

Models of Biological Interaction Among Species or Populations

1. Models of biological interaction

The bio-economic models examined so far in this course have typically considered just one population of a single biological species interacting with its natural environment (the biological component) and human harvesting of that population (the economic component). There are two circumstances in which it is sensible to develop a bio-economic model in this way. First, if the biological growth behaviour of a single population of interest is independent of that of any other population or species. In that case, there is no useful information to be brought into the modelling exercise by jointly studying the biological growth of this species and any other. It is most unlikely that any population will be strictly independent of all others, but it may be approximately so in some cases. As a practical matter, this might justify its analysis in isolation.

Second, we may accept that the behaviour of the population of interest is affected in many ways by many other populations or species, but with no single relationship being particularly dominant. In that case, a researcher might choose to regard all other populations/species as constituting (part of) that population's environment. The modeller would then give greater attention to modelling that environment – perhaps by treating it as being stochastic or uncertain in some way – but would not develop models of interaction between specific species or populations.

But there are circumstances where proceeding in this way is not appropriate. Of most importance are those cases where particular species interact in important ways. These relationships may be as predators and prey, as with big cats and herbivore mammals; they may involve parasitism in which one species inhibits the growth of another; they may exhibit mutualism (or symbiosis) where each species requires the other for its survival (such as some bacteria and hosts); or they may involve one of several other types of relationship.¹ Wherever the relationship between two or more populations is significant, the researcher into the behaviour of one of those populations is throwing away important and relevant information by ignoring that relationship. In this set of notes we investigate some models of biological interaction between populations, and then briefly show how such models can be used to shed light on the issues of biodiversity and sustainability.²

It will be helpful to begin by outlining a classification of models of biological interaction developed by Shone (1997). We shall also investigate some of the examples he considers. Suppose that there are two populations of different species, labelled F and P . Let f denote the net contribution of a 'representative' individual in F to the magnitude of population F , and let p denote the net contribution of one individual in P to the size of population P . We specify f and p in the following, relatively general, ways.

$$f = \alpha + \beta F_t + \chi P_t \quad (1)$$

$$p = \delta + \varepsilon P_t + \phi F_t \quad (2)$$

In Equations 1 and 2, the parameters α and δ are population-specific natural growth coefficients. They correspond to the parameter that we called the intrinsic growth rate of a fish population in the logistic growth model of a single population examined earlier.

Parameters β and ε are population-specific crowding (or self-limiting) coefficients, which can be interpreted in the following ways:

- If β and ε are both negative, both species are subject to (intra population) crowding effects, and so there will be limits to which the population size could grow, even in the absence of any limits imposed by relationships with other species.
- If β and ε are both positive, the fertility of each population increases the larger is the size of that population. There is a kind of mutualism *within* a population.

Mixed cases are, of course, also possible.

The parameters χ and ϕ relate to the interaction between different species or populations. In particular:

- χ, ϕ both negative implies inter species *competition*
- χ, ϕ both positive implies *mutually beneficial interaction* (mutualism or cooperation)
- χ, ϕ of opposite sign implies a *predator-prey* relationship (the population with the positive parameter being the predator, and with the negative being the prey)

In the absence of migration, the growth of each population is given by the product of the net contribution of a representative individual and the number of individuals in the population.

That is, in continuous time notation

$$\dot{F} = fF_t$$

$$\dot{P} = pP_t$$

and in discrete time notation

$$F_t - F_{t-1} = f_{t-1}F_{t-1}$$

$$P_t - P_{t-1} = p_{t-1}P_{t-1}$$

(In large part, we focus on using continuous time notation in these notes.)

By imposing restrictions on this general specification, various particular models of biological interaction are generated. We consider four of these. For reference purposes, we list these together with the parameter values being used in our modelling examples in the table below.

Model	α	δ	β	ε	χ	ϕ
Competition, with no self-limitation $\dot{F} = (a - bP_t)F_t \quad \dot{P} = (c - dF_t)P_t$	+	+	0	0	-	-
	a = 4	c = 3			b = 3	d = 1
Predator-prey with no self-limitation $\dot{F} = (a - bP_t)F_t \quad \dot{P} = (-c + dF_t)P_t$	+	-	0	0	-	+
	a = 1	c = 0.1			b = 1	d = 0.1
Predator-prey model with population-specific crowding for prey $\dot{F} = (a - bP_t - uF_t)F_t \quad \dot{P} = (c + dF_t)P_t$	+	-	-	0	-	+
	a = 1	c = 0.1	u = 0.1		b = 1	d = 0.1
Predator-prey model with population-specific crowding for prey and predators $\dot{F} = (a - bP_t - uF_t)F_t \quad \dot{P} = (c + dF_t - vP_t)P_t$	+	-	-	0	-	+
	a = 1	c = 0.1	u = 0.1	v = 1/8	b = 1	d = 0.1

1.1(a) Competition between species with no crowding or self-limitation

This model is obtained from the general specification (1 and 2) by imposing the restrictions $\{\alpha > 0, \beta = 0, \chi < 0\}$ and $\{\delta > 0, \varepsilon = 0, \phi < 0\}$. The population growth models may then be written as

$$\dot{F} = (a - bP_t)F_t \quad (a, b > 0) \quad (3)$$

$$\dot{P} = (c - dF_t)P_t \quad (c, d > 0) \quad (4)$$

What do these equations tell us? First, both intrinsic growth rate coefficients (here a and c) are positive, so in isolation each population becomes larger over time. Indeed, the absence of any self-limitation (strictly speaking, the property that $\beta = 0$ and $\varepsilon = 0$) means that in isolation the populations would grow without bounds. However, the populations are not in isolation; the negative coefficients in the terms $-bP$ and $-dF$ show that each species is in competition with the other for scarce resources. In Equation 3, for example, the term $-bP_t$ means that the net contribution to the F-population of one individual member of F is negatively related to the size of the other population, P. As this relationship is true for both populations, we have a ‘species competition’ model.

There are three possible outcomes to this interactive relationship. It may be helpful to think of the example of two competing garden plants (or perhaps a chosen plant and a weed) to visualise these. Two of these are equilibrium outcomes. The first – a trivial (uninteresting) solution - is that the equilibrium stock of each is zero. A second equilibrium outcome is that there is a positive stock of both, in which the competitive force that each exerts on the other is completely balanced. But such an equilibrium will be a ‘knife-edge’, or unstable, equilibrium.

Any event leading one population to become larger than its equilibrium level will precipitate a chain reaction sequence driving the other to zero. This points to the third kind of outcome: one species will become increasingly dominant, and the stock of the other will be driven towards zero.³

It will be helpful to give a numerical example. We assume (using Example 12.4 in Shone, 1997) that Equations 3 and 4 take the particular forms

$$\dot{F} = (4 - 3P_t)F_t \quad (5)$$

$$\dot{P} = (3 - F_t)P_t \quad (6)$$

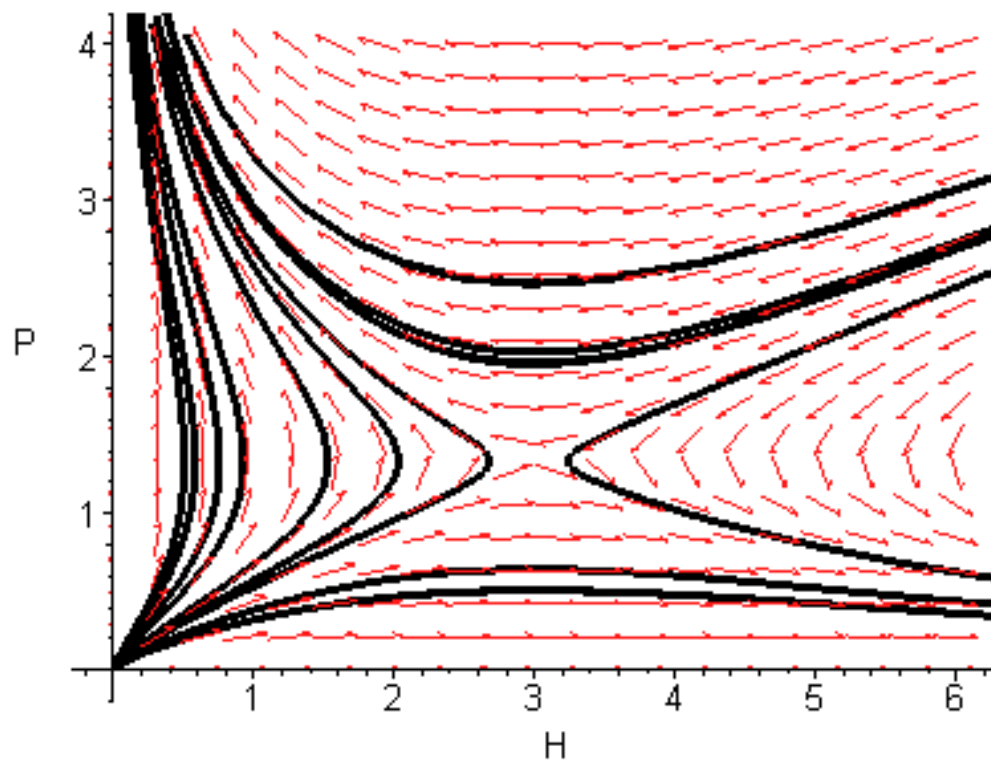
By definition, an equilibrium occurs where the two population levels are simultaneously constant, that is, $\dot{F} = 0$ and $\dot{P} = 0$. Imposing these equilibrium conditions on 5 and 6 gives

$$0 = (4 - 3P_t)F_t$$

$$0 = (3 - F_t)P_t$$

which yield the pair of solutions $\{F = 0, P = 0\}$ and $\{F = 3, P = 4/3\}$. These are shown in Figure 1 below (generated using Maple), the former at the origin, the latter by the intersection of the two straight lines representing $\dot{F} = 0$ and $\dot{P} = 0$. The arrows show the directions in which the two populations will move (defined by Equations 5 and 6) from any arbitrarily-chosen starting point. If sequences of these directional arrows are connected together, we obtain dynamic time paths for the two populations. Several such paths are shown in the diagram by the heavily-drawn curved lines.⁴ It is evident from that diagram that our previous conclusions are valid. A steady state equilibrium with positive values of F and P does exist. However, this is an unstable ‘knife edge’ equilibrium; any deviation from this equilibrium will lead to the population levels diverging even further, with one of the species becoming increasingly dominant and the other becoming ever-closer to zero with the passage of time. Moreover, almost all initial starting points fail to find that equilibrium and so – in the absence of deliberate management – the equilibrium is most unlikely to be achieved.

Figure 1 Equilibrium and dynamics of the competition with no crowding model.



1.1(b) Predator-prey model with no population-specific crowding or self-limitation

Suppose we wish to examine biological interaction between populations of a predator and a prey, but still retain the property that neither population is subject to crowding or self-limitation. This can be done by imposing the restrictions $\{\alpha > 0, \beta = 0, \chi < 0\}$ and $\{\delta < 0, \varepsilon = 0, \phi > 0\}$ on the general specification (equations 1 and 2). The resulting model – first developed by Lotka (1925) and Volterra (1931) – takes the form

$$\begin{aligned}\dot{F} &= (a - bP_t)F_t && (a, b > 0) \\ \dot{P} &= (-c + dF_t)P_t && (c, d > 0)\end{aligned}$$

In this predator-prey model, F is the prey population and P is the predator population. In the differential equation for F, the positive intrinsic growth rate a implies that in the absence of predation the prey population would increase through time. Moreover, the restriction $\beta = 0$ implies the absence of any self-limiting factor, and so this growth process would be without bounds: the prey population would expand indefinitely.

However, the prey population is constrained by its relationship with the predators. The term $-bFP$, found by multiplying out the terms within and outside brackets, shows that the prey population falls because of predation, and that this effect is larger the greater is the predator population.

In contrast, the negative intrinsic growth coefficient for the predator implies that the predator depends on the prey population for its existence: in the absence of F, the population P would collapse to zero. However, the presence of prey acts to increase the predator population; this effect is represented by the interaction term dFP .

What kind of outcome would one expect in this situation? Intuition suggests that we might find a balance between predator and prey populations. To see why, note that an equilibrium will, by definition, exist where both predator and prey populations are constant. The prey population will be constant where net recruitment (aF) equals net losses due to predation (bFP). The predator population will be constant when natural population loss (cP) is just balanced by growth associated with presence of the prey population (dFP). This gives us two equations; knowing values of the parameters a, b, c and d, these two equations could be solved for the two unknowns, the equilibrium levels of F and P. By way of example, we take the parameter values to be $a = 1, b = 1, c = 0.1$ and $d = 0.1$. The two equilibrium equations are then

$$P = 1$$

and

$$0.1F = 0.1$$

which yield the equilibrium solution $F^* = 1$ and $P^* = 1$.⁵

However, this intuition and ‘steady-state algebra’ both fail to reveal one of the important features of this model. Except fortuitously, or through deliberate management, the equilibrium outcome $F^* = 1$ and $P^* = 1$ will never be realised! Instead, what will happen is that populations of both F and P will continually fluctuate, cycling above and below those steady state levels but not actually converging to them.⁶ (This is shown in Figure 2b below.) Moreover the amplitude of the oscillations depends on the initial values of the variables: different initial values lead to different amplitudes. This can be observed by examining Figure 2a.⁷

Figure 2a Equilibrium and dynamics in the LV predator-prey model.

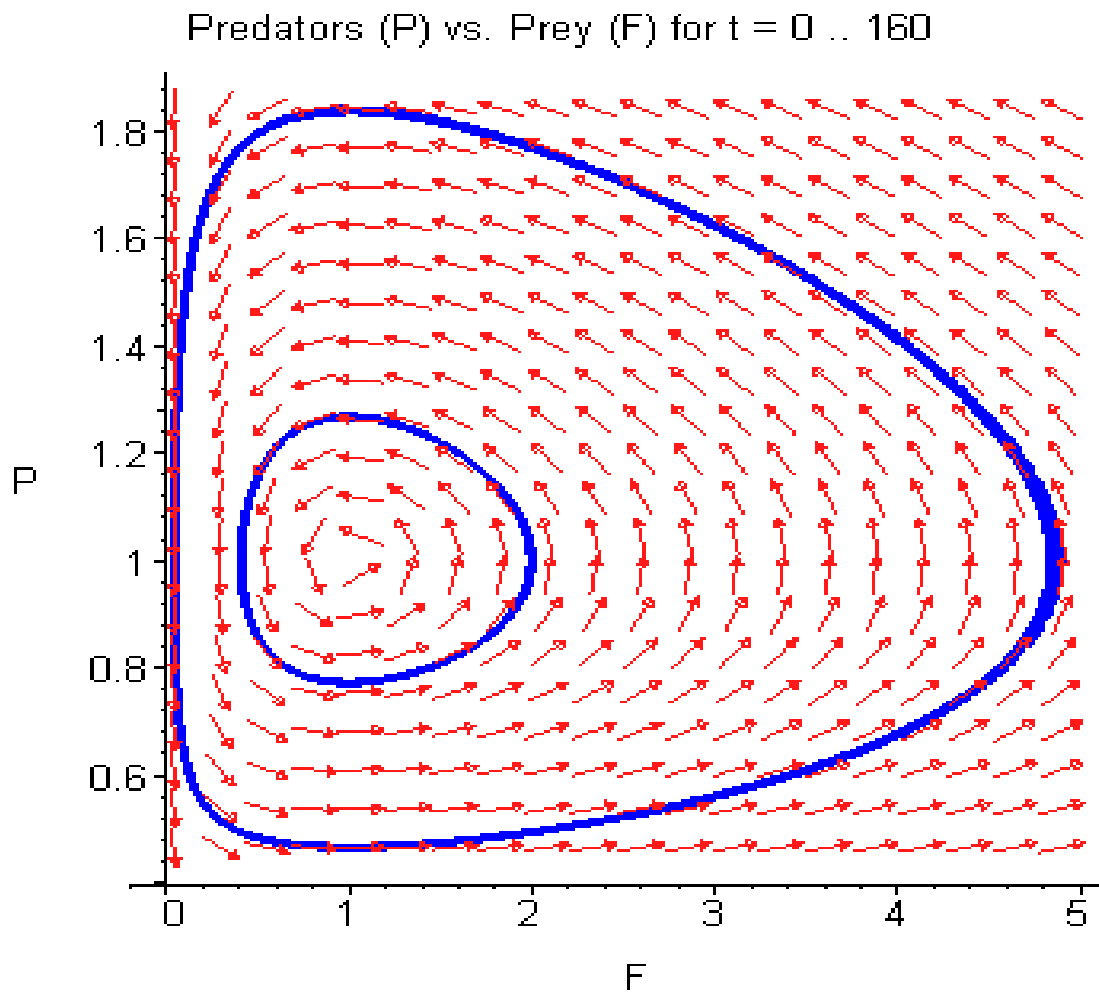
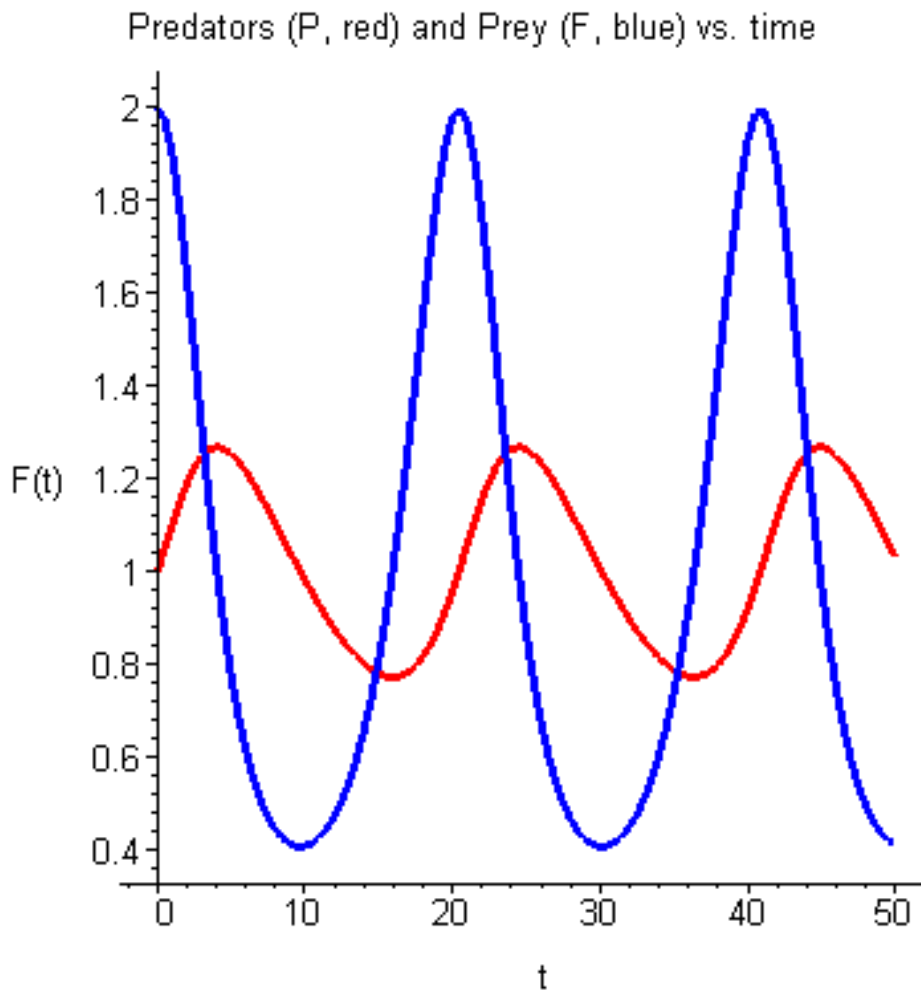


Figure 2b Population cycles in the predator-prey model where neither population is self-limiting.



1.1(c) Predator-prey model with population-specific crowding for prey

The cycling, non-convergent dynamic behaviour of the model examined in the section 1.1(b) is a mathematical property of the set of differential equations (and the associated parameter restrictions) which underlies the L-V predator-prey model. Many biologists regard these dynamic properties as being inconsistent with the observed evidence, or feel that they are overly restrictive. Various generalisations to the predator-prey model have been developed.

One such generalisation involves introducing upper limits to the population sizes of the prey, much as we did earlier when looking at biological models of fisheries. This can be implemented by making the parameter β in the general specification be negative (rather than zero). Then this model is obtained from the general specification (1 and 2) by imposing the restrictions $\{\alpha > 0, \beta < 0, \chi < 0\}$ and $\{\delta < 0, \varepsilon = 0, \phi > 0\}$. A predator-prey model with logistic-like population specific upper size on the prey thus can be specified with the following general structure

$$\begin{aligned}\dot{F} &= (a - bP_t - uF_t)F_t & (a, b, u > 0) \\ \dot{P} &= (c + dF_t)P_t & (c, d > 0)\end{aligned}$$

These equations imply that the prey population has a component that corresponds to a logistic form of biological growth function.^{8,9} To see that these equations do indeed contain logistic-like growth functions, consider the F population. Multiplying out terms and rewriting, the resultant equation gives

$$\dot{F}_t = (a - bP_t - uF_t)F_t = aF_t - uF_t^2 - bP_tF_t = aF_t \left(1 - \frac{uF_t}{a}\right) - bP_tF_t = aF_t \left(1 - \frac{F_t}{F_{MAX}}\right) - bP_tF_t$$

where $F_{MAX} = a/u$.

It is evident that there are here **two** limiting influences on the population of F:

1. F_{MAX} is the maximum carrying capacity of the population in the absence of the predator population P; as F rises from low levels, members of the F-population face increasingly intense “self-competition” given the environmental milieu in which they are located.
2. The multiplicative term $-bP_tF_t$ implies that the prey population, F, is negatively related to the size of the predator population, P.

For a numerical example we consider the following specific forms:

$$\dot{F} = aF_t \left(1 - \frac{F_t}{F_{MAX}}\right) - bF_tP_t = F_t \left(1 - \frac{F_t}{10}\right) - F_tP_t \quad (7)$$

$$\dot{P} = -cP_t + dF_tP_t = -0.1P_t + 0.1F_tP_t \quad (8)$$

which involves the following parameter value assumptions:

a = 1, b = 1, u = 1/10, c = 1/10, and d = 1/10.

Setting \dot{F} and \dot{P} equal to zero, and solving these two equations for F and P gives three equilibrium solutions: $F^* = 0$ and $P^* = 0$; $F^* = 10$ and $P^* = 0$; $F^* = 1$ and $P^* = 0.9$. The first of these is the empty or 'trivial' solution in which neither predators nor prey exist. The second is where predators are entirely absent, and the prey grow to maximum population size, 10.

The third solution, investigated further here, is that in which there is a joint equilibrium of one prey and 0.9 predators. (Note that we have not specified units in this example, so 0.9 may, for example, be in units of thousands, in which case $P = 0.9$ corresponds to 900 individuals.) The dynamics of this model are shown in Figure 3a. It is evident from looking at the directional arrows and the examples of dynamic adjustment paths (shown by the heavy continuous lines) that $F^* = 1$ and $P^* = 0.9$ is an equilibrium solution that will eventually be achieved provided that at least some individuals of both species exist; dynamic adjustment paths from any arbitrary position all lead to that equilibrium. Moreover, this is a stable equilibrium (a disturbance would only knock the system out of equilibrium temporarily as dynamic adjustments will restore the equilibrium). This is also evident in Table 3b showing

the convergent oscillatory dynamics of the two populations over time, starting from some arbitrarily chosen initial population levels.

Figure 3a Equilibrium and dynamics in the predator-prey model with logistic self-limiting (crowding) of the prey species.

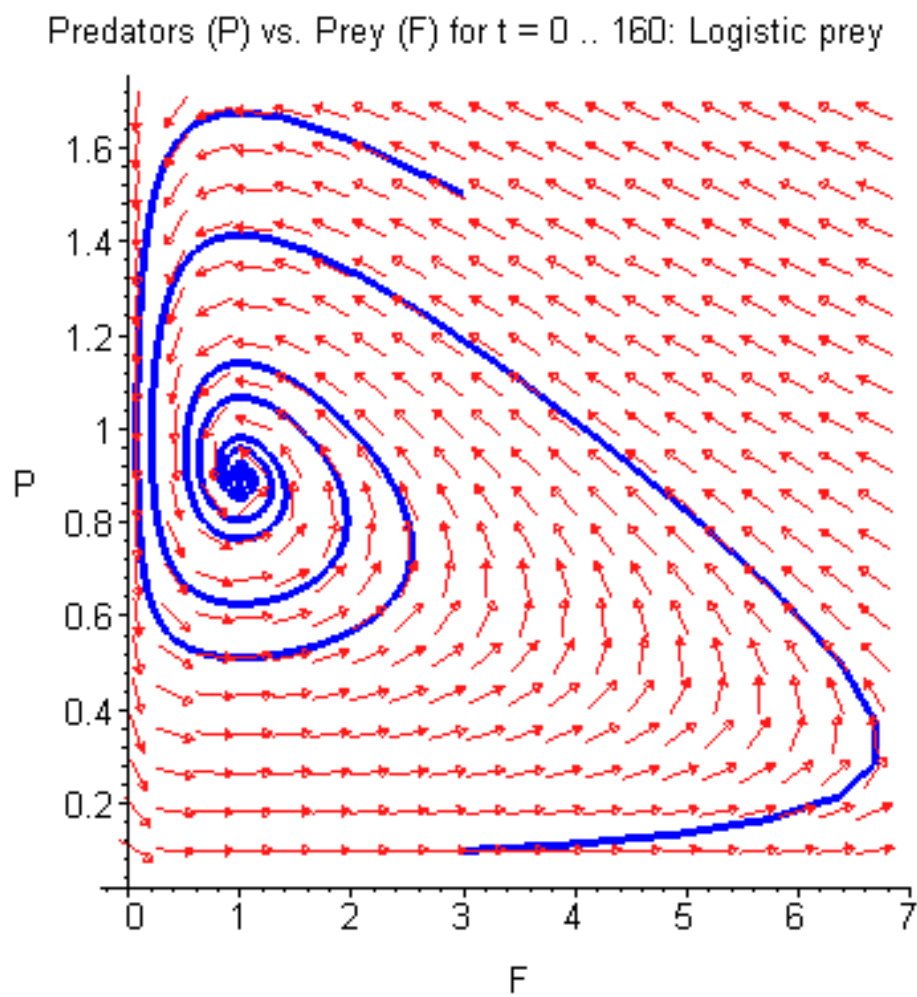
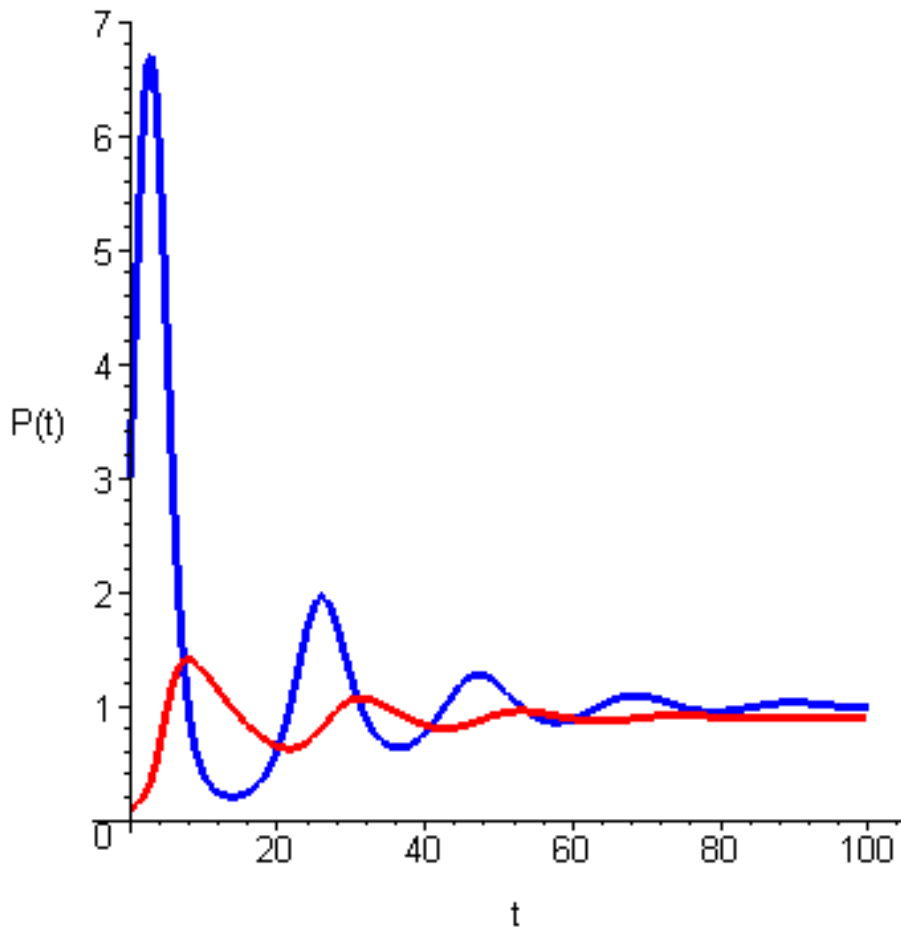


Figure 3b

Predators (P, red) and Prey (F, blue) vs. time: logistic prey



A useful exercise for you to do at this point would be to set up a discrete time counterpart to Equations 7 and 8 in a spreadsheet, and to verify the solution we have just described. Try a series of alternative starting values of F and P (ideally not too far away from the equilibrium values) and observe what happens. You might also like to see what happens as you change the parameter values of the model. If you wish to verify that you have set up your spreadsheet correctly, an example is provided in the file *Interaction.xls*.

1.1. (d) Predator-prey model with population-specific crowding for prey and predators

Next consider the case where there are upper limits to the population sizes of the predators and prey. This can be implemented by making the parameters β and ε in the general specification each be negative (rather than zero). A predator-prey model with logistic-like population specific upper size limits thus can be specified with the following general structure

$$\begin{aligned}\dot{F} &= (a - bP_t - uF_t)F_t & (a, b, u > 0) \\ \dot{P} &= (c + dF_t - vP_t)P_t & (c, d, v > 0)\end{aligned}$$

These equations imply that each population has a component that corresponds to a logistic form of biological growth function.¹⁰ We saw in the previous sub-section that these equations do indeed contain logistic-like growth functions; this time, consider the P population. Multiplying out terms and rewriting, the resultant equation gives

$$\dot{P}_t = (c - vP_t + dF_t)P_t = cP_t - vP_t^2 + dF_tP_t = cP_t\left(1 - \frac{vP_t}{c}\right) + dF_tP_t = cP_t\left(1 - \frac{P_t}{P_{MAX}}\right) + dF_tP_t$$

where $P_{MAX} = c/v$.

We see there are **two** influences on the population of predators:

1. P_{MAX} is the maximum carrying capacity of the population in the absence of the population F; as P rises from low levels, members of the P-population face increasingly intense “self-competition” given the environmental milieu in which they are located.
2. The multiplicative term $+ dF_tP_t$ implies that the predator population, P, is **positively** related to the size of the prey population, F.

For a numerical example we consider the following specific forms:

$$\dot{F} = aF_t\left(1 - \frac{F_t}{F_{MAX}}\right) - bF_tP_t = F_t\left(1 - \frac{F_t}{10}\right) - F_tP_t \quad (7^*)$$

$$\dot{P} = cP_t\left(1 - \frac{P_t}{P_{MAX}}\right) + dF_tP_t = 0.1P_t\left(1 - \frac{P_t}{0.8}\right) + 0.1F_tP_t \quad (8^*)$$

which involves the following parameter value assumptions:

$a = 1$, $b = 1$, $u = 1/10$, $c = 1/10$, $d = 1/10$ and $v = 1/8$.

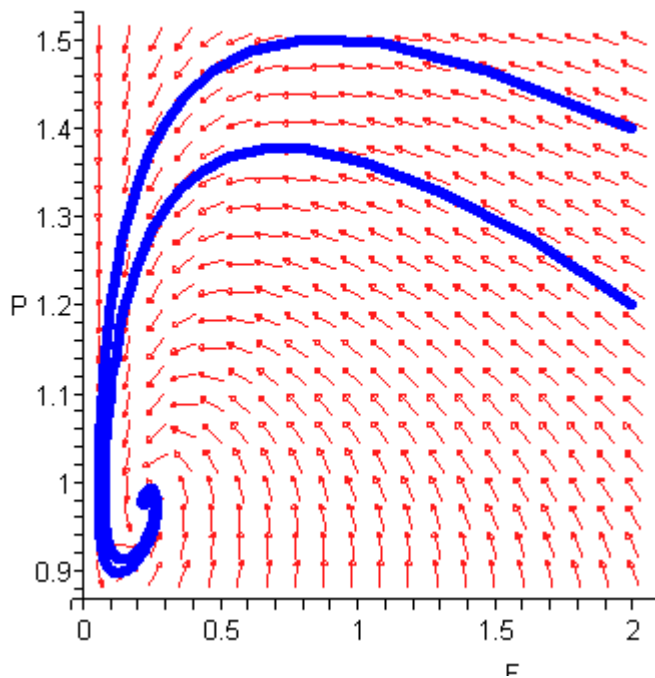
Setting \dot{F} and \dot{P} equal to zero, and solving these two equations for F and P gives the equilibrium solution $F^* = 2/9$ and $P^* = 44/45$.¹¹ The dynamics of this model are shown in Figure 4. It is evident from looking at the directional arrows and the examples of dynamic adjustment paths (shown by the heavy continuous lines) that $F^* = 2/9$ and $P^* = 44/45$ is an equilibrium solution that will eventually be achieved (dynamic adjustment paths from any arbitrary position all lead to it) and that it is a stable equilibrium (a disturbance would only knock the system out of equilibrium temporarily as dynamic adjustments will restore the equilibrium).

A useful exercise for you to do at this point would be to set up a discrete time counterpart to Equations 7 and 8 yourself in a spreadsheet, and to verify the solution we have just described. Try a series of alternative starting values of F and P (ideally not too far away from the equilibrium values) and observe what happens. You might also like to see what happens as

you change the parameter values of the model. If you wish to verify that you have set up your spreadsheet correctly, an example is provided in the file *Interaction.xls* in the *Additional Materials*.

Figure 4: Equilibrium and dynamics in the predator-prey model with crowding.

Predators (P) vs. Prey (F) for $t = 0 \dots 160$: Logistic P and F



1.2 Economic Policy

The various models of species interaction that we have examined in this note can be used to generate a number of policy implications. One way of doing so is to add, as an extra component to the model, a social welfare function (SWF). This could be specified in various ways. It might contain F and P as arguments, and so reflect society's relative valuations over the possible combinations of F and P populations. Alternatively, the arguments of the SWF might be the costs and benefits of harvesting each population at various rates. If the *in situ* stock size of F and/or P also contributes to utility, those benefits should also enter as arguments of the SWF.

Given a SWF, an optimisation exercise can then be undertaken, maximising social welfare subject to the constraints of the differential equations that are thought to be appropriate for F and P , and for given initial values of F and P . Note that an optimisation analysis of this kind will only be useful for policy purposes if populations of F and/or P can be controlled by human intervention. Hartwick and Olewiler (1998) do an analysis of this kind for two interacting species, sharks and tuna, and demonstrate how interesting policy inferences can be drawn from such an exercise.

An alternative way of deriving policy insight is to bring human intervention explicitly into the model being considered. One way of doing so is to introduce more species into the model, including one which is bred and maintained for human benefit, yet which also interacts with one or more species of our model. In most cases of interest, this third species will be some kind of domesticated livestock animal or farm crop. Conrad (1999, pages 173-182) investigates a three species model of grass-herbivore-predator interactions, and where farmers breed and maintain domesticated cattle which also compete for grass. This is a useful basis for studying policy implications of farming or agriculture, and so we shall examine a slightly modified version of his model, given by Equations 9-11. **Note that we now change notation slightly, using H rather than F for the herbivore.**¹²

Grass biomass (G) dynamics:

$$\dot{G} = gG_t \left(1 - \frac{G_t}{G_{MAX}} \right) - \alpha_1 H_t \quad (9)$$

Herbivore (H) dynamics:

$$\dot{H} = hH_t \left(1 - \frac{H_t}{\theta G_t} \right) - \beta H_t P_t \quad (10)$$

Predator (P) dynamics:

$$\dot{P} = pP_t \left(1 - \frac{P_t}{P_{MAX}} \right) + \chi H_t P_t \quad (11)$$

Examining these three equations, you will see that the first component on the right-hand side of each equation constitutes a logistic growth process, with the qualification that a fixed maximum herbivore population has been replaced by the term θG_t , indicating that the upper limit to which the herbivore population can grow is a fixed multiple of grass biomass.

The remaining terms on the right-hand side further specify the form of biological interactions. Grass is consumed by the herbivore population at the rate α per individual, and so at the rate $\alpha_1 H_t$ by the population at time t . The term $-\beta H_t P_t$ shows that herbivores are consumed by predators at a rate given by a fixed multiple of the product of the herbivore and the predator populations. In contrast, the predator population is positively related to that product. Once again, given knowledge of the parameter values and initial values for the variables G , F and P , one could identify steady state (equilibrium) populations, and simulate the dynamic evolution of these variables through time.

Next we follow Conrad by introducing a fourth population, domestic cattle, into the model. This is done by assuming that cattle consume grass at the rate α_2 per head. Equation 9 is then amended to become¹³

$$\dot{G} = gG_t \left(1 - \frac{G_t}{G_{MAX}} \right) - \alpha_1 H_t - \alpha_2 C \quad (12)$$

Note that in Equation 12, the variable C is not time-subscripted. That is, we are treating the cattle stock as a fixed constant, predetermined by economic agents.

At this stage of development, the model has become quite rich, and can be used in various ways. The researcher could leave the various equations of the model in general parametric form (as in 10 to 12 above) and could undertake qualitative analysis. Alternatively, particular parameter values and initial values of the variables G , F , P and P could be chosen and quantitative analysis be done. In either case, it would be possible to address the following types of questions:

- (1) Given particular choices of cattle stock, P , what are the steady-state equilibrium values of G , F and P ? How do those equilibrium values change as P is changed?
- (2) Using dynamic simulation, how do the paths of G , F and P vary over time in response to changes in the stock of domestic cattle? Do adjustment paths converge on a new steady state equilibrium?
- (3) What, if any, are the limits to which cattle stocks can be raised before the biological system breaks down (with one or more of the other stocks being driven to zero, or below some critical threshold)?
- (4) What level of cattle stocks maximise some appropriately specified social welfare function?

Conrad takes this kind of model one stage further by making the grass growth function stochastic rather than deterministic. This can be done by replacing the deterministic growth rate g in Equation 12 by g_t , a random variable with some suitably chosen distribution. It should be evident that, provided that the expected value of g_t is g , steady state equilibrium solutions will not be changed. However, the dynamic adjustments paths will now exhibit more variability. Moreover, if the variance of g_t is sufficiently large, these dynamic time paths may well breach biological threshold points leading to population collapses. In a stochastic environment, therefore, it is likely to be the case that human impacts on the system (measured in this case by the size of cattle stocks) will need to be smaller to avoid possible ecosystem collapse. This is one way of modelling the idea of a safe minimum standard of conservation that we described earlier. Alternatively, it is a useful way of modelling sustainability questions in a relatively simple bio-economic model framework.

This brief account of a multiple species bio-economic model has been given primarily as a pointer to how you might go about doing this kind of modelling yourself. We take it no further here in these notes. But the Conrad-type model is operationalised and simulated in both the Excel file and the Maple file referred to below. Using those files, you can examine the questions (1) to (4) that we listed above.

If you are interested in seeing how some of the issues here could be operationalised, a sensible option might be to follow the exposition in Conrad (1999), Chapter 8. Alternatively, we have provided in the *Additional Materials* to Chapter 17 of the Perman et al text an Excel file (*Interaction.xls*) which simulates a stochastic version the 'three species + cattle' model that has just been described, and which is used to explore the questions raised in this sub-section. You will also find in the *Additional Materials* the Maple file which has been used to generate all the results (and graphics) used in this set of notes, and which you can edit yourself if you wish to experiment further with simulations. (It uses version 9.5 of Maple.)

References: (Full details can be found in the Bibliography in the Perman et al text.)

Conrad, 1999

Dajoz, 1977

Hartwick and Olewiler (1998)

Lotka (1925)

Shone (1977)

Volterra (1931)

ENDNOTES :

¹ Ecologists recognise at least four other forms of biological interaction (see, for example, Dajoz, 1977): *competition*, where species are in competition for scarce resources; *cooperation*, where symbiotic relationships are chosen for common purposes, such as security against predation; *commensalism*, where one species benefits but the other neither suffers nor benefits; and *amensalism*, where one species is unaffected but the other suffers from a relationship.

² Discussions of this type sometimes refer to species interaction and sometimes to population interaction. Generally, it is the former which is relevant, provided we take care to note that the populations are of different species. In some special cases, the populations of interest may equate with entire species, in which case either is appropriate.

³ Mathematically, this kind of outcome is not an equilibrium outcome in this model, as no fixed point will ever be reached. It is worth noting that this property comes from the fact that this model has no (intra-population) crowding or self-limitation; hence there is no fixed point to which it can grow.

⁴ Figure 1 is an example of what is called phase plane analysis. A discrete time counterpart to the continuous time specification used for this model is given by:

$$F_{t+1} = F_t + (4 - 3P_t)F_t$$

$$P_{t+1} = P_t + (3 - F_t)P_t$$

The file *Interaction.xls* shows how this discrete time model can be analysed by means of an Excel spreadsheet.

⁵ There is also a second, trivial, solution $F = 0$ and $P = 0$.

⁶ Strictly speaking, this is only true in continuous time models. If a discrete time counterpart model is examined, cyclical behaviour will also be observed, but it will be explosive, with cycles of increasing amplitude (until the system collapses). This can be seen by examining sheet LV in the Excel file *Interaction.xls* in the *Additional Materials*.

⁷ Figure 2 was generated using Maple. A discrete time version can be found in the Excel file *Interaction.xls* (sheet = LV).

⁸ For the generalisation that we are discussing here to make sense, it is usual to specify that the parameter c in the predator equation is positive, unlike in the LV model *without* crowding effects (where it was negative).

⁹ Note that as $F_{\text{MAX}} \rightarrow \infty$, $F_t/F_{\text{MAX}} \rightarrow 0$, and so the logistic component disappears. Hence the linear form used in the L-V model can be regarded as a special form of logistic in which the quadratic collapses to a linear by virtue of there being an infinitely large upper limit to the population size.

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¹¹ Mathematically there are also three other solutions. Can you deduce what these are?

¹² The major variation concerns Equation 11 below. Unlike in our equation, Conrad specifies the predator population to be directly related to the herbivore population, and does not contain a logistic component in the form given by 11.

¹³ Conrad (1999) actually uses (in his Equation 8.7) a discrete time counterpart to our continuous time specification 12.