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<u>SCIENCE SIMULATIONS LABORATORY</u>

POPULATION DYNAMICS & COEXISTANCE

<u>STUDENTS' MANUALS (Version 1.02.2003)</u>

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STUDENTS' MANUAL A – INTRA-SPECIFIC COMPETITION

Population dynamics is the study of the changes which occur in the sizes of populations over periods of time and of the factors which influence these changes. The computer simulation ***Population Dynamics & Coexistance*** models two situations in population dynamics. In the first, populations of a single species grow on limited resources. Competition is thus between members of the same species (intra-specific competition). The second situation is that of two species in competition with each other for the same, limited resources (inter-specific competition). ***Population Dynamics & Coexistance*** allows you to investigate these different types of competition and, by altering variables such as the generation times and reproduction rates of the species, determine their relative importance in influencing the outcome of competition.

Suppose that a few members of a single species enter a habitat in which there is a constantly replenished, but limited, supply of all the resources essential to that species' existence. From the initial low number of organisms, the population will grow until it attains that number (known as the saturation population) which can only just be supported by the resources available. Typically it is found that the growth of the population follows an S-shaped, 'sigmoid' or 'logistic' pattern (Figure A1).

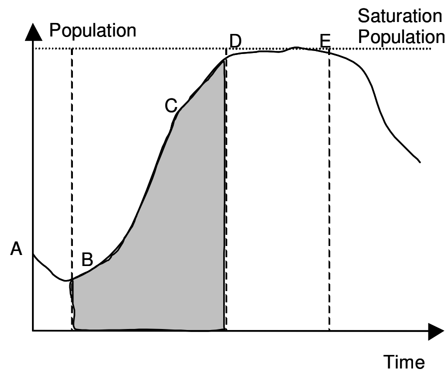

Figure A1 The sigmoid growth curve

From the 'seed' population (A), numbers usually fall for some while as the organisms adjust to their new environment. This phase is sometimes known as the 'lag' phase. However, at some point (B), the decline is reversed and the population starts to grow. The rate of growth (as well as the number of organisms) increases at first, until a maximum rate of growth is reached (C). This phase is sometimes known as the 'log' phase. There is then a period during which the number of organisms continues to rise, but the rate of population growth declines. When the saturation population is attained (D), the rate of population growth is, on average, zero. Numbers frequently fluctuate about this level for some time (DE) before declining (EF) due for example, to the accumulation of toxic waste products.

Population Dynamics & Coexistance models only the shaded part of Figure A1 properly. There is no 'lag' phase and, once the saturation population has been attained, the population size remains constant. There is no oscillation about the saturation population and no decline phase. The precise shape of the growth curve produced by ***Population Dynamics & Coexistance*** depends upon several factors, among which are:

a. The number of organisms at B, the 'initial population'.

b. The number of organisms at D, the 'saturation population'.

c. The potential number of offspring which can be produced by each member of the population. Note that 2 could represent either binary fission or the production of four offspring by a sexually reproducing pair of organisms.

d. The mean time between generations under ideal conditions for the particular species.

These four factors can be varied, and thus their relative importance determined, using ***Population Dynamics & Coexistance***.

STUDENTS' MANUAL B – *POPULATION DYNAMICS & COEXISTANCE* AND INTRA-SPECIFIC COMPETITION

To consider intra-specific competition you should click on the *INTRAspecific* button. You will be asked to specify whether there is to be one or two populations. Since we are studying intra-specific competition these populations are not competing against each other. The main purpose is to make comparisons between growth curves with different values for the four factors – initial population size, saturation population size, number of offspring and time between generations. Until you are completely familiar with the use of ***Population Dynamics & Coexistance*** it is better to specify only one species. In this example (figure B1) the initial population was just one organism, the environment could support 200 (the saturation population), each organism had the potential to leave two offspring and the generation time for this species was 5 units of time. You could imagine this species to be a micro-organism reproducing by simple division every 5 minutes. The population sizes could represent hundreds of thousands or millions. Note that it was also necessary to specify the time over which the population growth was to be plotted. Here 100 time units (equivalent to 20 generations) was specified. The resulting graph as shown in Figure B1 resembles a sigmoid growth curve.

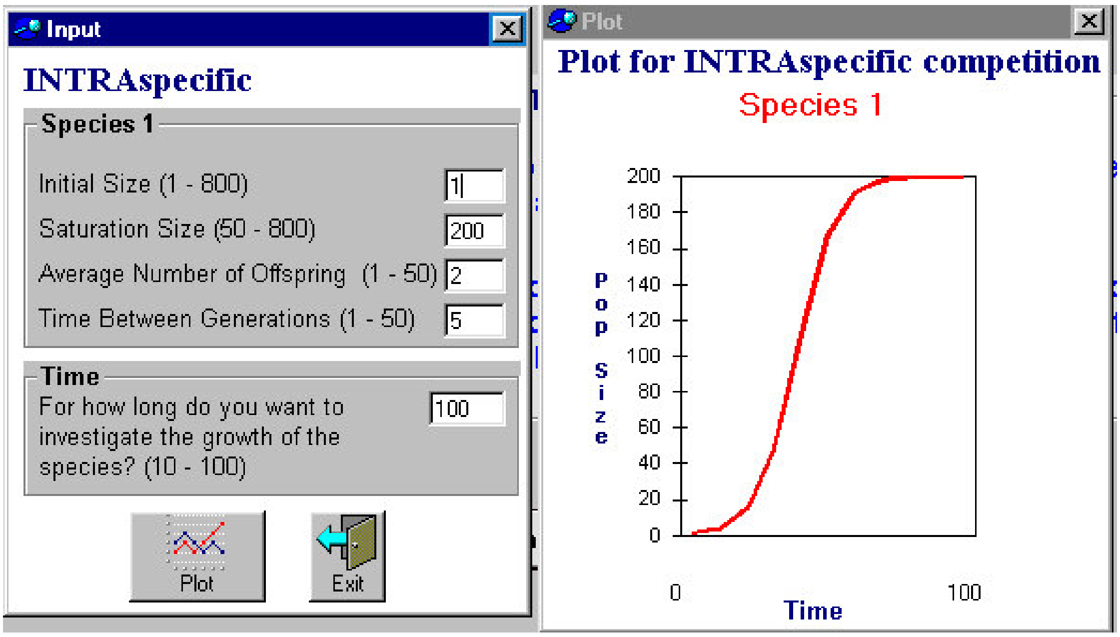

Figure B1 Screen printout showing results for Intra-specific competition with one species

Sometimes you may want to look at the results of the currently displayed competition over a different period of time – either longer, to see what happens later, or shorter, in order to see more detail. If so, respecify the time axis of the graph (*For how long do you want to investigate the growth of the species?*). However if you want to enter values for another species to compare with the first, you will have to click on the *Number of species* menu (top of screen). The growth curves of the two species will appear side by side so that you can make comparisons but remember that there is no competition between the species but only intra-specific competition within each.

STUDENTS' MANUAL C – INVESTIGATIONS ON INTRA-SPECIFIC COMPETITION

C1 What is the effect on the growth curve of lengthening the generation time?

Hint: On complete nutrient agar the bacterium *Escherichia coli*, has a generation time of 20 minutes (0.33 hours) at its optimum temperature (37ºC). On complete nutrient agar at 20 C it is about 120 minutes (2 hours). At 37ºC on glucose substrate (when the bacterium has to synthesise all the various amino acids, nucleic acids, etc. itself) it is about 60 minutes (1 hour). Compare the times taken to reach saturation population when the generation times are 0.33, 0.5, 0.67, 1, 1.5 and 2.0 hours. For the investigation to be valid all the variables except generation time should be kept constant. Suitable values for the others are:

Initial population	1
Saturation population	200
Number of offspring	2

You will need to determine an appropriate time course for each pair of curves.

C2 What is the effect on the growth curve of increasing the number of offspring?

Hint: Consider a sexually reproducing species which lives, on average, for one year. Compare the times taken to reach saturation population when the numbers of offspring are 1, 2, 5, 10, 15 and 20. Remember that in this model the number of offspring is defined as the potential number of offspring which can be produced per organism per lifetime. Suitable values for the other variables are:

Initial population	2
Saturation population	800
Generation time	1

C3 What is the relative influence on the growth curve of generation time and number of offspring?

Hint: If you have successfully tackled C1 and C2 you should know what the effects are of separately altering the generation time and the number of offspring. However, which of the two has the most influence? Keeping the initial and saturation populations constant (at 1 and 800 for instance), try the following series:

Number of offspring	2	4	8	16	32	64
Generation time	1	2	4	8	16	32

If the two variables are equally important the six graphs should be identical. What would happen if the number of offspring was the most important? What would happen if the generation time was most important? What actually happens?

STUDENTS' MANUAL D - GAUSE'S COMPETITIVE EXCLUSION PRINCIPLE

Seldom is a habitat occupied by only one or two species. Usually there are many species competing for the same resources. However, biologists have sometimes investigated such competition by considering simplified laboratory systems in which there are only two species. ***Population Dynamics & Coexistance*** can model such simplified situations, but not more complex multi-species ones.

It is quite possible for two species, although occupying the same area at the same time, to make almost totally different demands on it. The species would occupy different niches within the same habitat.

During the 1920s and 1930s a lot of research into competition was undertaken by scientists trying to obtain experimental evidence on whether two species having the same requirements could or could not coexist in the same habitat. One of the most prominent of these workers was the Russian, G.F. Gause.

Gause carried out an experiment involving two species of *Paramecium*, a protozoan which feeds on bacteria. Into culture bottles he put a solution upon which the bacterium, *Bacillus pyocyanaceus*, could live, but not reproduce, and he introduced the same amount of the bacterium into each of the bottles. Finally, he added the same total number of (a) *P. caudatum,* (b) *P. aurelia*or (c) *P. caudatum* and *P. aurelia* to the bottles and then let competition run its course. Growing in isolation, each of the *Paramecium* species survived and multiplied. However, in direct competition *P. caudatum* was always eliminated (figure D1).

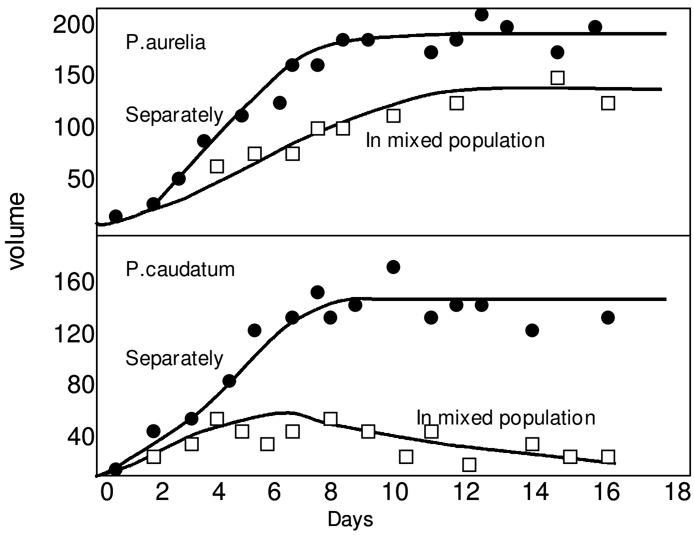

Figure D1 Growth of *P. aurelia* and *P. caudatum* in competition and isolation. (Note "Volume" is a measure of population density).

Similar results were obtained from other experiments and Gause generalised them into the conclusion that two species making the same demands on limited resources cannot coexist. Inevitably one of them would be more efficient, if only marginally, than the other and would come to dominate the niche to the exclusion of the other. This conclusion has been formulated as Gause' s Competitive Exclusion Principle.

It is thought that the particular bacterium in Gause's experiment excreted a substance which had a more detrimental effect on *P. caudatum* than on *P. aurelia. P. caudatum* was the less efficient of the two in this situation and was thus eliminated in competition. In a different environment, for example with a different bacterium, the relative efficiencies and thus the survivorship might well be reversed.

STUDENTS' MANUAL E – MORE IN INTER-SPECIFIC COMPETITION

Workers other than Gause carried out experiments on competition. For instance, in the 1940s Crombie studied competition between two species of flour beetle. In direct competition, *Tribolium* always eliminated *Oryzaephilus* (Figure E1). However, when small pieces of 1mm bore glass tubing was introduced into the habitat shared by the two beetles, *Tribolium* and *Oryzaephilus* appeared to coexist.

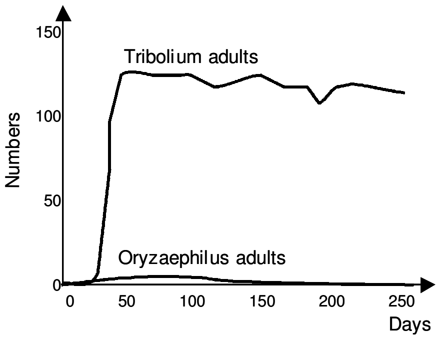

Figure E1 Direct competition between *Tribolium* and *Oryzaephilus.*

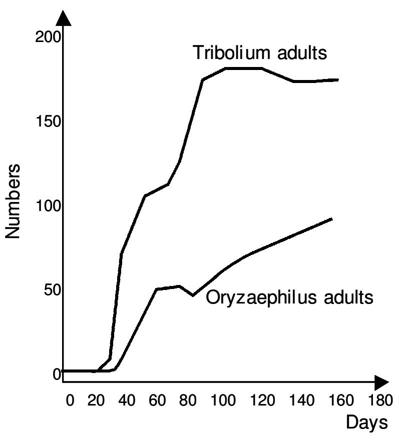

Figure E2 Effect of glass tubing on *Tribolium* and *Oryzaephilous* Competition.

E1 *Why, do you suppose, can Oryzaephilous survive in competition with Tribolium only in the presence of glass tubing?*

Supported by such experiments, the Competitive Exclusion Principle has become so much a part of the 'biological way of thinking' that if two species, apparently in equilibrium, are seen to occupy the same habitat simultaneously it is generally assumed that they fill different niches, even if no obvious differences in their demands upon the environment can be demonstrated.

It must not be imagined that Gause's ideas are never called into question. During the 1960s Ayala set out to test a hypothesis based on the Competitive Exclusion Principle. The hypothesis was that:

> If two species compete for a resource in short supply which is essential for their survival, one of the species must inevitably be eliminated.

By demonstrating the prolonged coexistence of *Drosophila pseudoobscura* and *D. serrata* on limited resources, Ayala claimed to have refuted Gause's Principle. As well as the interest in whether the Principle is valid under all circumstances or not, it is significant that scientists feel it is necessary to keep even such well established idea as those of Gause 'under review'.

For the most part, Gause's Principle remains accepted by population biologists and its mathematical basis provides the model for ***Population Dynamics & Coexistance***.

STUDENTS' MANUAL F – *POPULATION DYNAMICS & COEXISTANCE* AND INTER-SPECIFIC COMPETITION

When studying inter-specific competition, there is another factor which must be introduce, in addition to the four factors which apply in intra-specific competition, i.e. initial population, saturation population, number of offspring and generation. We shall call this the inhibitory factor.

Each of the two species in competition has an inhibitory factor. The inhibitory factor of species 1 is a measure of the detrimental effect species A has on species 2 in that particular environment. If the factor was zero, species 1 would have no detrimental effect on species 2 in that particular environment. If it was once, each member of species 1 would be taking as much of species 2's requirements from the environment as does each member of species.

If it was greater than one, each member of species 1 would be taking more of species 2's requirements than does each member of species 2. Simultaneously, of course, species 2 too would have an inhibitory factor and would inhibit species 1 to a greater or less extent.

F1 *Although inhibitory factors of less than zero are not allowed in* ***Population Dynamics & Coexistance****, it is possible to imagine such negative values. What would be the ecological significance for species 2 if species 1 had a negative inhibitory factor?*

To study inter-specific competition you should click on the *INTERspecific* button. It is necessary to specify the two competing species in detail and this is done by supplying the required values. Figure F1 shows the results that can be obtained.

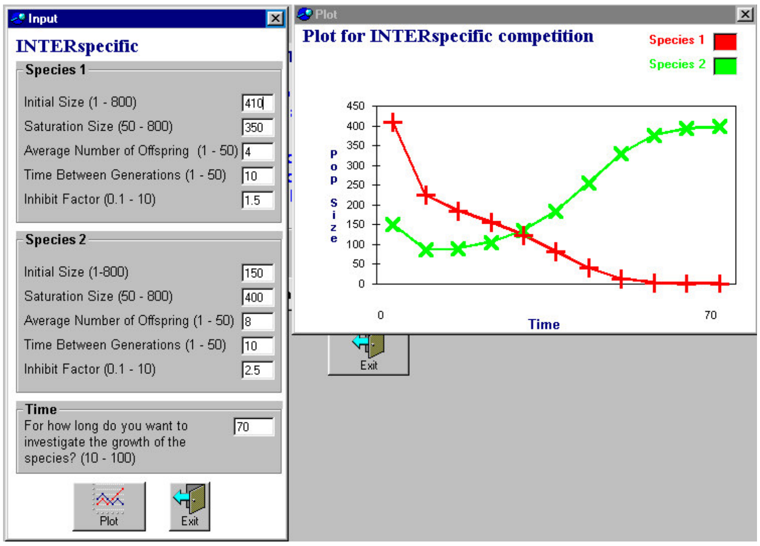

Figure F1 Screen print out from Inter-specific competition

Once the graph has been completed you might want to look at the result of the currently displayed competition over a different period of time – either longer, to see what happens later, or shorter, in order to see more detail. If so, just re-specify the time axis of the graph (*For how long do you want to investigate the growth of the species?*).

You will often want to change the values of one or a few of the factors while keeping all the others constant, just re-enter the values you want to change and click on the *Plot* button.

STUDENTS' MANUAL G – INVESTIGATIONS ON INTER-SPECIFIC COMPETITION

Four investigations are suggested in this Manual. In each, the five variables for the two competing species are set at particular values. The result, in terms of the outcome of competition, is different in each case. Your task is to formulate a general rule to explain the results. Since the saturation population, the number of offspring and the generation time should be kept constant (see below) and the same for each species, the outcome of competition clearly depends in some way on the initial populations and the inhibitory factors.

When you have formulated a general rule, use it to predict what might happen if some of the other factors are altered. Does your general rule stand up to experimental testing? Is the outcome of competition affected by altering any of these factors:

Saturation population
Number of offspring
Generation time

Start off with the following values for these three variables:

Saturation population	100
Number of offspring	4
Generation time	1

G1 *Set each inhibitory factor to 0.8. Keep the total initial population at 100, but vary the initial size of one population from 10 to 90 while the initial size of the other varies from 90 to 10. For example:*

Species	*1*	*10*	*20*	*30*	*40*	*50*	*60*	*70*	*80*	*90*
Species	*2*	*90*	*80*	*70*	*60*	*50*	*40*	*30*	*20*	*10*

What is the outcome of the competition?

G2 *Repeat G1, but with the inhibitory factor of one species set at 0.8 and that of the other at 1.2 What is the outcome of the competition?*

G3 *Repeat G1, but with the inhibitory factors reversed compared to G2 (i.e. 1.2 and 0.8). What is the outcome of the competition?*

G4 *Repeat G1, but with the inhibitory factors of each species set at 1.2. What is the outcome of the competitions?*

Remember that your task is now to formulate and test a general rule to explain these results.

STUDENTS' MANUAL H – THE MATHEMATICAL MODEL

If some quantity, N, changes during the course of time, we can say that the rate of change at any instant is dN/dt. So, if N is the size of the population, the rate of growth of the population can be expressed:

$$\text{Rate of growth} = \frac{dN}{dt}$$

Where the rate of growth is proportional to the size of the population, this can be expressed as:

$$\frac{dN}{dt} \propto N \qquad \text{.......................(1)}$$

where the symbol $\propto$ indicates proportionality. If the population was growing, this would mean that both the rate of growth and the size of the population would continue to grow indefinitely.

Clearly this equation is totally unrealistic. There is a limit to the number of organisms that a particular environment can support. This number is called the saturation population. A population may increase towards the saturation population (or decline if for some reason it is in excess of it) and the rate of change in the size of the population will tend to zero as the population approaches its saturation value. Mathematically, this can be written:

$$\frac{dN}{dt} \propto \frac{N(K-N)}{K} \qquad \text{........................(2)}$$

Where K is the saturation population, Notice that relationship (2) in the same as relationship (1), except that in (2) N is multiplied by the fraction.

$$\frac{(K-N)}{K}$$

Let us consider the effect of this change.

Suppose that N was very small, i.e. the population was nowhere near saturation level. Compared to K, we could afford to ignore the size of N. We would not introduce a very large error by writing.

$$\frac{(K-N)}{K} \text{ as } \frac{(K-0)}{K}$$

Which is equal to 1. So instead of relationship (2), we are back at relationship (1) with its unrealistically simple rate of growth.

Now, suppose that N was almost as large as K, i.e. the population was almost at its saturation level. In this case we could ignore the difference between K and N. We would not introduce a very large error by writing.

$$\frac{(K-N)}{K} \text{ as } \frac{(K-K)}{K}$$

which is equal to 0. So, the rate of growth must also be zero.

Thus relationship (2) provides us with the means of modelling population growth. When the population size is very small compared to the saturation population, the rate of growth is almost directly proportional to the population size. However, as population size approaches its saturation level the rate of growth declines until it becomes zero when the saturation population is reached. The next step is to modify relationship (2) so that it becomes an equation:

$$\frac{dN}{dt} = rN\,\frac{(K-N)}{K} \qquad \text{...........................(3)}$$

Where r is a constant for the species being modelled, called the intrinsic growth rate of the species.

The intrinsic growth rate is related to the number of offspring each organism could produce during its lifetime (R) and the mean generation time (T):

$$r = \frac{1nR}{T} \qquad \text{............................(4)}$$

where 1nR means the natural logarithm of R. Substituting for r in equation (3) we get:

$$\frac{dN}{dt} = \frac{1nR}{T} \cdot \frac{N\,(K-N)}{K} \qquad \text{.............................(5)}$$

And this is the equation upon which intra-specific competition in ***Population Dynamics & Coexistance*** is based.

In order to model inter-specific competition, equation (5) has to be modified slightly. We can consider the effect of species 2 on species 1 as being the equivalent of an increase in the number of species 1 requiring food, oxygen, etc. In other words the population is effectively nearer to its saturation level than one might suppose. This concept can be written into the equation:

$$\frac{dN}{dt} = \frac{1nR}{T} \cdot \frac{N\,(K-N-E)}{K} \qquad \text{...............................(6)}$$

Where E is the number of species 2 converted to the equivalent number of species 1 in terms of its nutrient requirement.

In inter-specific competition (as modelled in ***Population Dynamics & Coexistance***) there are two species (1 and 2) competing with each other. Each will have a rate of population growth at any instant:

$$\frac{dN_1}{dt} = \frac{1nR_1}{T_1} \cdot \frac{N_1(K_1-N_1-E_2)}{K_1} \qquad \text{............................(7)}$$

$$\frac{dN_2}{dt} = \frac{1nR_2}{T_2} \cdot \frac{N_2(K_2-N_2-E_1)}{K_2} \qquad \text{...........................(8)}$$

The terms E_1 and E_2 can be replaced by F_1N_1 and F_2N_2, where F_1 is the inhibitory factor of species 1 with respect to species 2 and F_2 is the inhibitory factor of species 2 with respect to species 1:

$$\frac{dN_1}{dt} = \frac{1nR_1}{T_1} \cdot \frac{N_1 (K_1 - N_1 - F_2N_2)}{K_1} \qquad \text{..........................(9)}$$

$$\frac{dN_2}{dt} = \frac{1nR_2}{T_2} \cdot \frac{N_2 (K_2 - N_2 - F_1N_1)}{K_2} \qquad \text{.........................(10)}$$

These are the equations upon which inter-specific competition in ***Population Dynamics & Coexistance*** is based.

STUDENTS' MANUAL I – CONDITIONS FOR EQUILIBRIUM

The rates of population growth for two species (1 and 2) competing with each other can be written:

$$\frac{dN_1}{dt} = \frac{1nR_1}{T_1} \cdot \frac{N_1(K_1-N_1-F_2N_2)}{K_1} \qquad \text{............................(1)}$$

$$\frac{dN_2}{dt} = \frac{1nR_2}{T_2} \cdot \frac{N_2(K_2-N_2-F_1N_1)}{K_2} \qquad \text{............................(2)}$$

At equilibrium the rates of growth of both species will be zero, i.e.

$\frac{dN_1}{dt} = 0$ and $\frac{dN_2}{dt} = 0$ this condition is fulfilled when:

$$(K_1-N_1-F_2N_2) = 0 \qquad \text{...........................(3)}$$

and $$(K_2-N_2-F_1N_1) = 0 \qquad \text{............................(4)}$$

Figure I1 is a graph of N_2 against N_1 when equation (3) holds true. Note that there are many values of N_1 and N_2 for which $dN_1/dt = 0$, but that two of them are:

$N_1 = 0$ and $N_2 = \frac{K_1}{F_2}$ (i.e. there is no species 1) and

$N_2 = 0$ and $N_1 = K_1$ (i.e. there is no species 2)

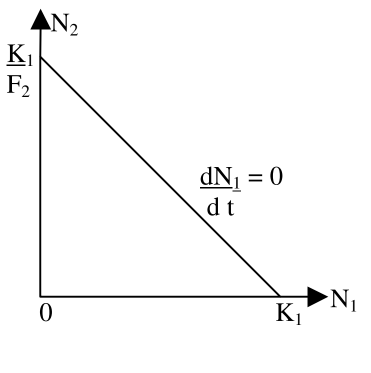

Figure I1 Equilibrium Species 1

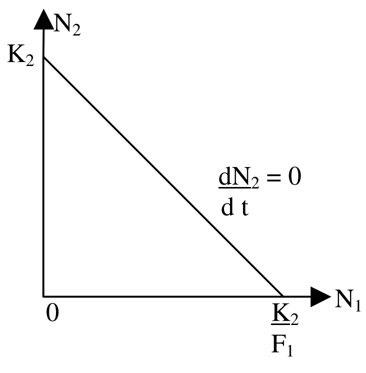

Figure I2 Equilibrium Species 2

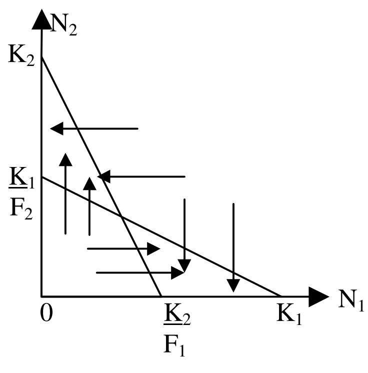

Figure I3 Case 1

Figure I2 is a graph of N_2 and N_1 when equation (4) holds true. Note that

$$\frac{dN_2}{dt} = 0,$$

when $N_2 = 0$ and $N_1 = \frac{K_2}{F_1}$ (i.e. there is no species 2) and
$N_1 = 0$ and $N_2 = K_2$ (i.e. there is no species 1).

These specific examples of equilibrium are rather trivial since they require one or other of the species to be either eliminated or never present. Can stability with coexistence of both species be achieved?

Figures I1 and I2 have the same axes and so can be superimposed. The line in each figure can have a gradient and so four different combined graphs can be obtained (Figures I3, I4, I5 and I6) depending on whether the lines cross or not, and which is above the other on the two axes. We will consider each in turn and relate it to one or other of the investigations on inter-specific competition.

Case 1 (Figure I3)

Here $K_2 > \frac{K_1}{F_2}$ and $K_1 > \frac{K_2}{F_1}$, which implies that $F_2 > \frac{K_1}{K_2}$ and $F_1 > \frac{K_2}{K_1}$

It can be seen that changes in population will favour either species 1 or species 2 depending upon the initial values of N_1 and N_2. There is unstable equilibrium.

I1 Which of the four investigations in Manual G corresponds to Case 1?

Case 2 (Figure I4)

Here $\frac{K_1}{F_2} > K_2$ and $\frac{K_2}{F_1} > K_1$ which implies that $F_2 < \frac{K_1}{K_2}$ and $F_1 < \frac{K_2}{K_1}$

All changes in population tend to equilibrium with both species coexisting. There is stable equilibrium.

I2 Which of the four investigations in Manual G corresponds to Case 2?

Case 3 (Figure I5)

Here $\frac{K_1}{F_2} > K_2$ and $K_1 > \frac{K_2}{F_1}$, which implies that $F_2 < \frac{K_1}{K_2}$ and $F_1 > \frac{K_2}{K_1}$

All changes in population tend to favour species 1, with species 2 invariably being eliminated.

I3 Which of the four investigations in Manual G corresponds to Case 3?

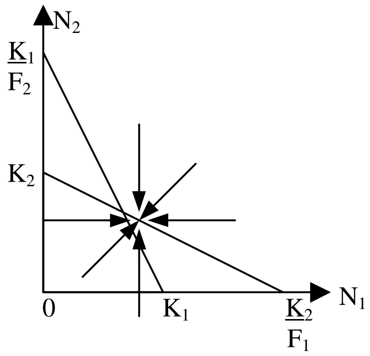

Figure I4 Case 2

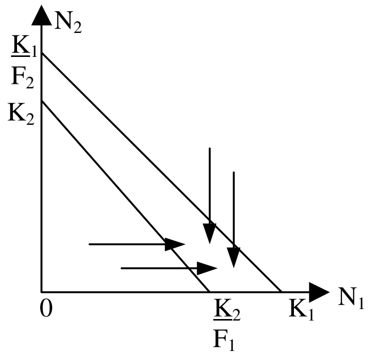

Figure I5 Case 3

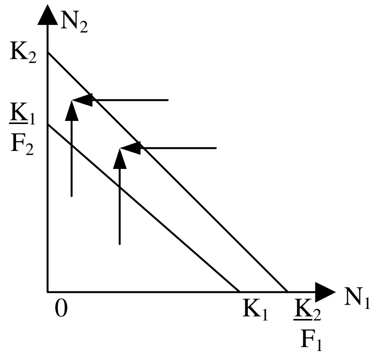

Figure I6 Case 4

Case 4 (Figure I6)

Here $K_2 > \frac{K_1}{F_2}$ and $\frac{K_2}{F_2} > K_1$ which implies that $F_2 > \frac{K_1}{K_2}$ and $F_1 < \frac{K_2}{K_1}$

All changes in population tend to favour species 2 with species 1 invariably being eliminated.

I4 Which of the four investigations in Manual G corresponds to Case 4?

STUDENTS' MANUAL J – ASSUMPTIONS OF THE MODEL

It should be obvious that there are huge differences in the levels of complexity of (a) a computer simulation such as ***Population Dynamics & Coexistance***, (b) the relatively simplified laboratory situations which are modelled by ***Population Dynamics & Coexistance***, and (c) real ecosystems, some aspects of which can be represented in the laboratory. In order to model even laboratory situations simplifying assumptions have to be made. In the case of the model ***Population Dynamics & Coexistance***, three important assumptions are made:

a. It is assumed that the organisms are living in an environment in which all the necessary resources (e.g. food, oxygen) are continuously replenished and therefore constant.

J1 What other arrangements could apply to the availability of such resources? What effects are such arrangements likely to have on the population growth curves?

b It is assumed that all the organisms respond instantly to changes in the environment.

This means that any change in, for example, reproductive rate is the result of the present state of the population and its environment and not to its history.

J2 What would be the likely effect on the population growth curves of relaxing this assumption? In general terms, what would have to be built into the model if changes in the environment were not to have instant effect?

c It is assumed that the generations are discrete, i.e. each generation dies out immediately it reproduces itself, leaving its offspring as the next generation.

This means that no account need be taken of the population's age structure.

J3 What effect would overlapping generations be likely to have on the response time of populations of different species competing with one another? In general terms, what changes to the model would have to be made in order to accommodate age structure?

J4 Apart from the three features of the model discussed above, what differences exist between the model **Population Dynamics & Coexistance** *and real ecosystems?*