

Chapter 3

Population Dynamics

3.1 The growth of single-species populations

We will now begin our first in depth consideration of a particular biological problem — the dynamics of how populations of organisms vary over time. Before delving into the discussion of mathematical models of such systems, it is worthwhile outlining the basic underlying biology. That is, how do species reproduce, and how do populations of species grow over time?

3.1.1 The biology of population growth

Different types of organisms have different modes of reproduction, and can differ fundamentally in qualitative patterns of population growth. Single-celled organisms reproduce primarily through asexual cell division. In some cases, such as bacteria and fission yeast, the cell division is largely symmetric — a single parent cell gives rise to two nearly identical offspring cells. In this case, it is impossible to identify one of the two offspring as being any more the “parent” than the other. In other cases, as in budding yeast, the cell division process is asymmetric — a smaller daughter cell is produced by “budding” off the parent cell. Here it is obvious from visual inspection which cell is the “parent” and which is the “child”. Regardless of which mode of division the cells follow, however, these organisms tend to grow and divide continuously as long as there are adequate resources (nutrients, space, *etc.*). This growth can be quite fast — *E. coli* bacteria can divide (and thus double the population) every 20 minutes under ideal conditions, and the yeast *S. cerevisiae* can double in population in roughly 2 hours. Under suboptimal conditions, however, this growth can be significantly reduced, or even halted completely.

What about other organisms? Multi-cellular organisms often have quite complicated life-cycles, involving multiple, distinct stages. Additionally, the life cycle is often coupled to particular periods of time. For example, many insects hatch from eggs to a larval stage, after sometime living as larvae — generally eating large amounts — they enter a pupal stage, in which the larvae remain in protective shells while developing into the adult form. The adults emerge from the pupae, mate and lay eggs. Often the adults eat minimally, existing primarily to lay eggs for the next generation. In house flies, the cycle is quite fast, with eggs hatching in as little as 1/2 a day, the larval and pupal stages lasting about 4 and 6

days respectively, and adults living perhaps two weeks. Each adult lays about 100-200 eggs several times, and thus can lay as many as 500 eggs before death. The times for hatching, larval growth, and time spend in the pupae are greatly affected by temperature, and can be lengthened as much as four-fold under sub-optimal conditions. So long as temperatures permit, each generation will continue through repeated cycles of reproduction. Horse flies (a biting fly) undergo a similar process with a larval and pupal stage, but with generations that are generally annual — eggs are laid in spring or summer, and hatch in about a week, but the larval stage lasts all year, and the pupal stage does not begin until the next year (lasting again about a week). The adults only live several weeks, during which time they lay the eggs of the next generation. Since most larvae enter the pupal stage at very close times (depending on the environmental conditions), the adults of a given species are only found during perhaps one month. This results in a discrete, step-wise growth each year, with a defined period of time when the adult population can be counted. Many other insects follow one or another of these life cycles — continuously cycling through generations, or following clear annual patterns. Not all go through a larval stage, but rather grow through several stages of an immature form known as a nymph or instar.

Some species of fish also follow live cycles in which reproduction is limited to a short period of time, shortly followed by death. For example, salmon eggs are laid in fresh water streams; after hatching, the fry may remain in the freshwater environment from as little as a few days (Chinook) to a year (Coho) or more depending on species; the smolt (as the are then called) travel downstream to the ocean, at which point they are considered adult; adults remain in the ocean for 1-7 years, depending on many factors, not only species. Ocean-living adult salmon do not reproduce, but eventually return to freshwater to lay eggs (spawn), after which they nearly immediately die. Amazingly, each adult salmon returns to the same stream from which it hatched! Other species of fish, however, will spawn each year, and even many times each year. Carp, for example, will continue spawning so long as the temperature and nutrition of the water is adequate, and will do so throughout a lifespan that can be as long as thirty years.

Most birds and reptiles have annual breeding patterns in which eggs are laid at a particular time of year, typically spring; many birds additionally have migratory patterns with separate spring/summer habitats and wintering grounds. Many larger land mammals also have well-defined mating and birthing seasons, typically timed around gestation, so that young are born during a season of plenty (spring in temperate climates). Smaller mammals, however, often will continuously breed while the environment is suitable; rabbits, for example, give birth roughly one month following breeding, and are immediately able to breed again. Humans, of course, have essentially completely decoupled their breeding habits from the seasons, and thus may be considered a continuously reproducing population.

Plants also can be divided into various growth classes, with some reproducing continuously and others tied very closely to annual cycles. Additional, some plants die immediately after bearing fruit, while others can grow for years (even hundreds of years for some species), and reproduce each year.

3.1.2 Models of continuously reproducing species

First, let's consider the growth of a species that reproduces continuously, such as single-celled organisms, humans, and certain plants and animals in tropical and sub-tropical climates. We will consider an initial time ($t = 0$) at which time the population is N_0 ; after some amount of time (τ), the population will double to $2N_0$. If the growth continues at a constant rate (per organism), then after waiting the same period of time (τ), the population will again double, but from $2N_0$, giving a new population of $4N_0$. After a third period of τ , the population will again double, this time to $8N_0$. We can describe this growth in terms the population at an arbitrary time:

$$N(t) = N_0 2^{\frac{t}{\tau}} \quad (3.1)$$

where τ is called the “doubling time”.

It seems intuitively reasonable to think of the growth of a population being well described by a doubling time. In single celled organisms, this would be the average time between cell-divisions, each of which creates two cells from one. In other populations, it would represent the average time it takes for an individual organism to produce an offspring. However, organisms also die, and thus we must take this into account. First, let's consider a population that does not reproduce, and thus the only changes in its size are due to death. It may be reasonable to assume a constant *per capita* death rate; this is equivalent to stating that at any given point in time, each individual, on average, has the same chance of dying. While there may be differences between mortality at different ages, if the population structure (distribution of ages) does not change over time, the average should remain constant. Such a model can be described simply by:

$$\frac{dN}{dt} = -\gamma N \quad (3.2)$$

where γ is the *per capita* death rate, and N is the number of individuals in the population. This is in the form of a differential equation, while the growth equation was written explicitly, so how might we combined them? First, note there is only one function whose derivative is equal to the function itself — this provides us with the solution to the differential equation above. Consider:

$$N(t) = N_0 e^{-\gamma t} \quad (3.3)$$

taking the derivative gives:

$$\frac{dN}{dt} = -\gamma N_0 e^{-\gamma t} = -\gamma N(t) \quad (3.4)$$

which is precisely the form we began with. Thus, we see that assuming a constant death rate leads to exponential decay, just as a constant growth rate leads to constant growth. Now, we initially wrote the growth equation in powers of two, since we used a doubling time, but we can easily convert this to an exponential in e , by noting that:

$$e^{(\ln 2)\frac{t}{\tau}} = \left(e^{\ln 2}\right)^{\frac{t}{\tau}} = 2^{\frac{t}{\tau}} \quad (3.5)$$

Thus:

$$N(t) = N_0 2^{\frac{t}{\tau}} = N_0 e^{(\frac{\ln 2}{\tau})t} = N_0 e^{\beta t} \quad (3.6)$$

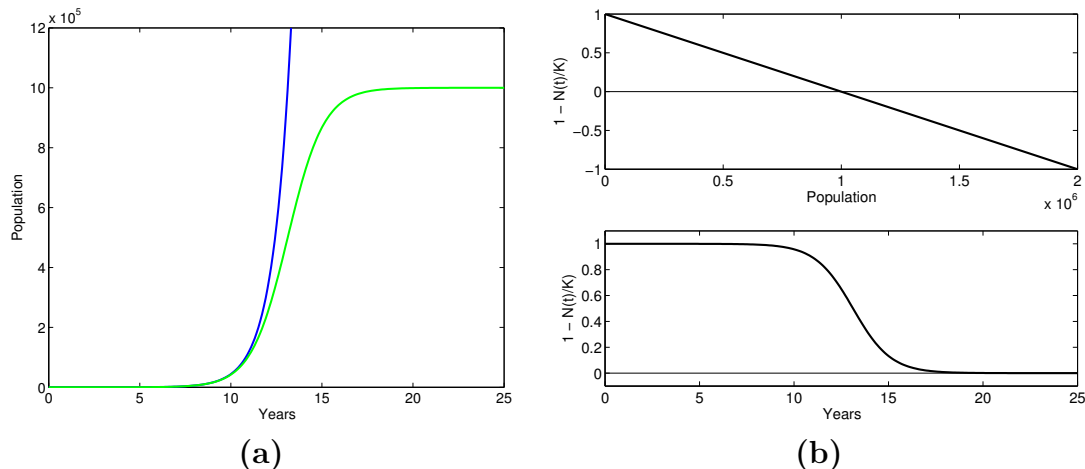


Figure 3.1: Population growth in a continuously-reproducing species. (a) While exponential growth (blue) continues unrestricted, logistic growth (green) is limited to a maximal capacity. (b) In logistic growth, the growth rate is scaled by a factor linearly dependent on population; over time, this scaling factors varies sigmoidally.

with $\beta = \frac{\ln 2}{\tau}$, and

$$\frac{dN}{dt} = \beta N_0 e^{\beta t} = \beta N(t) \quad (3.7)$$

This is the same form as the death model, where β thus describes the *per capita* growth (birth) rate. Now, in real populations, the *per capita* change will given by the difference between the growth and death rates:

$$\frac{dN}{dt} = \beta N(t) - \gamma N(t) = (\beta - \gamma)N(t) \quad (3.8)$$

Defining an *observed* growth rate of $R_o = (\beta - \gamma)$, this gives:

$$\frac{dN}{dt} = R_o N(t) \quad \rightarrow \quad N(t) = N_0 e^{R_o t} \quad (3.9)$$

So long as growth exceeds death ($\beta > \gamma$), the population will grow exponentially, and any time death exceeds growth ($\gamma > \beta$), the population will decay exponentially.

However, the observed behavior for most populations does not follow the predictions of this models. Even in highly-controlled environments, such as growth of bacteria or yeast in a lab fermenter, while exponential growth is observed at (relatively) low populations, the observed growth rate slows, and ultimately stops, at large populations. Why does this happen? Quite simply, the environment has a limited capacity, and can only support some maximal population size; the limits may be due to nutrition, physical space, energy, or other requirements.

When trying to develop or refine a model based on experimental observations, there are two basic approaches that can be taken. The first approach is to try to consider the underlying biology in more detail, and form a model based around this theory. The second is to make repeated observations, and try to fit a general, but reasonable, function to the

observed data. The first approach is clearly a more elegant approach, but can be very complicated. How does the observed growth rate slow with population density? Is the reproduction rate reduced, is the death rate increased or is it both? What is the expected form of these responses? Even if these questions could be answered, we would be left with an effective growth rate (R_o) that varies as a function of population, which is in turn a function of time:

$$\frac{dN}{dt} = R_o(N(t))N(t) \quad (3.10)$$

For most forms of $R_o(N(t))$, this will become very complicated to deal with. The second approach tries to choose a form of the equation based on the observed data, rather than on expectations about biological mechanisms. For example, consider the **logistic equation**:

$$\frac{dN}{dt} = R_o N(t) \left[1 - \frac{N(t)}{K} \right] \quad (3.11)$$

which corresponds to a model where the observed growth rate is given by the *non-limited* growth rate, scaled by the factor in brackets. This equation gives the desired qualitative behavior:

- When N is small, $\frac{dN}{dt} \approx R_o N(t)$, since $\left[1 - \frac{N(t)}{K} \right] \approx 1$ — that is, at small populations, growth is roughly exponential.
- When $N \approx K$, $\frac{dN}{dt} \approx 0$, since $\left[1 - \frac{N(t)}{K} \right] \approx 0$ — when the population is at its capacity (K), there is zero effective growth and the population is constant.
- When $N \gg K$, $\frac{dN}{dt} \ll 0$ — if a population is placed in an environment with a capacity much lower than its size, the population will decay until it reaches capacity. [Aside: One might note, however, that the decay is *not* exponential in form.]

The logistic equation can be integrated to give:

$$N(t) = \frac{K N_0 e^{R_o t}}{K - N_0 + N_0 e^{R_o t}} \quad (3.12)$$

and gives good agreement with growth in idealized laboratory conditions.

3.1.3 Models of discretely reproducing species

What about species that reproduce with a clear annual cycle, like horse flies, robins, or caribou? A differential equation, which describes the gradual population change over time, seems to be poorly suited to these dynamics. Rather it may seem more reasonable to count the population at a particular time of year (say, the number of breeding adults in mating season), and then describe the equivalent population at the same time the next year in terms of the current population. Presume that each adult will produce, on average, β new adults by the next season, and that each adult has a chance of dying before the next season given by γ . Note that β is not simply the birth rate, as it describes the number of offspring that survive to adult-hood; in some species (such as fish), millions of eggs may be laid, with very

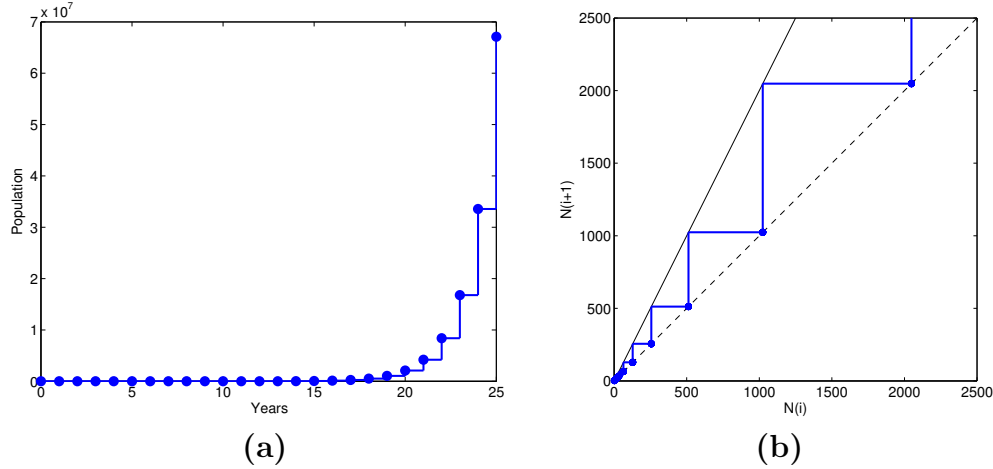


Figure 3.2: Population growth in a discretely-reproducing species. (a) The population grows exponentially over time, but in a step-wise fashion; (b) The growth dynamics can be understood by considering movement between the two curves on the $N(i+1)$ and $N(i)$ -plane: one describing the difference equation and the other corresponding to $y = x$.

few surviving to adult-hood. Given this model, the population in the next year, N_{n+1} , will be the population this year, N_n , plus the number of new adults to survive, minus the number of existing adults to die:

$$N_{n+1} = N_n + \beta N_n - \gamma N_n = (1 + \beta - \gamma)N_n = R_o N_n \quad (3.13)$$

where again, $R_o = (1 + \beta - \gamma)$ is the observed *per capita* growth rate. This sort of relationship, with a discrete future point described in terms of the current point, is called a *difference equation* relationship (as opposed to a differential equation).

This relationship also describes an exponential growth pattern, but the growth occurs in fixed intervals, rather than continuously — a plot of N versus time will have a step-like profile. The dynamics of difference equations can often be understood through the analysis of a plot of N_{n+1} vs N_n . Two curves are plotted: that of the difference equation of interest and the line of $y = x$; successive generations can be represented by steps between these two curves. That is, given a population N_0 , the next population is given by moving vertically from N_0 to the N_{n+1} curve, this begins the new “current” population, by a horizontal movement to $y = x$, defining N_1 . A second vertical motion to the N_{n+1} curve, followed by a horizontal movement back to $y = x$, gives N_2 , and so on. Given the above equation, we see a step-like pattern between two lines of different slope; the increasing step-size as we move up in N corresponds to the exponential growth with time, since each interval is a constant time period.

Now, we have already discussed how unlimited exponential growth is an unreasonable model for real biological systems. However, when many offspring are produced essentially at once, the competition for limited resources can be very different than in the case of continuous growth, where rates can gradually adjust to the available resources. There are two extreme models for competition between individuals in a locked reproduction cycle:

Contest competition: in this model, there are a fixed number of resources slots, N_c , such

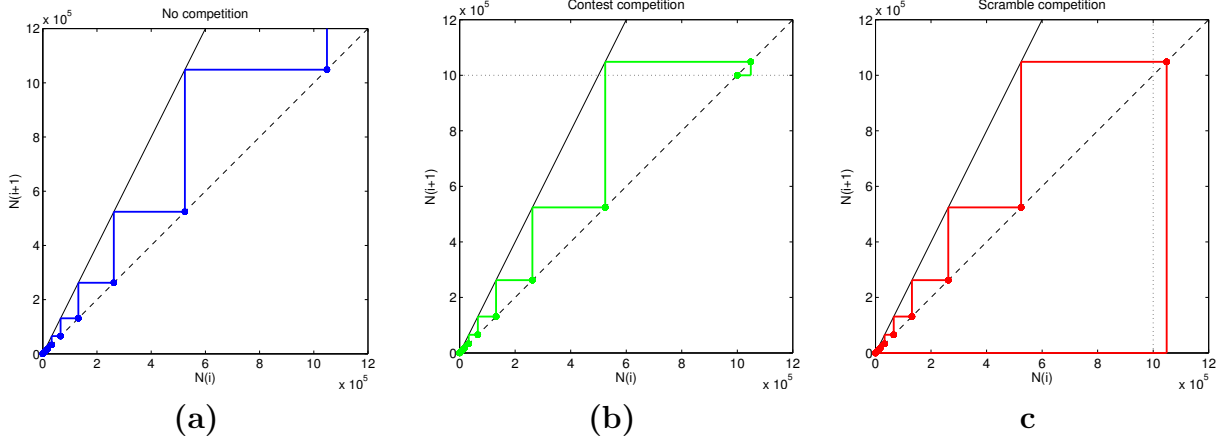


Figure 3.3: Resource-limited growth in a discretely-reproducing species. (a) Lack of competition leads to unrestricted growth; (b) Contest competition leads to a stable population size; (c) Scramble competition leads to extinction.

as suitable nesting sites. These are “easy to find” in the sense that all are always filled, but limited in number. Only those individuals that win the “contest” for these slots are able to reproduce. This gives the following difference equation relation:

$$N_{n+1} = \begin{cases} R_o N_n & \text{if } N_n \leq N_c \\ R_o N_c & \text{if } N_n > N_c \end{cases} \quad (3.14)$$

The population will thus plateau at a value of $R_o N_c$. Depending on how individuals are counted, and exactly when in the life cycle the slots are required for survival, the limiting equation may be replaced with $N_{n+1} = N_c$. In this case, we would define the population plateau at N_c .

Scramble competition: In the second model, there is a finite amount of a “shareable” resource (such as food), and all individuals are equally competitive in obtaining the resource. In other words, every individual gets an equal share of the resources. If this share is adequate for survival to reproduction, then all individuals survive and reproduce, but if the share is inadequate, then all individuals die without being able to reproduce. This gives a difference equation description of:

$$N_{n+1} = \begin{cases} R_o N_n & \text{if } N_n \leq N_c \\ 0 & \text{if } N_n > N_c \end{cases} \quad (3.15)$$

where N_c here describes the maximal number of individuals that the environment can successfully support. In this model, the population will increase until it exceeds N_c , at which point it will fall to zero (*i.e.* become extinct).

While the basic concepts in these models make sense, the implementation makes them too extreme. More realistically, one may expect contest competition to increase more smoothly — the greater the population, the harder it becomes to find “habitat” slots, some of which may be sub ideal. Thus, while at low populations, every individual successfully achieves a

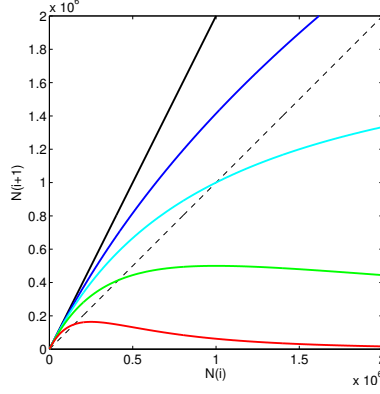


Figure 3.4: The Hassel equation with varying exponent. Black: $b=0.0$ (unlimited growth); blue: $b=0.5$; cyan: $b=1.0$ (exact compensation); green: $b=2.0$; red: $b=5.0$.

resource slot, when populations are close to the environmental capacity, some individuals will not successfully compete, and a small number of slots may remain unoccupied. Similarly, some individuals that find a (sub ideal) habitat may not successfully reproduce. The result should be a smoothing of the difference equation curve, while it still plateaus at a maximal capacity.

Similarly, scramble competition is very unlikely to lead to a *zero* reproducing population. Some individuals will compete more successfully, and thus even with populations that greatly exceed the carrying capacity of the environment, a small number of individuals may survive to reproduce. Again, the result is a smoother transition in the difference equation curve, as well as a long tail that asymptotically approaches zero, but never reaches it.

Again following the idea of finding a model functional form that describes the observed behavior, we introduce the Hassel equation:

$$N_{n+1} = \frac{R_o N_n}{(1 + a N_n)^b} \quad (3.16)$$

where a and b are positive constants. When $b = 0$, the Hassel equation simply becomes the difference equation for unlimited exponential growth, $N_{n+1} = R_o N_n$. When $b = 1$, we obtain a smoothed version of contest competition. Consider the limit of this curve when N_n becomes very large:

$$\lim_{N_n \rightarrow \infty} \frac{R_o N_n}{(1 + a N_n)} = \frac{R_o N_n}{a N_n} = \frac{R_o}{a} \quad (3.17)$$

Thus, we see that there is a finite, non-zero population that the population stabilizes to. If this population is denoted N_c , then $a = \frac{R_o}{N_c}$. The stable limit in population is reached because, as the population becomes large, the population loss due to competition for resources perfectly balances the reproduction rate (in the absence of competition). Thus, we say that the system displays **exact compensation**.

When $0 < b < 1$, there is a reduction in reproductive efficiency with increasing population, but it never is enough to fully balance the effect of increasing numbers of reproducing individuals, and thus the population still grows without bound (albeit at an ever-decreasing rate). These systems display **under-compensation**. When $b > 1$, the Hassel equation

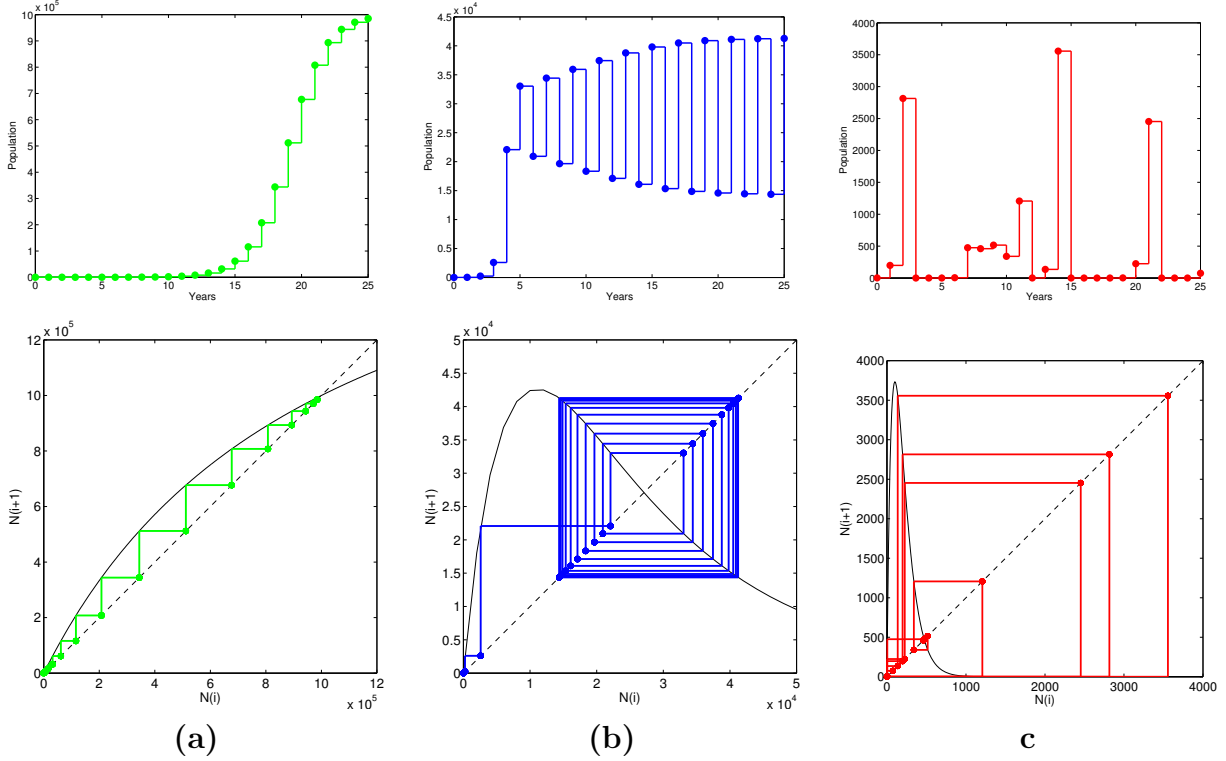


Figure 3.5: Resource-limited growth under the Hassel equation. (a) Exact compensation leads to a stable population size; (b) Moderate over-compensation leads to stable oscillations in population; (c) Extreme over-compensation leads to chaotic fluctuations.

describes systems with **over-compensation** — the loss of reproductive efficiency at large populations is such that it causes a reduction in the population beyond that imposed by the environmental capacity. The long term behavior of these systems, however, depends on the degree of over-compensation. At relatively low levels, the population is still able to achieve a stable population size; while approaching this stable point, the system oscillates between values that are slightly too high, and slightly too low, but the oscillations become smaller and smaller as generations progress. At moderate levels of over-compensation, the system still oscillates between values that are above and below the environmental capacity, but these oscillations continue with fixed magnitude — we say that the system is **oscillatorily stable**. At even higher levels of over-compensation, the system begins to oscillate with varying magnitude and period — there are dramatic variations in population from cycle to cycle — and at particularly high levels, the system descends into chaos, with the population from year to year fluctuating wildly in an impossible to predict manner.

Such great fluctuations would seem to run counter to evolutionary pressures to maintain the species, as any time the population drops to particularly low levels, it is susceptible to extinction from relatively minor adverse conditions. Thus, it is not surprising that in fits of the Hassel equation to most natural populations, the dynamics fall well within the stable or stable oscillatory region of the equation parameters.

3.2 Population dynamics in mixed-species groups

The previous section focused on the dynamics of the population of a single species, living and reproducing in isolation from any others. However, in the natural world, all organisms interact with other species in various ways. Again, let's begin by considering the biology of inter-species interactions; these can be broadly classified into four types: predation/parasitism, mutualism/symbiotism, commensalism, and competition.

3.2.1 The biology of inter-species interactions

Predation involves the consumption of one species by another. As a result, the *growth* (and reproductive fitness) of the predatory species is directly linked to the *reduction* of the prey species. This class of interaction includes classical predator-prey relationships (such as the interaction between foxes and rabbits, or between lions and zebra), but other types of interaction share similar characteristics. For example, *parasites* exert a negative effect on their host (thus reducing their reproductive fitness), while their own growth is increased. In some cases, the parasitic infection results in the death of the host (as is the case for many infections of insect larvae by parasitic flies and wasps), while in other instances death of the host is not assured (infections of mammalian hosts by similar parasitic flies can lead to open wounds that may heal, but may become infected and lead to death; diseases such as malaria and sleeping sickness are caused by single-celled parasitic organisms, and can have significant recovery rates).

Interactions between herbivorous species and the plants they consume can be more difficult to assess. In some cases, the interactions are clearly predator-prey-like — the consumption of plants by locusts during a swarm is a good example. Does the consumption of grass by grazing animals follow the same pattern, though? Certainly the biomass of the grass is reduced by consumption, but is the reproductive fitness of the grass reduced? In some cases, it could be increased! Additionally consider a fruit-eating animal — in many cases, the consumption of fruit directly enhances the reproductive fitness of the plant by distributing seeds and fertilizing them with dung. Since the biomass of a fruiting tree is minimally impacted by the eating of its fruit, the growth of both organisms is enhanced by the interaction. This type of positive interaction between species is referred to as **mutualism**. Many examples of cooperative interactions between species can be found — oxpecker birds which feed on parasitic insects on the hides of grazing animals, and bacteria which reside in the digestive tracks of mammals (and aid in digestion of some foods) are good examples. When the cooperative interaction is so ingrained in the life cycles of the organisms that they physically interact for extended periods we refer to them as *symbionts* — lichen are a symbiotic relationship between a fungus and algae.

In between these two extremes, there are interactions where one species benefits while the other is neither harmed nor benefits; this is referred to as **commensalism**. A good example is the nesting of birds in particular tree species. While we may categorize the interactions of species into these groups, it is important to remember that there is a continuum of degrees in all interactions. Thus, we may consider the effect on one organism ranging from highly negative (resulting in immediate death in the extreme), through weakly negative (bordering on commensalism), to weakly positive, and finally to highly positive. When the effects are

relatively small, it can be difficult to determine whether an interaction is truly commensal in the ideal sense.

In all the cases we have discussed above, one species always benefited from the interaction. However, we also may have interactions in which both species interfere with the growth and reproductive fitness of the other, a situation we refer to as **competition**. Competition may take many forms: there may be direct competition for food (seals and salmon both prey on herring, many grassland antelope have similar diets); there may be competition for energy (as in the competition for sunlight in forests or other areas of dense growth); and there may be competition for habitat (many small animals have similar preferences for nesting sites).

3.2.2 Developing models of predatory-prey relationships

In developing mathematical models of systems in which species interact, we will begin with our understanding of how individual, isolated populations behave, and add terms to our model that describe the interaction between the species. As the biology of predator-prey relationships is easy to understand, we will begin with these systems. One of the earliest (and simplest) models is the Lotka–Volterra model that was briefly discussed earlier.

The Lotka–Volterra model begins with very simple descriptions of isolated growth/decay:

- **Prey** (in the absence of predators) grow exponentially:

$$N_{prey}(t) = N_{prey,0}e^{+R_{prey,0}t} \quad (3.18)$$

$$\frac{dN_{prey}}{dt} = +R_{prey,0}N_{prey,0}e^{+R_{prey,0}t} = +R_{prey,0}N_{prey}(t) \quad (3.19)$$

- **Predators** (in the absence of prey) will die off exponentially:

$$N_{pred.}(t) = N_{pred.,0}e^{-R_{pred.,0}t} \quad (3.20)$$

$$\frac{dN_{pred.}}{dt} = -R_{pred.,0}N_{pred.,0}e^{-R_{pred.,0}t} = -R_{pred.,0}N_{pred.}(t) \quad (3.21)$$

Note that the intrinsic growth/death rates are taken to be positive by convention; thus growth is described with a positive coefficient, and decay by a negative. Now let's consider the assumptions we will make in describing the interaction:

- The *per capita* **predation rate** is linear in the prey population; that is, a given predator will kill prey in proportion to how many prey are available.
- Predators do not compete for prey, and thus the predation rate is linear in the predator population; predation is perfectly described by a *per capita* predation rate.

These assumptions lead a description of the predation rate by $\gamma N_{prey}(t)N_{pred.}(t)$, which gives an overall rate of change of the prey population of:

$$\frac{dN_{prey}}{dt} = +R_{prey,0}N_{prey}(t) - \gamma N_{prey}(t)N_{pred.}(t) \quad (3.22)$$

where γ is the predation constant. Additionally, we presume that predator growth (reproductive rate) is directly proportional to the predation rate. In other words, the more prey that are killed, the more that the predators reproduce. This gives a description of the predator population change as:

$$\frac{dN_{pred.}}{dt} = \epsilon\gamma N_{prey}(t)N_{pred.}(t) - R_{pred.,o}N_{pred.}(t) \quad (3.23)$$

ϵ is a constant that describes the relationship between the predation rate and predator growth. Note that this is the same form as we discussed before.

Now that we have a model, we can begin to analyze what we expect for the dynamics of the system. To do so, we first consider the stationary points of the system. First, we will simplify the notation by the following substitutions:

$$U = N_{prey}(t) \quad V = N_{pred.}(t) \quad \alpha = R_{prey,o} \quad \beta = R_{pred.,o} \quad (3.24)$$

giving:

$$\begin{aligned} \frac{dU}{dt} &= \alpha U - \gamma UV \\ \frac{dV}{dt} &= \epsilon\gamma UV - \beta V \end{aligned} \quad (3.25)$$

The stationary points are defined by setting both equations to zero:

$$\begin{aligned} \alpha U - \gamma UV &= 0 \\ \epsilon\gamma UV - \beta V &= 0 \end{aligned} \rightarrow \begin{aligned} \epsilon\alpha U - \epsilon\gamma UV &= 0 \\ \epsilon\gamma UV - \beta V &= 0 \end{aligned} \rightarrow \epsilon\alpha U - \beta V = 0 \rightarrow \epsilon\alpha U = \beta V = 0 \rightarrow V = \frac{\epsilon\alpha}{\beta}U \quad (3.26)$$

where we have scaled the first equation, then added the equations together, and rearranged the result. We can then substitute this result into the first equation:

$$\alpha U - \gamma UV = 0 \rightarrow \alpha U - \gamma U \left(\frac{\epsilon\alpha}{\beta} U \right) = 0 \rightarrow \alpha U \left(1 - \frac{\gamma\epsilon}{\beta} U \right) = 0 \quad (3.27)$$

Thus we have two possible solutions for U :

$$U = 0 \quad 1 - \frac{\gamma\epsilon}{\beta} U = 0 \rightarrow U = \frac{\beta}{\epsilon\gamma} \quad (3.28)$$

Substituting for V gives:

$$V = \frac{\epsilon\alpha}{\beta} 0 = 0 \quad V = \frac{\epsilon\alpha}{\beta} \frac{\beta}{\epsilon\gamma} = \frac{\alpha}{\gamma} \quad (3.29)$$

Thus our two stationary points are:

$$(U, V) = (0, 0) \quad (U^*, V^*) = \left(\frac{\beta}{\epsilon\gamma}, \frac{\alpha}{\gamma} \right) \quad (3.30)$$

We have found that the system has two stationary points, but are they stable or unstable? There are two approaches to answering this question. The first is a qualitative assessment using the **null clines** of the system. A null cline is a line corresponding to one of the

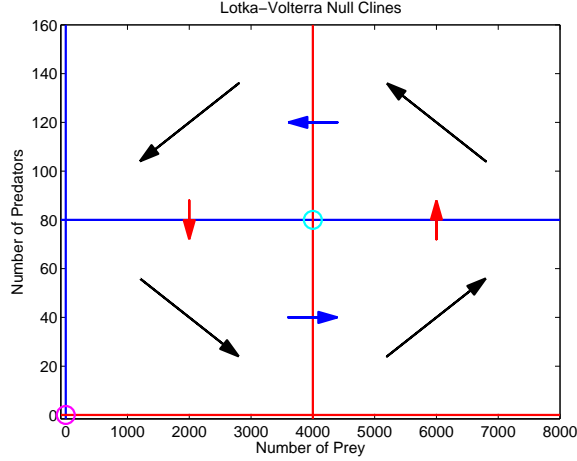


Figure 3.6: Null cline analysis of the Lotka–Volterra model. Blue lines indicate prey null clines, and red lines predator null clines; two stationary points exist at the intersection of these. The general direction of motion is indicated by the arrows.

velocity equations being equal to zero; we thus define a set of null clines for each variable in the system. In this system, for U :

$$\frac{dU}{dt} = \alpha U - \gamma UV = U(\alpha - \gamma V) = 0 \quad (3.31)$$

giving two solutions:

$$U = 0 \quad \text{or} \quad \alpha - \gamma V = 0 \rightarrow V = \frac{\alpha}{\gamma} \quad (3.32)$$

Similarly, for V :

$$\frac{dV}{dt} = \epsilon\gamma UV - \beta V = V(\epsilon\gamma U - \beta) = 0 \quad (3.33)$$

again giving two solutions:

$$V = 0 \quad \text{or} \quad \epsilon\gamma U - \beta = 0 \rightarrow U = \frac{\beta}{\epsilon\gamma} \quad (3.34)$$

Now, what information do the null clines provide? First, we note that a stationary point (requiring *all* velocities to be zero), correspond to the *intersection* of the null clines of each variable. Taking the first null cline for U , we find an intersection with the V null cline of $V = 0$, but no intersection with $U = \frac{\beta}{\epsilon\gamma}$. Taking second null cline of U , $V = \frac{\alpha}{\gamma}$, we get no intersection with the V null cline of $V = 0$, but we do have an intersection with $U = \frac{\beta}{\epsilon\gamma}$. These intersections are consistent with the stationary points that we derived earlier. Null clines provide much more information than this, however. If we consider only the direction of motion along a given variable (that is, the sign of the velocity), we note that the direction of motion can only change when crossing a null cline — a continuous variable can not change sign without crossing zero (the Mean Value Theorem). This property allows us to *qualitatively* describe the direction of motion in each region of space delineated by the null clines.

As neither U nor V can take negative values (they represent populations, and negative populations do not make physical sense), we can largely ignore the $U = 0$ and $V = 0$ null clines. Considering the null cline of U defined by $V = \frac{\alpha}{\gamma}$, we find that:

$$\text{if } V > \frac{\alpha}{\gamma} \rightarrow \gamma V > \alpha \quad \therefore \quad \alpha(U) - (\gamma V)(U) < 0 \quad (3.35)$$

and conversely:

$$\text{if } V < \frac{\alpha}{\gamma} \rightarrow \gamma V < \alpha \quad \therefore \quad \alpha(U) - (\gamma V)(U) > 0 \quad (3.36)$$

Thus, in a plot of V versus U , $\frac{dU}{dt}$ is negative above the line of $V = \frac{\alpha}{\gamma}$ and positive below it; the system moves to the right (higher U) when V is low, and to the left (lower U) when V is high. Moving onto the null cline of V , defined by $U = \frac{\beta}{\epsilon\gamma}$, we similarly find that:

$$\text{if } U > \frac{\beta}{\epsilon\gamma} \rightarrow \epsilon\gamma U > \beta \quad \therefore \quad (\epsilon\gamma U)(V) - \beta(U) > 0 \quad (3.37)$$

and:

$$\text{if } U < \frac{\beta}{\epsilon\gamma} \rightarrow \epsilon\gamma U < \beta \quad \therefore \quad (\epsilon\gamma U)(V) - \beta(U) < 0 \quad (3.38)$$

That is, $\frac{dV}{dt}$ is positive to the right of the line $U = \frac{\beta}{\epsilon\gamma}$ (in a plot of V vs U), and negative to the left; the system moves upwards (higher V) at large U , and downwards (lower V) at low U . We thus find that there are for qualitatively distinct regions of motion, separated by the null clines:

- at low U and V , V decreases while U increases
- at low V , but high U , U and V both increase
- at high V and U , V increases while U decreases
- at high V but low U , both U and V both decrease

Graphically, this suggests that the dynamics of the system correspond to an orbit around the stationary point.

Let's briefly return to the biology, and consider what these four qualitative regions represent:

- When both predator and prey populations are low, the predator population decreases while the prey population increases. This makes sense, since with low prey populations, the predator population lacks resources for growth, while the prey population is free to increase with limited predation.
- When the predator population is low, but prey populations have grown to a large value, the predator population will increase, as food (prey) is now abundant; since predators are still rare, the prey population will continue to rise.

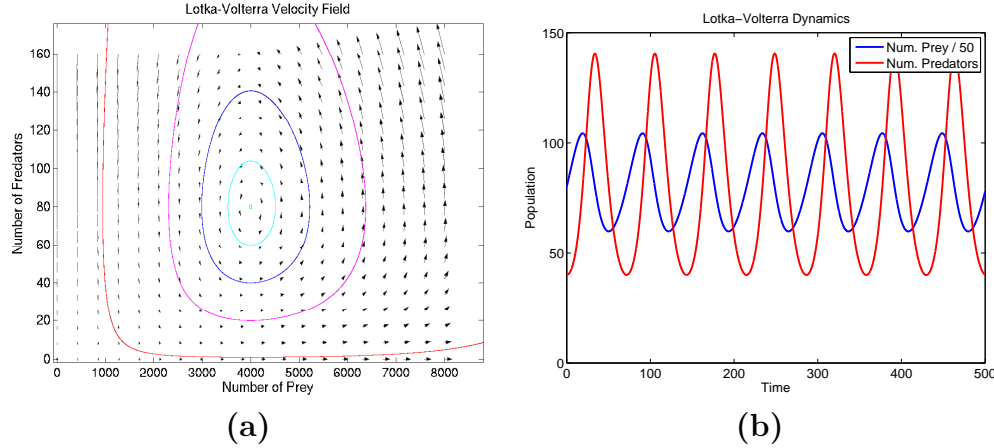


Figure 3.7: Dynamics of a Lotka–Volterra system. (a) The velocity field and sample trajectories; (b) Population dynamics as a function of time for one trajectory.

- When the predator population reaches a large value (with prey also abundant), the increase in predation rate will lead to a decrease in prey populations. As resources for predators remain ample, the predator population will continue to grow.
- Finally, as prey populations drop to low values due to predation, the predator population will fall due to lack of resources. While the predator population remains significant, the prey population will also continue to fall.
- This will return both populations to low values, and the cycle begins again.

The oscillatory pattern suggested by the mathematical analysis can be interpreted in a straightforward manner with respect to the underlying biology.

Note: The following discussion of Jacobian matrices is somewhat beyond the level of mathematics assumed for the class. While all students should read this section and make their best attempt to understand it, a mastery of all the details is not necessary. We can also characterize the motion around each stationary point by asking the question of how do $\frac{dU}{dt}$ and $\frac{dV}{dt}$ vary if U and V are shifted slightly from the stationary points. This corresponds to taking the *partial derivative* of $\frac{dU}{dt}$ and $\frac{dV}{dt}$ with respect to U and V :

$$\begin{aligned}
 \frac{\partial}{\partial U} \left(\frac{dU}{dt} \right) &= \frac{\partial}{\partial U} (\alpha U - \gamma UV) = \alpha - \gamma V \\
 \frac{\partial}{\partial V} \left(\frac{dU}{dt} \right) &= \frac{\partial}{\partial V} (\alpha U - \gamma UV) = -\gamma U \\
 \frac{\partial}{\partial U} \left(\frac{dV}{dt} \right) &= \frac{\partial}{\partial U} (\epsilon \gamma UV - \beta V) = \epsilon \gamma V \\
 \frac{\partial}{\partial V} \left(\frac{dV}{dt} \right) &= \frac{\partial}{\partial V} (\epsilon \gamma UV - \beta V) = \epsilon \gamma U - \beta
 \end{aligned} \tag{3.39}$$

The **Jacobian matrix** for the system is a matrix of these partial derivatives, constructed by assigning each *row* to either $\frac{dU}{dt}$ or $\frac{dV}{dt}$ and each *column* to $\frac{\partial}{\partial U}$ or $\frac{\partial}{\partial V}$:

$$\mathbf{J} = \begin{bmatrix} \alpha - \gamma V & -\gamma U \\ \epsilon \gamma V & \epsilon \gamma U - \beta \end{bmatrix} \tag{3.40}$$

The Jacobian matrix depends on the values of U and V , representing that the dynamics of how the system responds to small changes in the populations depends the initial population

state. As we are interested in the behavior near each stationary points, we evaluate the Jacobian at each of these points. At $(U, V) = (0, 0)$:

$$\mathbf{J}(0, 0) = \begin{bmatrix} \alpha - \gamma 0 & -\gamma 0 \\ \epsilon \gamma 0 & \epsilon \gamma 0 - \beta \end{bmatrix} = \begin{bmatrix} \alpha & 0 \\ 0 & -\beta \end{bmatrix} \quad (3.41)$$

This is a diagonal matrix, which greatly simplifies the analysis. Consider how this can be interpreted. The first column describes how the system will evolved when U is moved slightly (in the positive direction); the result is α in the U direction and 0 in the V direction. In other words, if the system is perturbed slightly in the U direction, it will follow a path that continues along increasing U . The second column describes the dynamics given a small movement in the V direction; the result is 0 in the U direction, and $-\beta$ in V . This indicates that, given a small perturbation in the V direction, the system will evolve back towards the stationary point, along V . This is behavior characteristic of a saddle point — the velocity lines point, towards the stationary point in one direction, and away from it in the other. Keep in mind that U and V correspond to populations of two species. Thus, only positive values are biologically realistic; the only perturbations that are relevant around the point $(0, 0)$ are shifts in the positive directions.

Now what about the second stationary point? At $(U^*, V^*) = (\frac{\beta}{\epsilon \gamma}, \frac{\alpha}{\gamma})$, the Jacobian is:

$$\mathbf{J}(U^*, V^*) = \begin{bmatrix} \alpha - \gamma \left(\frac{\alpha}{\gamma}\right) & -\gamma \left(\frac{\beta}{\epsilon \gamma}\right) \\ \epsilon \gamma \left(\frac{\alpha}{\gamma}\right) & \epsilon \gamma \left(\frac{\beta}{\epsilon \gamma}\right) - \beta \end{bmatrix} = \begin{bmatrix} \alpha - \alpha & -\frac{\beta}{\epsilon} \\ \epsilon \alpha & \beta - \beta \end{bmatrix} = \begin{bmatrix} 0 & -\frac{\beta}{\epsilon} \\ \epsilon \alpha & 0 \end{bmatrix} \quad (3.42)$$

How can we interpret this? Again, consider that the first column represents the evolution rule for a small shift in (positive) U — the system will not move in U (the entry is 0), and will move in the positive V direction. With a perturbation towards the negative U direction, the movement will simply be negated — no movement in U and movement towards the negative V direction. For perturbation along V , we consider the second column — a positive shift in V will result in motion in the negative U direction with no motion V , while negative shift in V will lead to motion in the positive U direction. What do these results imply? The motion of the system is found to be *orthogonal* to the direction of perturbation. This suggests that the motion in the neighborhood around the stationary point is best characterized by a loop — the system neither moves away from the point, nor closer to it, but rather cycles around it continuously; note that this result is wholly consistent with the earlier result.

We can extend this analysis by considering the *eigenvalues* of the Jacobian matrix at each point. The eigenvalues of a matrix, \mathbf{A} are solutions to the characteristic equation:

$$\det(\lambda \mathbf{I} - \mathbf{A}) = 0 \quad (3.43)$$

For a diagonal matrix, this leads to the result that the eigenvalues are the diagonal entries; for an arbitrary (non-diagonal) matrix, the determinant above gives an n^{th} -order polynomial in λ (where n is the size of the matrix), for which we must find the roots. Typically this is done numerically, but for the simple 2×2 system here, it can be easily done by hand.

We have already mentioned that the eigenvalues of a diagonal matrix are the diagonal entries, so for the stationary point $(0, 0)$, we have $\lambda_1 = \alpha$ and $\lambda_2 = -\beta$. For the second

stationary point, $(U^*, V^*) = (\frac{\beta}{\epsilon\gamma}, \frac{\alpha}{\gamma})$, we must solve for the roots of the characteristic equation:

$$\det(\lambda \mathbf{I} - \mathbf{J}(U^*, V^*)) = \left| \lambda \begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix} - \begin{bmatrix} 0 & -\frac{\beta}{\epsilon} \\ \epsilon\alpha & 0 \end{bmatrix} \right| = \left| \begin{bmatrix} \lambda & \frac{\beta}{\epsilon} \\ -\epsilon\alpha & \lambda \end{bmatrix} \right| \quad (3.44)$$

$$\det(\lambda \mathbf{I} - \mathbf{J}(U^*, V^*)) = \lambda^2 - \left(\frac{\beta}{\epsilon}\right)(-\epsilon\alpha) = \lambda^2 + \alpha\beta = 0 \quad \rightarrow \quad \lambda^2 = -\alpha\beta \quad (3.45)$$

As α and β are positive constants, the only solutions are imaginary:

$$\lambda = \pm i\sqrt{\alpha\beta} \quad (3.46)$$

How do these results help us understand the stability of a stationary point? There are a set of simple rule that we can use:

- If all the eigenvalues of the Jacobian are *real* and *positive*, then all velocity lines point away from the point, and it is **unstable**.
- If all the eigenvalues are real and *negative*, on the other hand, then all velocity lines point towards the point, and it is **stable**.
- If all the eigenvalues are real, but some are positive and some are negative, then we have a **saddle point**.
- If all the eigenvalues are *purely imaginary* (that is, there is no real component), the stationary point will exhibit **periodic motions** about the point.

More generally, we may say that if the *real component of all eigenvalues* are positive, the point will be stable, and if the real component of all eigenvalues are negative, the point will be unstable.

These results arise from what we call a *linearization* of the model; that is, we approximate the full non-linear system by a linear system that agrees well with the non-linear model *in the immediate neighborhood of the point of interest*. While the linearization should be rigorously correct in the limit of an infinitely small neighborhood, it can be difficult to predict how far from the point of interest the linear model will remain a reasonable approximation. Thus, while a great deal of insight can be gained by linearization, one should always keep in mind that it is an approximation.

How do the results from the Lotka–Volterra system fit in this model? Well, for the stationary point at the origin, we obtain one positive and one negative real eigenvalue. Thus, this point is a saddle point (in the linearized model), which is consistent with our earlier analysis. For the non-zero stationary point, we obtained purely imaginary eigenvalues, which indicate periodic solutions in the linear model. However, the non-linearities in the model could perturb the dynamics to give one of three results:

- Trajectories near the stationary point could oscillate in a strictly periodic manner, for infinite time.
- Trajectories may spiral inwards towards the stationary point (*damped oscillations*).

- Trajectories may spiral away from the stationary point, with oscillations of increasing amplitude.

While we will not go into the details here, it turns out that in this system, the dynamics are truly periodic. However, the model lacks what we term *structural instability*; that is, if the parameters of the model are changed slightly, the dynamics can change in a significant manner. Additionally, while every set of (non-zero) starting conditions gives a periodic solution, they do not give the *same* periodic solution — the system does not have a stable *limit cycle*.

3.2.3 Comparison of Lotka–Volterra model with observation.

The Lotka–Volterra model was very simple in its conception, but seems to make intuitive sense — one can easily imagine the sort of periodic trends in predator/prey populations. However, as we are trying to develop models that will be useful in the understanding of natural systems, we need to ask the question — what are the observed dynamics of *actual* predator-prey systems. This is a very challenging question for a number of reasons; not the least of which is the availability of long-term measurements of the populations of predator and prey species in a given region over extended periods. One often-cited example of such data involves estimates of the populations of lynx and hares in northern Canada during the late 19th century; the Hudson Bay Company kept detailed records on the number of pelts brought in by fur traders during each season, and it may be reasonable to presume that this number is proportional to overall population of each species.

At first glance, these data seem to strongly support the model — the populations of both lynx and hare vary in a periodic fashion throughout the period. However, closer examination reveals a significant inconsistency in the *phase* of the oscillations. That is, at some points in time, the populations vary in the predicted pattern, but at other times they move opposite to the predicted trends; the model predicts a counter-clockwise movement on the predator versus prey plot, but clockwise movements are sometimes seen in the data. What could be the origin of the discrepancy?

Other factors affecting populations. The natural system is not an isolated environment in which lynx and hare populations are the only variables. For one, there are other predator species for which hare may be the prey (wolves, cougars, foxes, eagles, and so on), and lynx may also prey on other species (squirrels, mice, and more). Additionally, weather can have annual variations — a particularly harsh winter may kill large number of both predators and prey, while a dry summer may limit hare growth due to limited vegetative growth. There are also disease epidemics that can dramatically affect populations of a particular species, independent of predation rates. These, and many more examples, all are factors which are not included in the model. Some of these factors can not easily be incorporated into the model, without a vast more amount of information about the system. Weather variations, for example, might be added into to model after the fact, but can not be predicted *a priori*. This is a general limitation that must be accepted — no model can account for all the possible influences in natural systems. Thus, rather than aiming for a goal of perfectly reproducing

observation, our goal should be to find *reasonable* models that agree well, but not necessarily perfectly, with what occurs in natural systems.

Imperfect modeling of included terms. While one source of error may be neglected factors in the model, another is that the model is poorly capturing effects that are, in fact, included in the model. For example, the Lotka–Volterra model presumes that, in absence of predation, prey will grow exponentially. However, from our previous discussions, we know that this is not the observed behavior for single species populations in nature. Rather, at high population levels, growth slows to zero, an effect well described by the logistic equation. If predation strongly limits the prey population, so that it never reaches values in which competition for resources becomes an issue, then exponential growth of prey may be reasonable, but it is not clear that this is, in fact, the case. We have additionally assumed that, in the absence of prey, the predator population will decay exponentially; this may be reasonable for a perfect two-species system, although if alternate prey source is available, we may expect deviations.

Another concern is how we have modeled the interaction between predators and prey: with a predation rate linear in both predators and prey. A linear response to prey populations may be reasonable when prey are scarce, as the ability of a predator to find prey could increase with prey populations. However, predators are not wanton killers that increase their predation rate beyond what is needed for healthy survival. Thus, at high abundance of prey, it may be expected that the *per capita* predation rate would be independent of prey levels. Again, at very low prey levels, deviations from linearity could also be seen when alternate prey are present. The linear dependence of the predation rate on predator population — which can equivalently be stated as having a *per capita* predation rate that is independent of predator population — can be interpreted as a lack of any competition (or cooperation) between predators for prey. In solitary animals, cooperation is not expected to play a role, although in pack animals such as wolves, it may. Competition, however, is somewhat more difficult to assess; at high populations, there may be direct competition for prey, particularly when prey are not highly abundant. Thus, deviations from a linear dependence on predator populations might not be surprising, but it is difficult to predict the expected form of the deviation.

This competition at high predator densities could also play a role in the assumption that predator growth is directly proportional to the predation rate. At high predator populations, there may not only be competition for prey, but also for habitat (den sites, mates, hunting territory, and so on) which could lead to non-linear relationships between predation rate and population growth. Again, the exact form of these non-linearities may be difficult to predict.

It is important to note, that while the Lotka–Volterra model may not be *correct* in many ways, a great deal can still be learned from it. This includes both that the significant deficiencies in the model are (*i.e.* what approximations are *reasonable* and what are not), as well as fundamental ideas about how dynamical systems would behave under certain conditions.

3.2.4 Improving the predator response model

Of the issues raised above, two may seem most significant: the assumption of unlimited, exponential growth of prey in absence of predators, and the unbounded increased in predation rate with prey populations. The first of these can easily be dealt with by use of a logistic-based growth expression, which leaves us to improve the model of how predation rates vary with prey. To do so, first consider how an individual predator spends its time: (1) a hungry predator searches for prey; (2) upon identifying a prey target, it makes a kill; (3) the predator then eats; and (4) rests until it is hungry again. In many cases, a single kill will satisfy one or more predators for several days.

To develop a model of this, we will begin with an assumption that the time for steps 2–4 (kill/eat/rest) is constant (on average) for every kill, and we will denote this time by h . A constant average time for eating/resting may be considered equivalent to an assumption that the average prey size is constant, and thus provides a constant amount of sustenance. That the average time between identifying a prey target to making a kill would be constant also seems reasonable. Secondly, presume that all time not spent in the kill/eat/rest stage is spent actively searching for prey. That is, once a predator becomes hungry, it searches until it finds suitable prey. Now, let T be some arbitrary period of time (a week, a month, a year, *etc.*) over which several kills will be made by an individual predator, with N being the number of kills made. The total time searching, τ , will then be given by:

$$\tau = T - hN \quad (3.47)$$

That is, the total time less the product of the number of kills and the time “occupied” per kill. Now, it may be reasonable to presume that to total number of prey that are caught increases both with prey density, U , and with the time spent searching, τ . The simplest model will have a linear dependence on each of these, giving:

$$N = sU\tau = sU(T - hN) \quad (3.48)$$

where s is proportionality constant. Manipulating this expression gives:

$$N = sUT - shUN \quad \rightarrow \quad N(1 + shU) = sUT \quad \rightarrow \quad \frac{N}{T} = \frac{sU}{(1 + shU)} \quad (3.49)$$

The ratio, $\frac{N}{T}$, is the number of prey caught by one predator in a given time period, which is precisely the definition of the *per capita* predation rate; the expression we obtain is known as Holling’s disc equation. Note that this expression is very similar in functional form to the Hassel equation (with $b = 1$) and to the Michaelis–Menten expression:

$$N_{n+1} = \frac{R_o N_n}{1 + aN_n} \quad v = \frac{V_{max} S}{K_m + S} \quad (3.50)$$

This is not a coincidence, but rather is a result of each of the expressions describing a type of **saturated growth** — a very common phenomenon in biological systems. In this case, saturation occurs because as prey become abundant, the search time approaches zero, but the time for the killing/eating/resting phase remains constant; the maximal predation rate

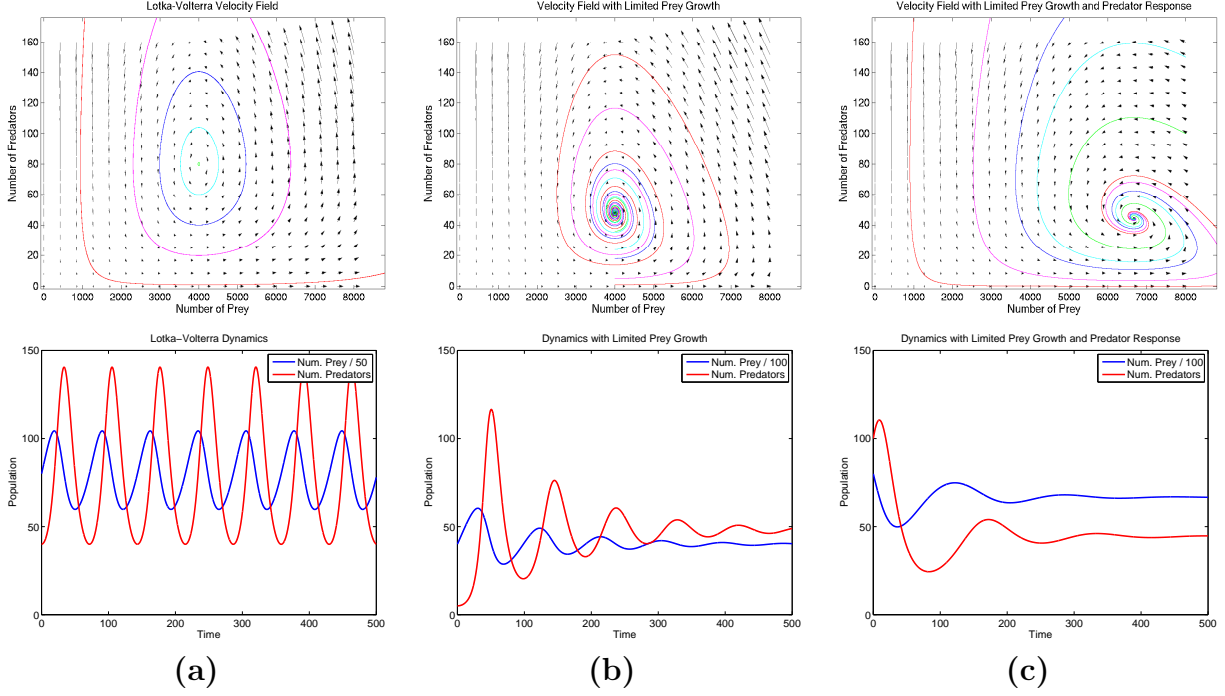


Figure 3.8: Dynamics of predator–prey systems. (Top) The velocity field and sample trajectories; (bottom) Population dynamics as a function of time for one trajectory. (a) Lotka–Volterra; (b) LV, with total prey population growth limited by a logistic model; (c) LV, with logistic prey growth and the predator-response described by the Holling’s Disk equation.

is reached when predators no longer need to spend any amount of time searching for a prey target.

Now, the Lotka–Volterra model was based on an unlimited prey growth model (described by a fixed growth constant, α), and an unlimited predator response (with a constant predation constant, γ). We can derive an improved model simply by substituting the logistic equation for prey growth and the Holling’s disk equation for the predator response. That is:

$$\begin{aligned} \frac{dU}{dt} &= \alpha U - \gamma UV \\ \frac{dV}{dt} &= \epsilon \gamma UV - \beta V \end{aligned} \quad \rightarrow \quad \begin{aligned} \frac{dU}{dt} &= A(U)U - \Gamma(U)V \\ \frac{dV}{dt} &= \epsilon \Gamma(U)V - \beta V \end{aligned} \quad (3.51)$$

where:

$$A(U) = \alpha \left(1 - \frac{U}{K}\right) \quad \Gamma(U) = \frac{sU}{1 + shU} \quad (3.52)$$

Note that $\lim_{U \rightarrow 0} A(U) = \alpha$, and $\lim_{U \rightarrow 0} \Gamma(U) = \gamma U$ if we take γ to be equivalent to s ; this model is equivalent to the Lotka–Volterra model at low prey numbers, but differs at large prey populations, where the underlying assumptions of the Lotka–Volterra model break down.

3.2.5 Interspecies competitions for resources

Direct interactions between species, as in predator–prey relationships, are common, but many species also interact more indirectly, by competing for similar resources. To develop

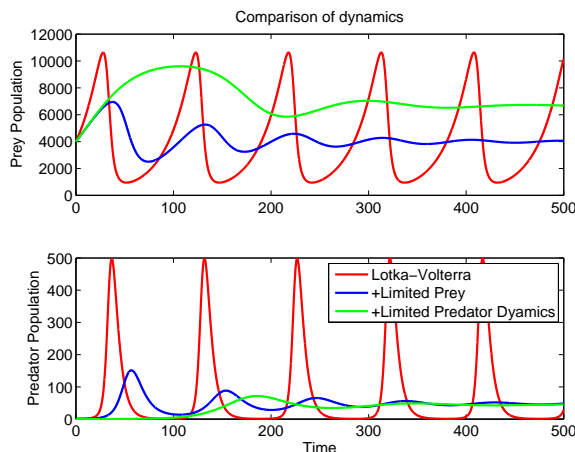


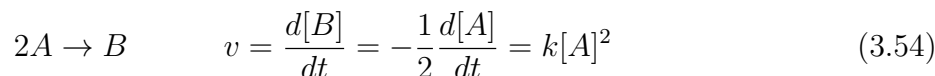
Figure 3.9: Comparison of dynamics of the Lotka–Volterra model and modified variants. The top panel displays prey population and the bottom the predator population. All trajectory begin with the same initial conditions of 4000 prey and a single predator.

a model for this, we can begin by thinking about how we dealt with competition within a single population (*intraspecies* competition). In that case, we replace a uniform growth constant with a saturating term, through the logistic equation:

$$\frac{dU}{dt} = R_o U \quad \rightarrow \quad \frac{dU}{dt} = R_o U \left(1 - \frac{U}{K}\right) = R_o U - \frac{R_o U^2}{K} \quad (3.53)$$

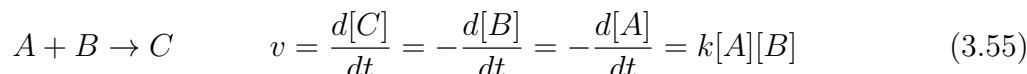
With R_o being the intrinsic (unlimited) *per capita* growth rate and K is the environmental carrying capacity for the population. Writing the logistic in this form, we see that we have two terms. The first is simply the unrestricted, positive growth term that is linear in U , and the second is a decay term (negative) that is quadratic in U .

What is the significance of this quadratic term? In a system of randomly moving identical particles, the rate of collision between any two particles is proportional to N^2 , where N is the particle density (or the number of particles in a fixed volume system). This quadratic dependency give rise to the quadratic rate law in bimolecular chemical reactions:



This is known as the Law of Mass Action. We can consider the decay term in the logistic equation in a similar manner — random interactions between individuals within the population (collisions) lead to the death of one individual. These interactions do not need to interpreted as directly leading to death, but rather that with increased interaction there is an increased likelihood of death (for example, due to lack an inability to find food or a suitable nesting site).

Now, in physical systems involving two distinct sets of randomly moving particles, the collision rate between these different particles is proportional to NM , where N and M are the densities of the two particles. Again, this is the source of the chemical rate equation for a mixed bimolecular reaction:



Thus, by extending our interpretation of intraspecies competition, perhaps interspecies competition should involve the addition of another decay term, proportional to the product U_1U_2 , for two populations with numbers U_1 and U_2 . Thus, if we consider that there is also intraspecies competition within each population, we obtain:

$$\begin{aligned}\frac{dU_1}{dt} &= R_{o,1} - \frac{R_{o,1}U_1^2}{K_1} - aU_1U_2 \\ \frac{dU_2}{dt} &= R_{o,2} - \frac{R_{o,2}U_2^2}{K_2} - bU_1U_2\end{aligned}\tag{3.56}$$

where $R_{o,i}$ and K_i are the intrinsic growth constants and environmental capacities of each species, and a and b are interspecies competition constants. Now, if we scale the constants a and b according to the growth and capacity of each species:

$$\alpha = \frac{aK_1}{R_{o,1}} \quad \leftrightarrow \quad a = \frac{\alpha R_{o,1}}{K_1} \quad \beta = \frac{bK_2}{R_{o,2}} \quad \leftrightarrow \quad b = \frac{\beta R_{o,2}}{K_2}\tag{3.57}$$

then we get the result:

$$\begin{aligned}\frac{dU_1}{dt} &= R_{o,1} - \frac{R_{o,1}U_1^2}{K_1} - \frac{\alpha R_{o,1}U_1U_2}{K_1} = R_{o,1}U_1 \left(1 - \frac{U_1 + \alpha U_2}{K_1}\right) \\ \frac{dU_2}{dt} &= R_{o,2} - \frac{R_{o,2}U_2^2}{K_2} - \frac{\beta R_{o,2}U_1U_2}{K_2} = R_{o,2}U_2 \left(1 - \frac{U_2 + \beta U_1}{K_2}\right)\end{aligned}\tag{3.58}$$

These expressions are very similar in form to the logistic equation for intraspecies competitive growth, but the competitive population size is *increased* by αU_2 or βU_1 . We can think of the **competition coefficients** α and β as indicating how strong of a negative effect an individual of one population has on another. If the two species are very close in ecological niche — that is they share almost identical habitat, food sources, nesting sites, and so on — then one might expect an inverse relationship between α and β :

$$\alpha = \frac{1}{\beta} \quad \leftrightarrow \quad \alpha\beta = 1\tag{3.59}$$

That is, if one species competes more strongly for the identical set of resources, the other must necessarily compete less strongly by a similar amount. If, on the other hand, there is not a perfect overlap of ecological niche (the species compete for some resources, but not all), then no clear relationship between α and β is required.

3.2.6 Dynamic analysis of competitive systems

What will the dynamics of a competitive system of populations be? Can two competing species successfully coexist? To address these questions, we must consider what our model predicts. To do this, we will use the graphical approach centered on determination of the null clines for the system. For species (1), the null clines are given by:

$$\frac{dU_1}{dt} = R_{o,1}U_1 \left(1 - \frac{U_1 + \alpha U_2}{K_1}\right)\tag{3.60}$$

which has two solutions:

$$U_1 = 0 \quad \text{or} \quad 1 - \frac{U_1 + \alpha U_2}{K_1} = 0 \rightarrow U_1 + \alpha U_2 = K_1 \rightarrow U_2 = \frac{-1}{\alpha}U_1 + \frac{K_1}{\alpha}\tag{3.61}$$

Similarly, for species (2), the null clines are given by:

$$\frac{dU_2}{dt} = R_{o,2}U_2 \left(1 - \frac{U_2 + \beta U_1}{K_2}\right) = 0 \quad (3.62)$$

which again has two solutions:

$$U_2 = 0 \quad \text{or} \quad 1 - \frac{U_2 + \beta U_1}{K_2} = 0 \rightarrow U_2 + \beta U_1 = K_2 \rightarrow U_2 = -\beta U_1 + K_2 \quad (3.63)$$

We see that each variable has two null clines, one consisting of its own axis, and the other of a linear function of U_1 and U_2 .

To find the stationary points of the system, we consider the intersection points of these null clines; there are four possibilities, matching each member of two pairs.

1. $U_1 = 0$ and $U_2 = 0$.
2. $U_1 = 0$ and $U_2 = -\beta U_1 + K_2$. Substituting $U_1 = 0$ gives $U_2 = K_2$.
3. $U_2 = \frac{-1}{\alpha}U_1 + \frac{K_1}{\alpha}$ and $U_2 = 0$. Substituting $U_2 = 0$ gives $\frac{1}{\alpha}U_1 = \frac{K_1}{\alpha}$ and thus $U_1 = K_1$.
4. $U_2 = \frac{-1}{\alpha}U_1 + \frac{K_1}{\alpha}$ and $U_2 = -\beta U_1 + K_2$. Equating these expressions and solving for U_1 gives:

$$U_1 = \frac{\alpha K_2 - K_1}{\alpha\beta - 1} \quad (3.64)$$

Now substituting this result into either of the original expressions: ²

$$U_2 = \frac{\beta K_1 - K_2}{\alpha\beta - 1} \quad (3.65)$$

We have found four stationary points, whose significance we may briefly examine:

1. $(U_1, U_2) = (0, 0)$: This is the trivial stationary point corresponding to neither species being present; populations can not arise from nothing.
2. $(U_1, U_2) = (0, K_2)$: Here we have species (1) non-existent and species (2) at its environmental carrying capacity. This point should be expected, as we know that a single population with logistic growth will reach a steady population.
3. $(U_1, U_2) = (K_1, 0)$: This is simply the reversed case of the previous point — species (2) is not present, and thus species (1) reaches its environmental carrying capacity.
4. $(U_1, U_2) = (\frac{\alpha K_2 - K_1}{\alpha\beta - 1}, \frac{\beta K_1 - K_2}{\alpha\beta - 1})$: This result gives non-zero populations for both species, and thus is the key point of interest; understanding the stability and dynamics about this point will provide insight into whether *stable coexistence* is feasible.

¹ $\frac{-1}{\alpha}U_1 + \frac{K_1}{\alpha} - \beta U_1 + K_2 \rightarrow (\beta - \frac{1}{\alpha})U_1 = K_2 - \frac{K_1}{\alpha} \xrightarrow{\frac{1}{\alpha}(\alpha\beta - 1)} U_1 = \frac{\alpha K_2 - K_1}{\alpha\beta - 1}$
² $U_2 = -\beta U_1 + K_2 = \beta \left(\frac{\alpha K_2 - K_1}{\alpha\beta - 1} \right) + K_2 = \frac{-\beta(\alpha K_2 - K_1) + (\alpha\beta - 1)K_2}{\alpha\beta - 1} = \frac{-\beta\alpha K_2 + \beta K_1 + \alpha\beta K_2 - K_2}{\alpha\beta - 1} = \frac{\beta K_1 - K_2}{\alpha\beta - 1}$

Although we have found a stationary point, we must additionally consider whether the stationary point makes physical and biological sense, and the nature of the dynamics of the system about the point. First, for biological consistency, we require that the populations are both *finite* and *non-negative*. First, we see that to achieve a finite solution:

$$\alpha\beta - 1 \neq 0 \rightarrow \alpha\beta \neq 1 \quad (3.66)$$

Recall, however, that if two species share identical niches, then we expect $\alpha\beta = 1$, directly leading to a non-physical solution for the stationary point. This is a manifestation of the **principle of competitive exclusion**, which states that no two species can stably occupy identical ecological niches.

Now, consider the case where $\alpha\beta < 1$, and thus $\alpha\beta - 1 < 0$. For the solutions to be positive, we require that:

$$\alpha K_2 - K_1 < 0 \rightarrow \alpha K_2 < K_1 \rightarrow \alpha < \frac{K_1}{K_2} \quad (3.67)$$

and:

$$\beta K_1 - K_2 < 0 \rightarrow \beta K_1 < K_2 \rightarrow \beta < \frac{K_2}{K_1} \quad (3.68)$$

Also note that, if $\alpha < \frac{K_1}{K_2}$ and $\beta < \frac{K_2}{K_1}$, then:

$$\alpha\beta < \frac{K_1}{K_2} \frac{K_2}{K_1} = 1 \quad (3.69)$$

and thus the results are consistent.

Now we may consider the stability of this point; we will approach this by considering the null clines. In this case, the null clines are not simply horizontal or vertical lines, and thus our analysis of their crossing must be slightly more involved. We have two lines, one with slope $\frac{-1}{\alpha}$ and intercept $\frac{K_1}{\alpha}$, and the other with slope $-\beta$ and intercept K_2 . Now:

$$\text{if } \alpha < \frac{K_1}{K_2} \text{ then } \frac{1}{\alpha} > \frac{K_2}{K_1}, \text{ but } \beta < \frac{K_2}{K_1} \therefore \frac{1}{\alpha} > \beta \quad (3.70)$$

Thus we see that the null cline of U_1 has a slope that is greater in magnitude (but negative) than that of U_2 . Also:

$$\frac{1}{\alpha} > \frac{K_2}{K_1} \rightarrow \frac{K_1}{\alpha} > K_2 \quad (3.71)$$

and thus the intercept of the U_1 null cline is also greater than that of the U_2 null cline. This allows us to sketch these lines on a plot of U_2 versus U_1 , and consider the qualitative dynamics in each region of the plot; recall that we are only concerned with positive values of each variable. In the region below and to the left of both null clines, both U_1 and U_2 are increasing, and thus we indicate a general motion upwards and to the right — biologically, both populations are below their capacity, and thus increase. Similarly, in the region above and to the left of both null clines, both U_1 and U_2 are decreasing, indicated by a general motion downwards and to the left — the populations are both above their capacity, and thus decay. Now, there is a region above and to the left of the stationary point, which is above

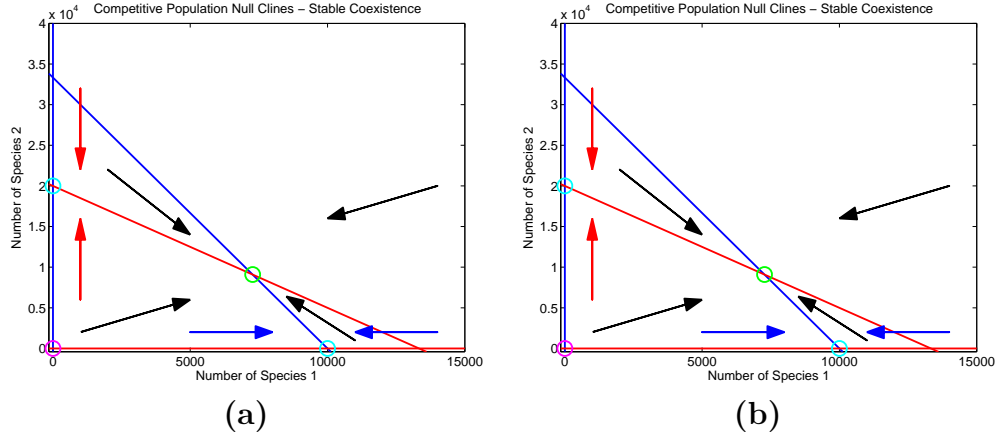


Figure 3.10: Dynamics of competitive populations. (a) Weakly competitive systems lead to stable coexistence due to a stable stationary point with both populations non-zero; (b) In strongly competitive systems, the stationary point with non-zero populations for both species is a saddle point; the system evolves to extinction of one or the other species, dependent on history.

the U_2 null cline, but below the U_1 null cline. Here, U_1 will still be increasing, but U_2 will be decreasing, and thus the general direction of motion is down and to the right. Similarly, there is a region below and to the right of the stationary point where the reverse is true — U_1 is decreasing but U_2 is increasing, as we are above the U_1 null cline but below that of U_2 — and here, the motion is up and to the left. In both these regions, one population is above its capacity, while the other has not yet reached it. In all these regions, the general direction of motion is *towards* the stationary point, and thus the point is **stable** (it is an attractor).

A stable stationary point indicates that the two populations can stably co-exist, and that regardless of the initial populations of the two species, they will reach (over time) two stable and constant population densities. Now, what is the biological significance of the parameter range for which this is true? We found this result required:

$$\alpha < \frac{K_1}{K_2} \quad \beta < \frac{K_2}{K_1} \quad (3.72)$$

That is, the competitive coefficient for the effect of species (2) on species (1) (α) must be less than the relative carrying capacity of species (1) to that of (2). This can be interpreted as meaning that species (2) competes less with species (1) than (1) does with itself. In considering β , we get the reciprocal requirement — species (1) must compete less with (2) than (2) does with itself. Two species can stably coexist so long as both compete imperfectly; this will likely be the case in most situations where there is partial, but incomplete overlap of resources consumed by each species.

To get this result, we assumed that $\alpha\beta < 1$, so what happens if we consider the case where $\alpha\beta > 1$, or $\alpha\beta - 1 > 0$. In these case, for the solutions to be positive, we require that:

$$\alpha K_2 - K_1 > 0 \rightarrow \alpha K_2 > K_1 \rightarrow \alpha > \frac{K_1}{K_2} \quad (3.73)$$

and:

$$\beta K_1 - K_2 > 0 \rightarrow \beta K_1 > K_2 \rightarrow \beta > \frac{K_2}{K_1} \quad (3.74)$$

Again note that, if $\alpha > \frac{K_1}{K_2}$ and $\beta > \frac{K_2}{K_1}$, then:

$$\alpha\beta > \frac{K_1}{K_2} \frac{K_2}{K_1} = 1 \quad (3.75)$$

and thus the results are consistent. Thus we also can have a physically relevant stationary point when both competitive coefficients are *greater* than the ratios of the carrying capacities of each species. However, is this stationary point stable?

To answer this, again we may consider the slopes and intercepts of the null clines.

$$\text{if } \alpha > \frac{K_1}{K_2} \text{ then } \frac{1}{\alpha} < \frac{K_2}{K_1}, \text{ but } \beta > \frac{K_2}{K_1} \therefore \frac{1}{\alpha} < \beta \quad (3.76)$$

Thus we see that in this case, the null cline of U_1 has a slope that is lower in magnitude than that of U_2 . Also:

$$\frac{1}{\alpha} > \frac{K_2}{K_1} \rightarrow \frac{K_1}{\alpha} < K_2 \quad (3.77)$$

and thus the intercept of the U_1 null cline is also lower than that of the U_2 null cline. These changes do not change the qualitative behavior in the region above and to the right, or below and to the left, of both null clines — the system still tends to move down and the to the left, or up and to the right, respectively. However, in the regions bounded by the two null clines, the order in which the null clines are crossed is reversed. These leads to a complete reversal of direction in these areas; in the region above and to the left of the stationary point, the system evolves further upwards and left, while in the region below and to the right of the stationary point, the system evolves further down and right. Thus, in these regions, the general direction of motion is *away* from the stationary point. With some lines of motion directed towards the stationary point, and others away, we find that this is a **saddle point**.

The result of this is that the system will evolve through time to one of the stationary points on the axes — one population will go extinct while the other will stabilize at its environmental carrying capacity. However, which population survives depends on the initial conditions. There is a repelling manifold in this system, following a straight line through the origin and through the saddle point — all starting points above this manifold will lead to survival of species (2), and all starting points below will lead to survival of species (1). Biologically, the meaning of this regime of behavior is that each species competes more strongly with each other than with themselves. One may hypothesize that this could happen if two species shared nearly identical ecological niches, but showed a preference for conflict with the unlike species. However, we do not see such relationships in nature — consistent with the result that this is not a stable point.

Analysis of the slopes and intercepts also allows to consider the cases where there is no intersection of the null clines in the positive domain, and thus no stationary points without at least one of the populations at 0. When the null cline of (1) has an intercept above that of (2) (*i.e.* $\frac{K_1}{\alpha} > K_2$) but the difference in slope is not enough to lead to a non-negative crossing point, then there will only be three regions of general motion. As always, in the region of

low U_1 and U_2 , both populations tend to increase. Similarly, in the region of high U_1 and U_2 , both populations decrease. However, between the two null clines, as we move above the U_2 null cline but below that of U_1 , U_1 will increase while U_2 decreases. This yields motion down and to the right — the overall result is that all paths (regardless of initial condition) lead to the $(K_1, 0)$ stationary point. That is, species (1) survives, and species (2) goes extinct; the relation of the competitive coefficients is such that species (1) competes against (2) much more strongly than (2) does against one. When the null cline of (1) has an intercept below that of (2) ($\frac{K_1}{\alpha} < K_2$), but there is no positive crossing point, then motion in the region between the null clines will point towards increasing U_2 and decreasing U_1 . Under these conditions, species (2) always survives, and species (1) goes extinct; here species (2) is the stronger competitor.

3.3 Ecosystems modeling

So far, competition for resources in our models has been *implicit*. That is, we describe competition as a decay term proportional to degree of interaction (a quadratic in populations in the models we have worked with). This has a benefit in that it can describe a large range of competitive interactions — competition for food or for space, direct conflict between individuals, and so on. However, in some cases we know the primary resource underlying conflict, and may wish to treat this explicitly. Additionally, some organisms play an essential role in ecosystems without *directly* interacting with others (such as species which promote decay and recycling of resources from dead plants and animals). When these features are added into our models, we classify them as *ecosystems models*.

In developing these models, we will still consider populations of organisms and describe their rates of growth and death by differential equations. We will then add an explicit consideration of key resources, and describe the variation in the amount of these materials in a similar way.

3.3.1 A minimal ecosystem model

Consider a simple system with vegetative growth and a single herbivorous species. We might think of this as an isolated island with grass and rabbits, or a marine environment consisting of phytoplankton (plant-like) and zooplankton (animal-like). Now, let's briefly consider the essential biology.

Plants grow largely by harnessing solar energy through photosynthesis, and building biological macromolecules from fundamental components; these components — carbon, nitrogen, oxygen, phosphorous, sulfur, hydrogen, as well as metals and salts — are essential to growth. Carbon is taken from the atmosphere in the form of CO_2 and hydrogen from the soil as H_2O ; both of these also provide oxygen. Salts and trace metals are also typically present in all ground water, and thus are generally easily obtained. Nitrogen, phosphorous and sulfur generally must be taken up from the soil, but are not present in usable forms in inorganic dust or gravel. Nitrogen, for example, is present in large quantities in the air (80%), but as N_2 , which is unusable by most plants. Rather, plants require nitrogen that has been “fixed”, or converted to forms such as ammonia (NH_3) or nitrate (NO_3^-). While some plants have

symbiotic relationships with bacteria that are able to convert atmospheric nitrogen into a usable form, most must uptake fixed nitrogen from the soil. This fixed nitrogen almost always comes from decayed plant or animal matter.

For simplicity, we will begin by only keeping track of nitrogen, and assume that the availability of other nutrients is either not limiting, or proportional to nitrogen levels. Thus our system will be governed by three basic rules:

- Plants grow in a manner dependent on nitrogen availability, and nitrogen is incorporated into the plant during growth.
- Herbivores take all nutrition from plants, and grow based on plant availability; nitrogen is transferred from animals to plants in this process
- The death and decay of both plants and animals restores nitrogen to the environment.

Before we go further, it is worthwhile to briefly discuss the issue of units. In simple modeling of animal populations, considering numbers of individuals in a particular area is a reasonable choice of units. However, for plant growth, an individual can not always be clearly identified (consider grass for example), and thus it is more reasonable to keep track of the *biomass* (the total mass of the population). It is also perfectly reasonable to consider animal populations in terms of biomass as well; one can convert between the number of individuals and the biomass by the average animal mass. For an fundamental resource like environmental nitrogen, the units that make the most sense are mass, as this directly measures the total quantity of the material. Now, the chemical composition of a given plant or animal is very uniform — there is generally a strong linear correlation between the mass of an organism and the mass of key elements within the individual. As a result, biomass can be measured either in total mass, or in mass of a particular key element. In some cases, total carbon mass may be most significant, while here (where we are explicitly tracking nitrogen levels), total nitrogen mass may be more appropriate. It may seem odd to count an animal population in terms of kilograms of nitrogen, but keep in mind that these units can be directly converted into numbers of individuals, simply by knowing the average nitrogen content of an individual.

Now we can begin to develop our model. We will consider three “species”, defined as follows:

- P : total plant biomass (as nitrogen content)
- Z : total animal (herbivore) population (measured as biomass of nitrogen)
- N : mass of free, fixed nitrogen in the environment

With three species, we will need three differential equations to describe their time variation. These must capture the fundamental processes of growth and death:

- Plant biomass increases by growth, which is dependent on nitrogen availability, and decreases both by natural death and through consumption by herbivores.
- Herbivore biomass increases by growth dependent on plant consumption, and decreases by natural death.

- Environmental nitrogen decreases through uptake by plants during growth, and increases through decay of dead plants and animals.

A key assumption is that nutrient transfer is perfectly efficient. That is, every unit of nitrogen that is taken up during plant growth is either transferred to an animal during consumption or returns to the soil when the plant decays, and all nitrogen taken up by an animal returns to the soil upon decay of the animal. There is no loss of nitrogen from the system (**Law of Conservation of Mass**).

The simplest model assumes linear, unlimited responses for each process:

- Plant death/decay: αP
- Animal death/decay: βZ
- Plant growth: γNP
- Animal growth: δPZ

Since we have chosen to use units of nitrogen mass for all values, and because of our assumption of perfect resource transfer, we have:

- Increase in free nitrogen = plant + animal death/decay.
- Plant reduction by consumption = animal growth
- Decrease in free nitrogen = plant growth

This leads to the differential equations:

$$\begin{aligned}\frac{dN}{dt} &= \alpha P + \beta Z - \gamma NP \\ \frac{dP}{dt} &= \gamma NP - \alpha P - \delta PZ \\ \frac{dZ}{dt} &= \delta PZ - \beta Z\end{aligned}\tag{3.78}$$

Note that:

$$\frac{dN}{dt} + \frac{dP}{dt} + \frac{dZ}{dt} = 0\tag{3.79}$$

which is a statement of the conservation of mass in the system. This can be integrated to give:

$$N + P + Z = N_{tot}\tag{3.80}$$

where N_{tot} is a constant describing the overall nitrogen content of the whole ecosystem.

3.3.2 Dynamical systems analysis of ecological model

To understand how this system behaves, we begin with defining the null clines. For Z :

$$\frac{dZ}{dt} = \delta PZ - \beta Z = (\delta P - \beta)Z = 0\tag{3.81}$$

which gives:

$$Z = 0 \quad \text{or} \quad \delta P - \beta = 0 \rightarrow P = \frac{\beta}{\delta}\tag{3.82}$$

For P :

$$\frac{dP}{dt} = \gamma NP - \alpha P - \delta PZ = (\gamma N - \alpha - \delta Z)P = 0 \quad (3.83)$$

giving:

$$P = 0 \quad \text{or} \quad \gamma N - \alpha - \delta Z = 0 \rightarrow Z = \frac{\gamma N - \alpha}{\delta}, N = \frac{\alpha + \delta Z}{\gamma} \quad (3.84)$$

Finally, for N :

$$\frac{dN}{dt} = \alpha P + \beta Z - \gamma NP = 0 \quad (3.85)$$

As this expression is not factorizable, and all three variables are involved, we can not simplify it.

To find stationary points, we look for the intersection of the null clines. We have well defined null clines for P and Z (two each). While we could not simplify the expression for $\frac{dN}{dt} = 0$, we note that the law of conservation of mass gives:

$$\frac{dN}{dt} + \frac{dP}{dt} + \frac{dZ}{dt} = 0 \rightarrow \frac{dN}{dt} = -\frac{dP}{dt} - \frac{dZ}{dt} \quad (3.86)$$

Thus, when both $\frac{dP}{dt}$ and $\frac{dZ}{dt}$ are zero, so will $\frac{dN}{dt}$. With two pairs of null clines to consider, we will have four possible intersections.

First, consider $Z = 0$ and $P = 0$. We additionally have the constraint of conservation of mass:

$$N + P + Z = N_{tot} \rightarrow N = N_{tot} \quad (3.87)$$

Thus, there is a stationary point at $(N, P, Z) = (N_{tot}, 0, 0)$. Of course, this is the trivial result that if there are neither plants nor animals present, the system will remain unchanging, with all available nitrogen in the environment. Is this point stable? Consider a point near the stationary point, but slightly shifted in Z , $(N_{tot} - \Delta Z, 0, \Delta Z)$ (remembering that mass must be conserved). Here:

$$\frac{dP}{dt} = (\gamma N - \alpha - \delta Z)P = 0 \quad \frac{dZ}{dt} = (\delta P - \beta)Z = -\beta(\Delta Z) \quad (3.88)$$

Thus, the system will move in the negative Z direction, back towards the point. Now consider a point shifted in P from the stationary point, $(N_{tot} - \Delta P, \Delta P, 0)$. Here:

$$\frac{dP}{dt} = (\gamma N - \alpha - \delta Z)P = (\gamma N_{tot} - \gamma(\Delta P) - \alpha)\Delta P \quad \frac{dZ}{dt} = (\delta P - \beta)Z = 0 \quad (3.89)$$

The direction of motion in P depends on the sign of $\gamma N_{tot} - \gamma(\Delta P) - \alpha$; this expression will be positive if:

$$\gamma N_{tot} > \gamma \Delta P + \alpha \rightarrow N_{tot} > \Delta P + \frac{\alpha}{\gamma} \quad (3.90)$$

and negative if:

$$N_{tot} < \Delta P + \frac{\alpha}{\gamma} \quad (3.91)$$

As we are considering a very small shift, we may presume that $\Delta P \ll \frac{\alpha}{\gamma}$, and thus we get the conditions that:

$$\frac{dP}{dt} > 0 \quad \text{if} \quad N_{tot} > \frac{\alpha}{\gamma} \quad \text{and} \quad \frac{dP}{dt} < 0 \quad \text{if} \quad N_{tot} < \frac{\alpha}{\gamma} \quad (3.92)$$

If the total nitrogen in the environment is below a critical value ($\frac{\alpha}{\gamma}$), then the direction of motion is in the negative P direction, back towards the stationary point. Thus, under these conditions, the stationary point is *stable*. However, if the nitrogen levels are above this value, the direction of motion is towards positive P , and thus we have a saddle point. What does this mean biologically? If there is inadequate nitrogen in the environment, the system does not stably support any life; but once a threshold is reached, plant life can grow.

How consider the next intersection, of $Z = 0$ and $N = \frac{\alpha + \delta Z}{\gamma}$, which gives:

$$Z = 0 \quad N = \frac{\alpha}{\gamma} \quad P = N_{tot} - N - Z = N_{tot} - \frac{\alpha}{\gamma} \quad (3.93)$$

Thus we have a stationary point at:

$$(N, P, Z) = \left(\frac{\alpha}{\gamma}, N_{tot} - \frac{\alpha}{\gamma}, 0 \right) \quad (3.94)$$

Biologically, this represents a point with plant biomass of $N_{tot} - \frac{\alpha}{\gamma}$, and no animal population. Note that the plant biomass will only be a physically reasonable value (positive) if $N_{tot} > \frac{\alpha}{\gamma}$, which is the same threshold value that we found for stability of the first stationary point. We also see that free nitrogen level is independent on the total nitrogen level — once a threshold level of total nitrogen is available, all the nitrogen above that level will go into supporting plant life. Again, we may evaluate the stability of this point by considering small perturbations in each direction. Shifting the plant biomass, we see that at $(\frac{\alpha}{\gamma} - \delta P, N_{tot} - \frac{\alpha}{\gamma} + \Delta P, 0)$:³

$$\frac{dP}{dt} = -\gamma(\Delta P) \left(N_{tot} - \frac{\alpha}{\gamma} + \Delta P \right) \quad (3.95)$$

and

$$\frac{dZ}{dt} = (\delta P - \beta)Z = 0 \quad (3.96)$$

The second term must be positive for any realistic perturbation, since it represents total plant biomass. Thus, the direction of motion will always oppose the direction of the perturbation, and the system will move back towards the stationary point. Now consider a shift in the direction of animal population (only positive shifts are meaningful, since the stationary point is at $Z = 0$). We will make the perturbation consistent by modifying the free nitrogen mass, leaving plant biomass fixed, and thus we are looking at the point $(\frac{\alpha}{\gamma} - \Delta Z, N_{tot} - \frac{\alpha}{\gamma}, \Delta Z)$:

$$\frac{dP}{dt} = (\gamma N - \alpha - \delta Z)P = \left(\gamma \frac{\alpha}{\gamma} - \gamma(\Delta Z) - \alpha - \delta(\Delta Z) \right) P = -(\gamma + \delta)(\Delta Z)P \quad (3.97)$$

³ $\frac{dP}{dt} = (\gamma N - \alpha - \delta Z)P = \left(\gamma \frac{\alpha}{\gamma} - \gamma(\Delta P) - \alpha \right) \left(N_{tot} - \frac{\alpha}{\gamma} + \Delta P \right) = -\gamma(\Delta P) \left(N_{tot} - \frac{\alpha}{\gamma} + \Delta P \right)$

$$\frac{dZ}{dt} = \left(\delta \left(N_{tot} - \frac{\alpha}{\gamma} \right) - \beta \right) \Delta Z = \left(\delta N_{tot} - \frac{\alpha\delta}{\gamma} - \beta \right) \Delta Z \quad (3.98)$$

The most important term involves the direction of motion in Z , the animal population, and the direction of this motion will depend on the sign of $\delta N_{tot} - \frac{\alpha\delta}{\gamma} - \beta$. The animal population will grow if:

$$\delta N_{tot} - \frac{\alpha\delta}{\gamma} - \beta > 0 \quad \rightarrow \quad N_{tot} > \frac{\alpha}{\gamma} + \frac{\beta}{\delta} \quad (3.99)$$

and decrease otherwise. The motion in P is always negative, essentially a direct consequence of animals consuming plant matter when the growth and natural death rates of the plants were constant. If Z decreases, this will lead to an intersection with the P -axis ($X = 0$), at which point P will increase to the stationary point. Thus, when $N_{tot} < \frac{\alpha}{\gamma} + \frac{\beta}{\delta}$, the stationary point is stable. When N_{tot} is above this second threshold, the point loses its stability (becoming a saddle point). This has a very simple interpretation. Just as there is a minimum nitrogen level required to support plant life ($\alpha\gamma$), there is a greater minimum level required to support both animal and plant life; the excess nitrogen required is $\frac{\beta}{\delta}$. If this threshold is not reached, then an introduced animal population will die out, and only plant life will remain.

Now, there are two more possible intersections to consider. Taking the null clines of $P = \frac{\beta}{\delta}$ and $P = 0$, we clearly have no intersection, leaving us only with the null clines $P = \frac{\beta}{\delta}$ and $N = \frac{\alpha}{\gamma} + \frac{\delta Z}{\gamma}$. First, we see that:

$$\frac{dN}{dt} = \alpha P + \beta Z - \gamma NP = \alpha \frac{\beta}{\delta} + \beta Z - \gamma \left(\frac{\alpha}{\gamma} + \frac{\delta Z}{\gamma} \right) \frac{\beta}{\delta} = \frac{\alpha\beta}{\delta} + \beta Z - \frac{\alpha\beta}{\delta} - \beta Z = 0 \quad (3.100)$$

Thus we again see that this expression is satisfied for all values of Z . Using the conservation of mass law, we have:

$$Z = N_{tot} - P - N = N_{tot} - \frac{\beta}{\delta} - \left(\frac{\alpha}{\gamma} + \frac{\delta Z}{\gamma} \right) = N_{tot} - \frac{\beta}{\delta} - \frac{\alpha}{\gamma} - \frac{\delta Z}{\gamma} \quad (3.101)$$

$$\rightarrow \quad \left(1 + \frac{\delta}{\gamma} \right) Z = N_{tot} - \frac{\beta}{\delta} - \frac{\alpha}{\gamma} \quad \rightarrow \quad \left(\frac{\gamma + \delta}{\gamma} \right) Z = N_{tot} - \frac{\beta}{\delta} - \frac{\alpha}{\gamma} \quad (3.102)$$

Thus we can the final result for our stationary point, (N^*, P^*, Z^*) :

$$Z^* = \frac{\gamma}{\gamma + \delta} \left(N_{tot} - \frac{\beta}{\delta} - \frac{\alpha}{\gamma} \right) \quad P^* = \frac{\beta}{\delta} \quad N^* = N_{tot} - P^* - Z^* \quad (3.103)$$

While we not go into the details here, this point is stable for all values of total nitrogen above the second threshold of $N_{tot} > \frac{\alpha}{\gamma} + \frac{\beta}{\delta}$ (the point does not exist below this threshold, taking on a non-physical value of Z). What about the biological significance? First, we see that P^* is independent of total nitrogen levels — in a system with animals present (and enough nitrogen to support both plant and animal life), increasing the total nitrogen content will **not** lead to more plant growth, but only to increased animal population. Secondly, this constant plant level is determined by the constants related to the animal population (consumption, β , and animal death, δ), not by plant-specific growth terms. Additionally, this is not the same

plant level that is found in the absence of animals — if $\frac{\beta}{\delta} < \frac{\alpha}{\gamma}$, then the plant population will decrease when animals are present, while if $\frac{\beta}{\delta} > \frac{\alpha}{\gamma}$, the plant population will increase. In the latter case, however, the total nitrogen content required to support animals and plants is more than double that needed to support only plants. Finally, we note that the animal population at the steady state is directly proportional to the excess nitrogen above the threshold value; the constant of proportionality is the ratio of the plant growth constant and the sum of the plant and animal growth constants.

3.3.3 Deviations of model from observation

Many natural systems (such as the levels of phytoplankton and zooplankton in the ocean) show oscillations in populations, rather than a constant steady state. What is missing from the model? One key aspect is seasonal variations — plant growth rates depend not only on nitrogen levels, but also on the amount of sunlight, which varies through the year. In other words, γ should be considered a function of time (or explicitly of sunlight levels, which would then vary in time). The issue is not fundamentally a deficiencies of the model, *per se*, but rather with the assumption of time-invariant constants. While this would lead to a significantly complicated model, for fast growing organisms like plankton, the changes in sunlight are slow compared to the changes in populations, and thus a series of models with different (but static) values of γ may be applied.