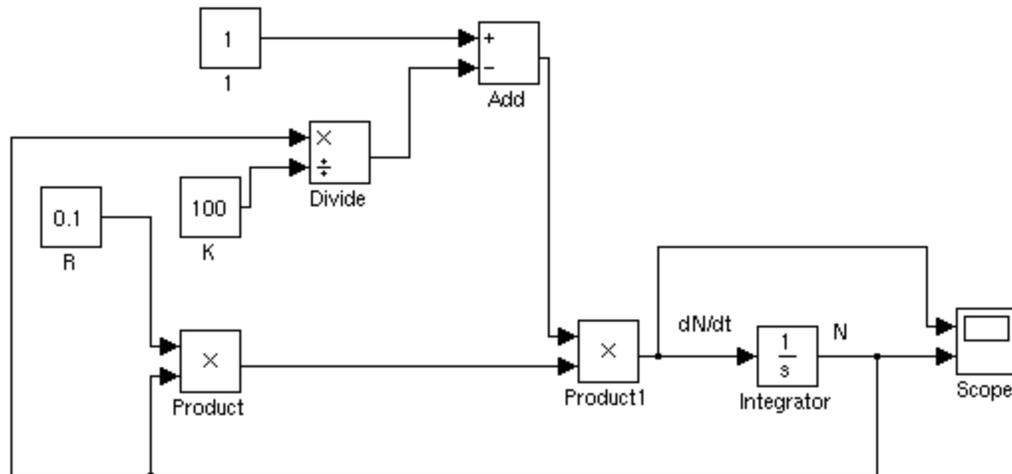
[1]

In integral form this equation becomes

$$N = \frac{k}{1 + a \cdot e^{-rt}}$$

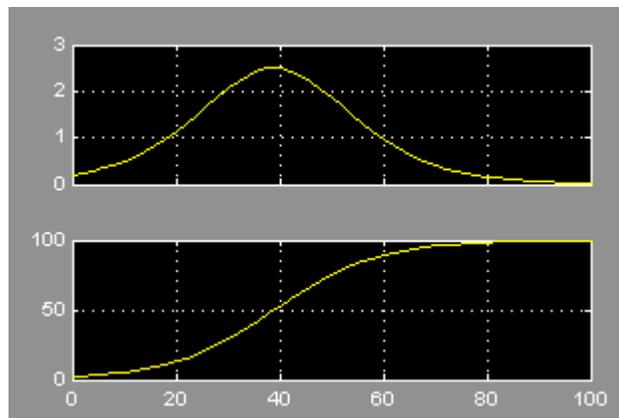
Where: a = Defines the inflect point of the curve

When this model is implemented in Simulink (once again, building the equation as an input into dN/dt) we get:



Where: $N = 2$ (initially)
 $r = 0.1$
 $k = 100$

The output scopes are:



The upper output is the rate of growth for the population, while the lower curve is the total number of individuals in the population. The shape of the lower curve is known as a “logistic” curve.

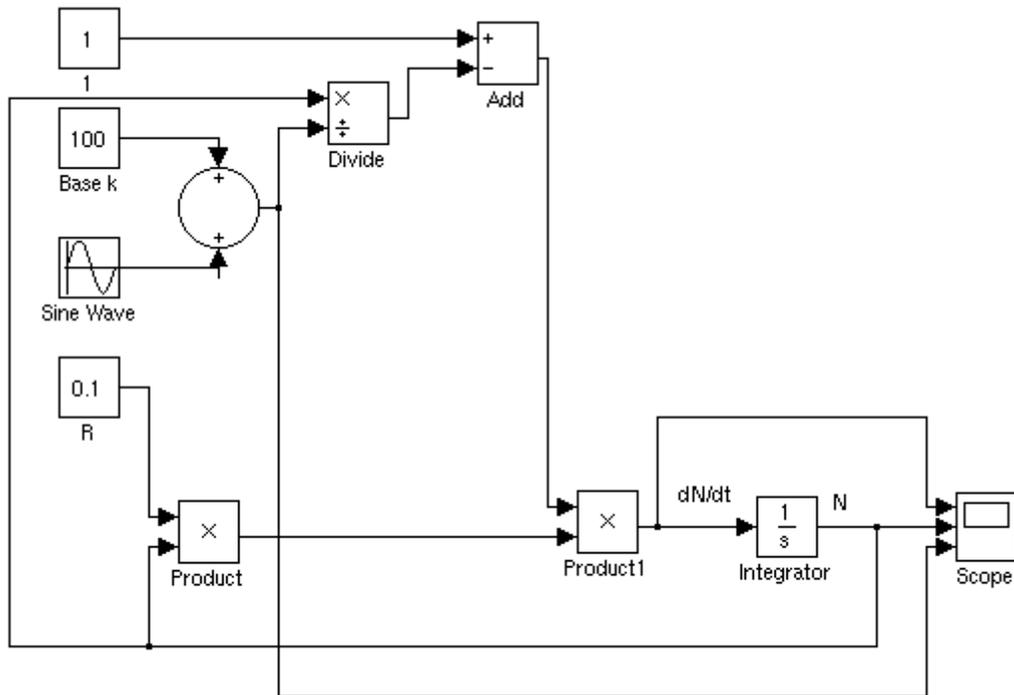
Variable Carrying Capacity

The above simulation is still somewhat limited, since the carrying capacity of an ecosystem is not a constant. Instead, there is a periodic variability in the carrying capacity throughout the year.

- Note that if: $N > k$ carrying capacity is exceeded and the population decreases.
- $N < k$ population increases.
- $N = k$ population is stable.

The extent to which the population follows depends on the “Population’s Response Time” = 1/r.

One way to implement this variability in the Simulink model is to add a sine component to k. This has been done in the model below:

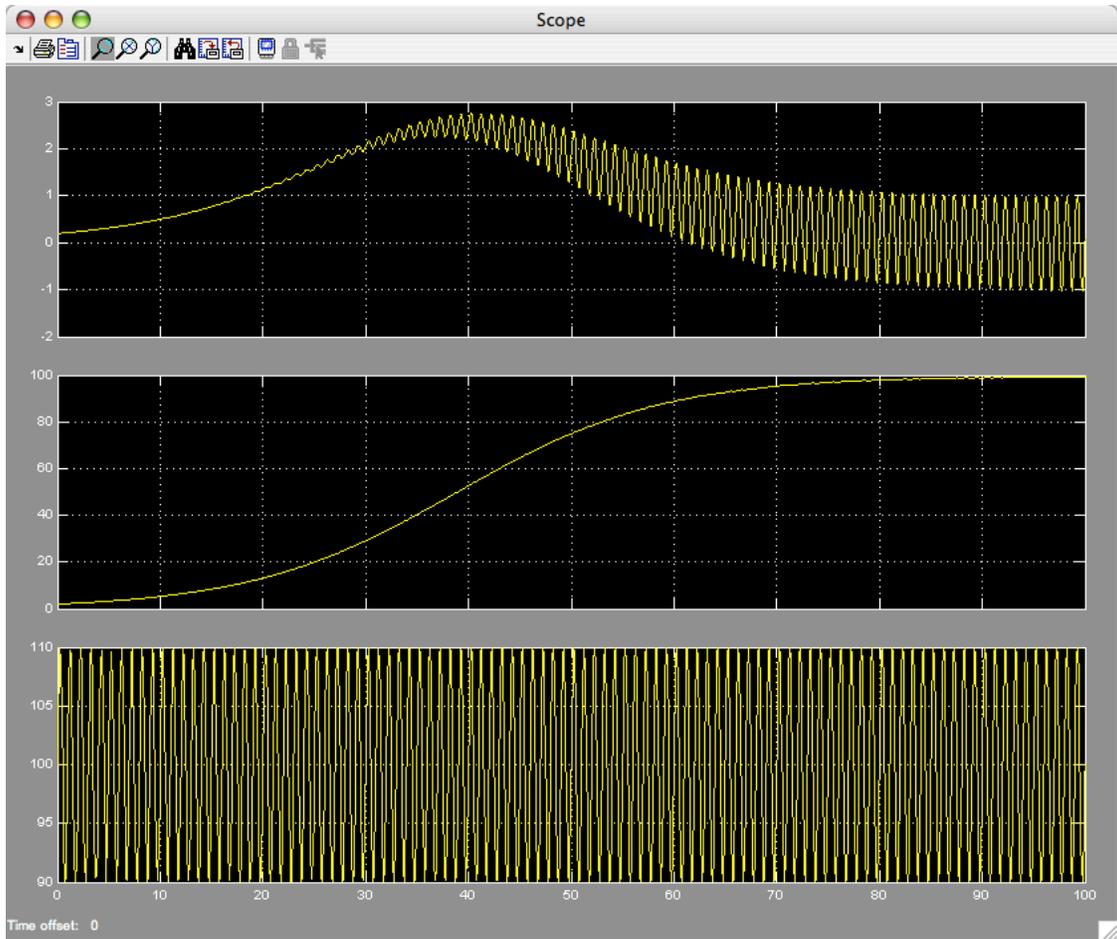


where: $k = 100 + 10 \cdot \text{sine}(2 \cdot \pi \cdot t)$

This results in a final equation for the logistic growth curve of:

$$\frac{dN}{dt} = r \cdot N \cdot \left(1 - \frac{N}{100 + 10 \cdot \text{sine}(2 \cdot \pi \cdot t)} \right)$$

To get a correct output from this model, you will need to use a stiff equation solver and reduce the relative tolerance to 1e-6. An extra input has been added to the scope to display the value of k. The outputs shown on the scope (from top to bottom) are dn/dt, N, and k. This is shown below:



As you might expect, during the early (exponential) phase of growth, the population is unaffected by the variability in the carrying capacity. However, once the population is near the carrying capacity it oscillates at the same frequency as the carrying capacity, with some of the population dying off.

Population Dynamics Models II

Density dependence is not usually instantaneous. Due to organism generation time or environmental recovery. This can be expressed as the equation:

$$\frac{dN}{dt} = r \cdot N \cdot \left(\frac{k - (t - T)}{k} \right)$$

Where: T = Time lag

The systems response varies as a function of $(T, 1/r)$ as is shown in Figure 7.6.

The time lag term can be combined into the existing logistic growth with variable carrying capacity to yield

$$\frac{dN}{dt} = r \cdot N \cdot \left(\frac{(100 + 10 \cdot \sin(2 \cdot \pi \cdot t)) - (t - T)}{100 + 10 \cdot \sin(2 \cdot \pi \cdot t)} \right)$$

This is why we use numerical integration routines

Discrete Generations

Generally, these models are framed as difference equations. Time is a discrete variable.

$$N_{(t+1)} = F(N_t)$$

$$N_{t+1} = \lambda \cdot N_t$$

The difference equation equivalent of

$$\frac{dN}{dt} = r \cdot N$$

Then, the number of individuals at time t

$$N_{@t} = \lambda^t \cdot N_0$$

Where: λ = Finite rate of increase

t = Number of times the population multiplies itself/generation

$$r = \ln \lambda$$

This equation also results in geometric growth.

If one then allows the equivalence of a carrying capacity:

$$N_{t+1} = N_t e^{r \left(1 - \frac{N_t}{K}\right)}$$

Based on this equation a wide range of theoretical patterns are possible. See Figure 13.1[1] for some possibilities.

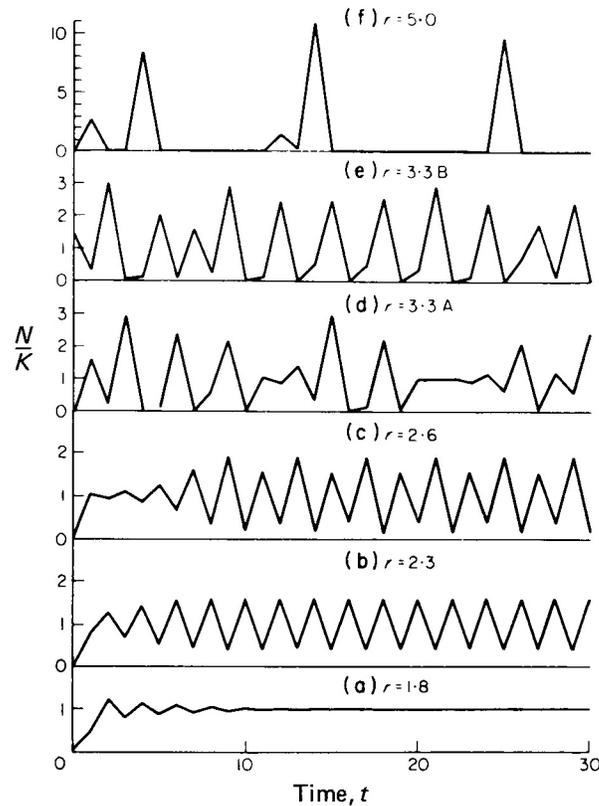


Figure 13.1: The Spectrum of Dynamical Behaviour of the Population Density, N_t/K , as a Function of Time, t , as Described by Difference Equations for Various Values of r . Specifically: (a) $r = 1.8$, stable equilibrium point; (b) $r = 2.3$, stable 2-point cycle; (c) $r = 2.6$, stable 4-point cycle; (d to f) in the chaotic regime, where the detailed character of the solution depends on the initial population value, with (d) $r = 3.3$ ($N_0/K = 0.075$), (e) $r = 3.3$ ($N_0/K = 1.5$), (f) $r = 5.0$ ($N_0/K = 0.02$). Source: From May, 1976b.

What is wrong with these equations?

- 1) Ignores competitors.
- 2) Ignores predators.
- 3) Ignores abiotic environment.
- 4) Ignores interactions between populations in community.
- 5) Ignores age effects in the population.

Life Table Approach

- 1) Used only for overlapping generations.
- 2) Contains age distribution information.
- 3) Used most effectively for a relatively constant population.
- 4) Requires mortality information.

Start by defining a pivotal age group size.

e.g. Man - 10 Years
 Insects - Days or Weeks
 Bacteria - Hours

Tradition requires starting at 1000 or normalizing to 1000 initial population.

Death rates are determined either by aging a sample population or by studying remains. The latter method is more subject to sampling bias.

A Hypothetical Time-Specific Life Table.[1]

x	l_x	$\log l_x$	d_x	q_x	e_x	L_x	T_x
1	1000	3.0	550	550	1.21	725	1210
2	450	2.7	250	556	1.08	325	485
3	200	2.3	150	750	0.80	125	160
4	50	1.7	40	800	0.70	30	35
5	10	1.0	10	1000	0.50	5	5

Where:

- x = Pivotal age class
- l_x = Number of the 1000 surviving at start of age class
- d_x = Number dying during interval
- q_x = (fraction dying) x 1000
 e.g. at start of age class 2, $q_x = (250/450) \times 100$
- L_x = Average number of individuals between age x and age x+1 (i.e. $L_x = (l_x + l_{x+1})/2$)
- T_x = Total number of individuals of aged x and beyond (determined by adding midpoints from bottom up to point)
- e_x = Life expectancy for individuals attaining age x
 $= T_x/l_x$

You can obtain a visual representation by plotting l_x or x. However plotting $\log_{10} l_x$ vs x. This yields information as to how survival rate changes. In this case the same proportion of the organisms die each year.

Survivorship data showing a constant death rate.

l_x	$\log l_x$	d_x
1000	3.0	300
500	2.7	250
250	2.4	125

125	2.1	63
63	1.8	

When plotted, this data looks like [1]:

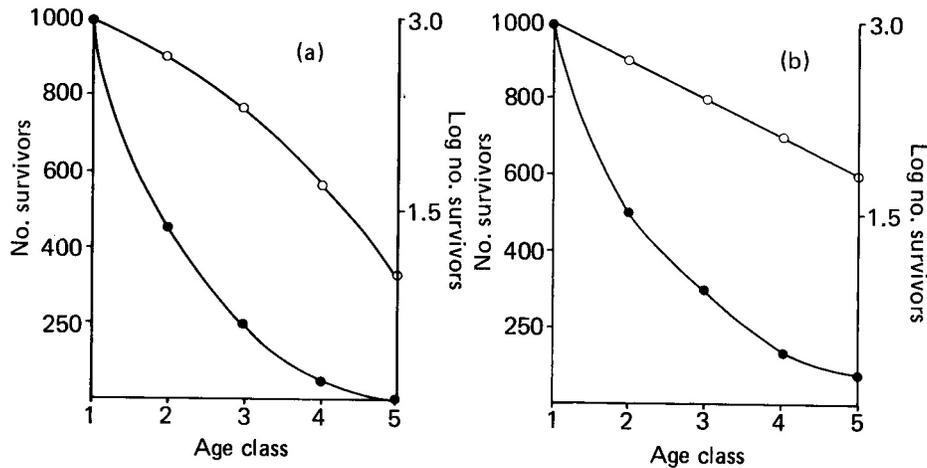


Figure 7.7: Survivorship Curves on Arithmetical and Log Axes for the Data in (a) Table 7.2 and (b) Table 7.3.

Organisms may be ecologically classified, as either:

- “r-Selected” - Exploits short duration habitats. Maximizes r while staying below k . Density dependence is low.
- “k-Selected” - Relatively low reproduction rate. Density dependence is important in population processes.

This classification is based on their approach to survival of the species. r – selected organisms count on rapidly responding to a favorable environmental change by rapidly producing large numbers of young. Because of the large numbers of young parental care is not possible and large numbers of offspring die. In the case of k – selected organisms, only a few young are produced, but there is significant parental involvement in the child rearing process.

If the numbers of individuals is plotted as a function of age, the result is known as a “survivorship” curve. There are three major classes of survivorship curves [1].

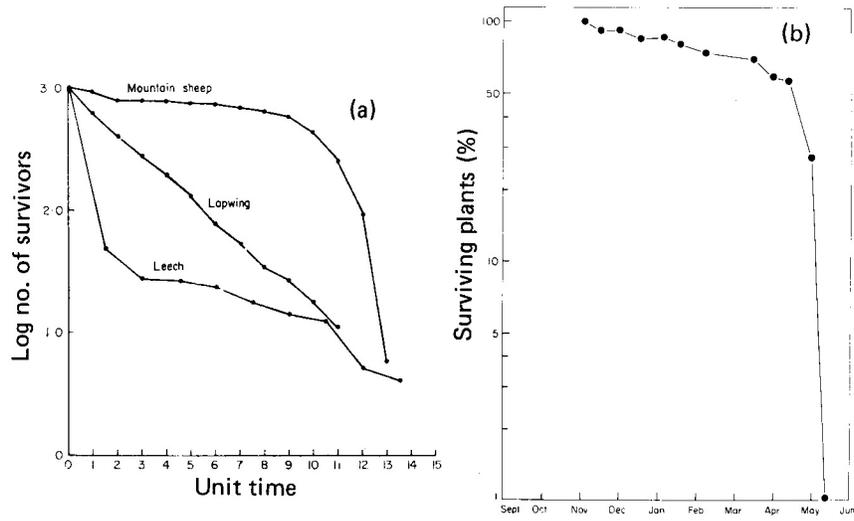


Figure 7.8: (a) Survivorship Curves for the Mountain Sheep (Murie, 1944), the Lapwing (Lack, 1943) and the Leech, *Glossiphonia* (Mann, 1957). (From Dempster, 1975). (b) Survivorship Curve for the Chickweed (*Cerastium atrovirens*) on Fixed Dunes at Aberffraw, North Wales. Source: From Mack, 1976 and Silvertown, 1982.

- Type 1 Curve - Mammals, K-Selected, Exhibit parental care
 - Mountain Sheep
- Type 2 Curve - Constant Survivorship
 - Lapwing
 - Obtained from banded birds
 - Omits infant mortality
 - Reality is between types 2 and 3
 - Die before they are old
- Type 3 Curve - r-Selected Organisms
 - Insects, Fish, Parasites, Annual Plants
 - Leech

One must be careful in expecting these sorts of curves. In the lapwing curve in 7.8a [1], the results are for banded birds only, eliminating the higher death rate of chicks. In the figure below (7.9)[1], the age structure has been broken by environmental factors. In this case, lump is due to severe winter storms clearing mussels off of rocks. This provided space for settling of a large number of spat.

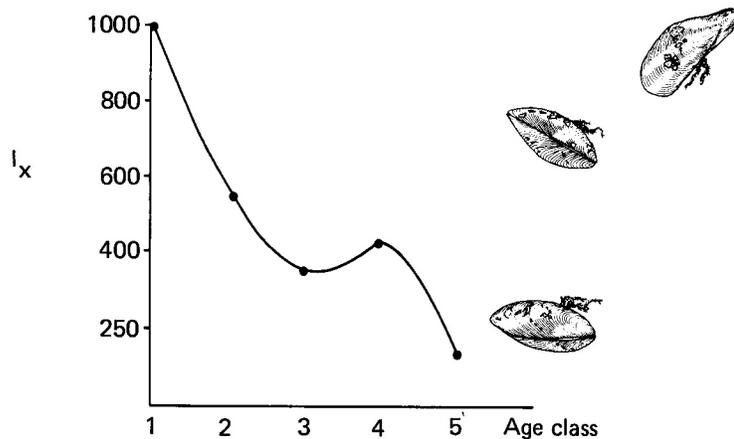


Figure 7.9: A Survivorship Curve for a Population of Mussels (*Mytilus edulis*) Which did not Exhibit a Constant Age Structure.

Competition

When 2 organisms occupy the same ecological niche, they influence each other through competition. In general there are two types of competition:

1. Intraspecific Competition - Same species
2. Interspecific Competition - Different species

Competitors must require the same resource and that resource must be limiting or potentially limiting. If this is not the case, then there is no competition. Competition occurs by either or both of the following:

Interference Competition - Direct interactions of competitors for the same resource, thus interfering with each other's uninterrupted access to and use of that resource; e.g. plants & space or light.

Exploitation Competition - One individual affects another's uninterrupted use of a resource through prior exploitation. Competitors do not meet, but use by one diminishes the amount of the resource available for the other.

Use of one resource by 'A' that affects the use of another by 'B' that is not used by 'A' is *not* competition.

In general, intraspecific competition leads to diversity/variation in the population and 'broadens' the niche occupied. This may lead to new species.

Both inter- and intraspecific competition are mechanisms used to regulate population size.

Intense interspecific competition results in: 1) Extinction of one competitor or 2) Movement of one competitor into a new niche.

Remember that

$$\frac{dN}{dt} = r \cdot N \cdot \left(1 - \frac{N}{k}\right)$$

for organisms with overlapping generations. In this equation, much of what we are compensating for is intraspecies competition.

In the case of interspecies competition, we must compensate for the effects of the second species. This requires the inclusion of an additional term (for Species 2 or Species 1). This term needs to:

- 1) be negative in sign,
- 2) include the carrying capacity for Species 1, and
- 3) include a competition coefficient $\alpha_{1,2}$

The equation then becomes

$$\frac{dN_1}{dt} = r_1 \cdot N_1 \cdot \left(1 - \frac{N_1}{k_1}\right) - r_1 \cdot N_1 \cdot \left(\alpha_{1,2} \cdot \frac{N_2}{k_1}\right)$$

or

$$\frac{dN_1}{dt} = r_1 \cdot N_1 \cdot \left(1 - \frac{N_1}{k_1} - \alpha_{1,2} \cdot \frac{N_2}{k_1}\right)$$

Geometric Growth	Effect of Species 1 on itself	Effect of Species 2 on Species 1
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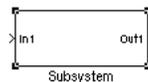
Note the labeling of the components of the equation.

Similarly for Species 2

$$\frac{dN_2}{dt} = r_2 \cdot N_2 \cdot \left(1 - \frac{N_2}{k_2} - \alpha_{2,1} \cdot \frac{N_1}{k_2}\right)$$

$\alpha_{1,2}$ and $\alpha_{2,1}$ are reflections of the degree to which growth is restricted.

In the case of these equations, they can only be implemented as a pair in Simulink. This is because, when they are assembled the “N” term from the other model must be included. The easiest way to build the model is to build the first equation, do a copy and paste, and link the two equations. This can be done using “subsystems.” The subsystem block is shown below:

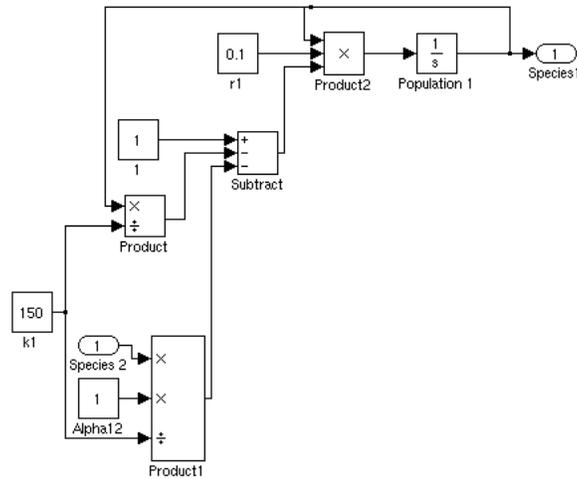


[3]

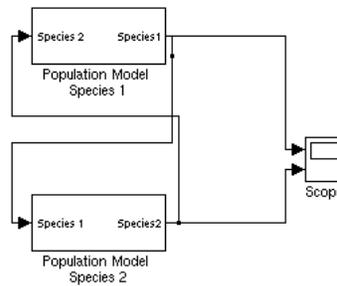
When this block is opened, an inport and an outport block are visible with a signal between them.



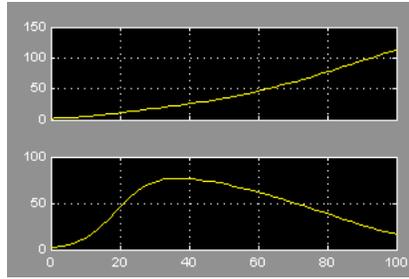
Build the model for each species between the blocks as shown below:



If you close the subsystem block, you can copy and paste it in the top level of your model. The models for the two species are then connected as shown:



The population model for the second species will need to be opened and the constants changed to those for the second species. In the simulation below, species one has out competed species 2.



This approach of using subsystems presents several advantages. First, it is easier to see the relationships between the two species. Second, as was performed in this model, it is easy to cut and paste additional modules into the model. Finally, a model containing multiple subsystems can be easily upgraded as additional information is available, by simply replacing the appropriate subsystem.

Note that a term (and an appropriately configured subsystem) can be added for each additional competing species, i.e.

$$\frac{dN_2}{dt} = r_2 \cdot N_2 \cdot \left(1 - \frac{N_2}{k_2} - \alpha_{2,1} \cdot \frac{N_1}{k_2} - \alpha_{2,3} \cdot \frac{N_3}{k_2} \right)$$

Additional terms may be added for each resource under competition.

Also note that the sign on the “Competition” term may be altered

- ,- Competition
- ,+ Parasitism
- +,+ Mutualism, Symbiosis
- +,0 Use of one organism as the host for another
- ,0 Incidental damage, e.g. trampling of plants

It has been said that 2 species with the same ecologies (or niche) can not coexist in the same environment. Theory, however, gives two possibilities. These possibilities are shown below:

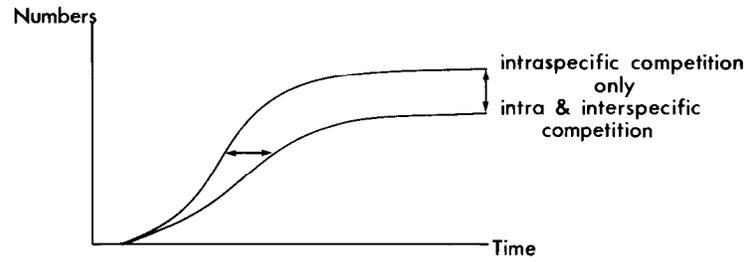


Figure 6.3: Effects of Introducing an Element of Interspecific Competition into the Population Equations of Page 131. Population growth is demonstrated here for a theoretical population but compare with Figure 6.7.

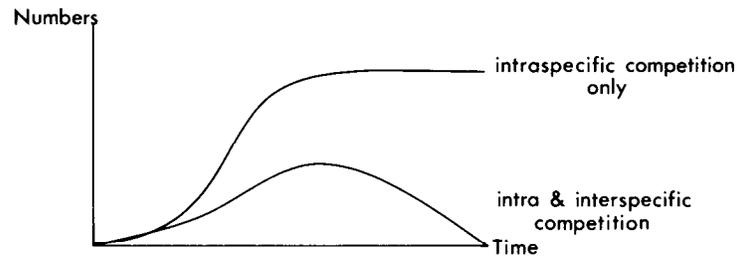


Figure 6.4: As Figure 6.3, but Strength of Competition Has Increased Such as to Cause Extinction.

In general, this is true as shown in Figure 6.5.

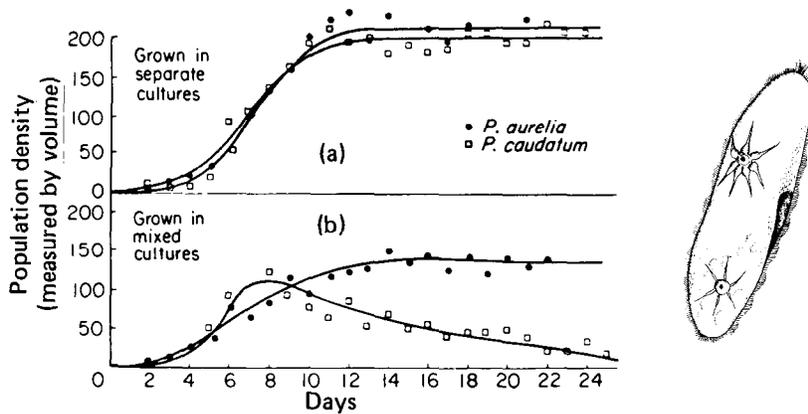


Figure 6.5: Growth of *Paramecium* Populations (*P. caudatum*, *P. aurelia*) in Separate Culture (a) and in Mixed Culture (b). Source: After Gause, 1934.

In some cases this is not true, as shown in Figure 6.7.

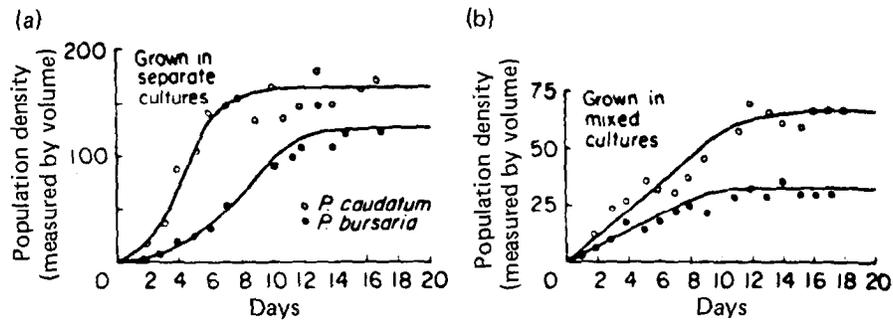


Figure 6.7: Coexistence of *Paramecium caudatum* and *P. bursaria* in Mixed Culture (b). Population curves for the two species in separate culture are shown in (a).

The outcome is dependent on:

- A) Initial population densities
- B) Environmental conditions
- C) Genetic constitution of the strains of the competing species.

An example of (B) considering

Drosophila pseudo obscura
Drosophila serrata

At 23°C the 2 species exist in competition.

At 25°C *D. serrata* out competes *D pseudo obscura*.

At 22°C *D. pseudo obscura* wins.

Competition may also exist in a “patchy” environment where spatial heterogeneity gives each of 2 species a local advantage in an area. The victor is also a function of the period by which the environment favors one organism over another (where time is in terms of generational length).

Some of these possibilities are shown in Figure 6.8.

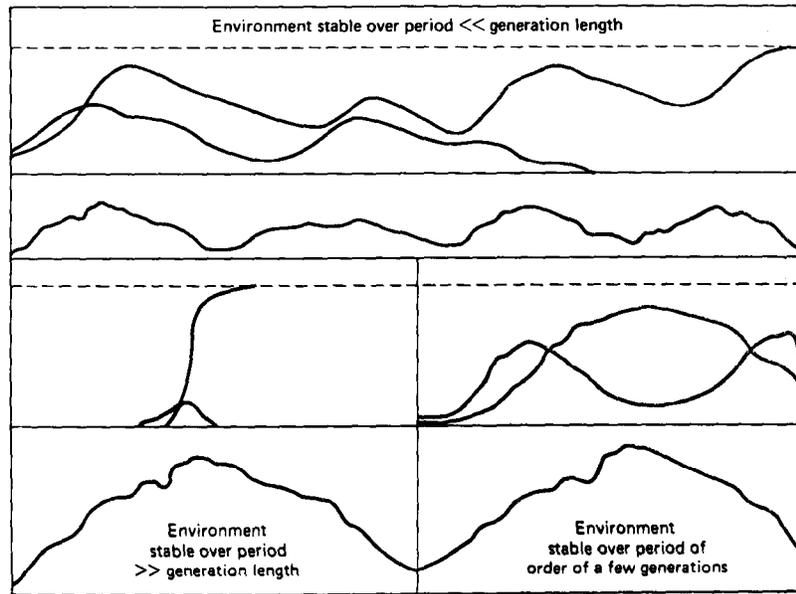


Figure 6.8: Ideal Course of Competition Between Two Species as Regulated by the Relation Between Generation Length and the Period over which the Environment may be Taken to be Stable. Source: From Hutchinson, 1953 after Collier *et al.*, 1973.

Note also that competition does not need to be direct. (Indirect competition))

e.g. 2 Species which do not occupy the same dietary niche may share a predator. If one species becomes scarce the predator may switch species.

e.g. 2 predatory species which do not eat the same prey, but whose prey species compete. If one prey species outcompetes the other, the predators will be affected.

Interspecific Competition in Natural Systems

Reynoldson and Bellamy (1970) established a set of criteria for establishing the existence of competition in the field.

1. The comparative distribution and/or relative abundance of the two potentially competing species should be amenable to explanation based on competition.
2. It is necessary to show that the competing species are utilizing a common resource that may provide the basis of competition.
3. There should be evidence from the performance of the particular species populations in the field that intraspecific competition is occurring. This may relate to fecundity, survival growth rate of individuals or some other appropriate parameter. This criterion assumes that

if persistent interspecific competition is occurring then intraspecific competition must also be taking place.

4. Both the resource which is being competed for and the population should be manipulated separately in the field with predictable results based on the hypothesis that competition is occurring. It is insufficient to manipulate only the absolute amounts of a resource since its availability may be altered irrespective of the competition process. For example, many populations are likely to respond to an increase in food whether or not competition is occurring because the same amount (or more) may be obtained with less expenditure of energy.
5. Events following the introduction or removal (or reduction) of a competing species should be consistent with the competition hypothesis. This criterion differs from criterion 4 since it concerns interspecific events only. Criteria 4 and 5 are clearly the most crucial to observe: results of criterion 5 enable the empirical determination of the competition coefficients α .

Lecture Sources

- [1] R. J. Putman and S. D. Wratten, *Principles of Ecology*. Berkeley and Los Angeles: University of California Press, 1984.
- [2] B. M. Hannon and M. Ruth, *Modeling dynamic biological systems*. New York: Springer, 1997.
- [3] Mathworks, *Using Simulink*. Natick, MA: The Mathworks, Inc., 2004.