Extra Exercises for Chapter 20
on Predator-Prey Cycles

Confirming the Competitive Exclusion Principle

These exercises[1] call for an expansion the model in chapter 20 to confirm the competitive exclusion principle. The model in the book has a single predator and a single prey. If you are interested in predators, you might add a second predator to the model. You would then simulate two predator populations attacking the same prey population. If you are interested in prey populations, you might add a second prey to the model. You would then simulate one predator population attacking two prey populations.

The competitive exclusion principle suggests that one of the two predator populations will dominate, and the other will be excluded from the system. Similarly, the principle suggests that one of the prey populations will dominate over time, and the other will be excluded. You can read about this principle in Odum's *Fundamentals of Ecology*:

Interspecific competition can result in equilibrium adjustments by two species, or it can result in one species population replacing another or forcing it to occupy another space or to use another food, whatever is the basis on competitive action. It is often observed that closely related organisms having similar habitats or life forms often do not occur in the same places. If they do occur in the same places, they use different food, are active at different times, or are otherwise occupying somewhat different niches … No two species can have exactly the same niche, of course, and still be different, but species, especially if they are closely related (and hence have similar morphological and physiological characteristics), are often so similar that they have virtually the same niche requirements. Experimental and observational research has shown that in a high proportion of cases there is one species to a niche. The explanation for the widely observed ecological separation of closely related (or otherwise similar) species has come to be known as the ***competitive exclusion principle*** *(Hardin 1960) or Gause's principle (after the Russian biologist who first confirmed the principle experimentally.*

Modeling Exercises

Let's expand the model from Fig. 20.2 in the book. This model shows plausible oscillations in a deer and cougar population (see Figs 20.7 and 20.9) when we adopt the 2nd shape for the predation function (see table 20.1). For these exercises, we will expand the model to include two predator populations. And we will expand the representation of the deer population as well.

[1] I appreciate the good work of Monica Roth and Rachel Emswiler, two students who earned their BS in Environmental Science from WSU in 2004. Their project in my environmental modeling class dealt with the competitive exclusion principle, and they helped with the preparation of these exercises.

Expanding the Deer Sector

The original model (Fig. 20.2) uses a single stock for the deer population with a starting value of 4,000. A new view of the deer population is shown in Fig. 1. The deer population is comprised of fawns, does, and bucks. Let's initialize the model with 2,000 fawns, 1,000 does, and 1,000 bucks. The model in the book uses "net births" to keep track of the net effect of births and deaths. Fig 1 is much more description. Deer births increases the stock of fawns and their maturation leads to either does or bucks. Deer births depend on the number of does and how many fawns they give birth to every year.

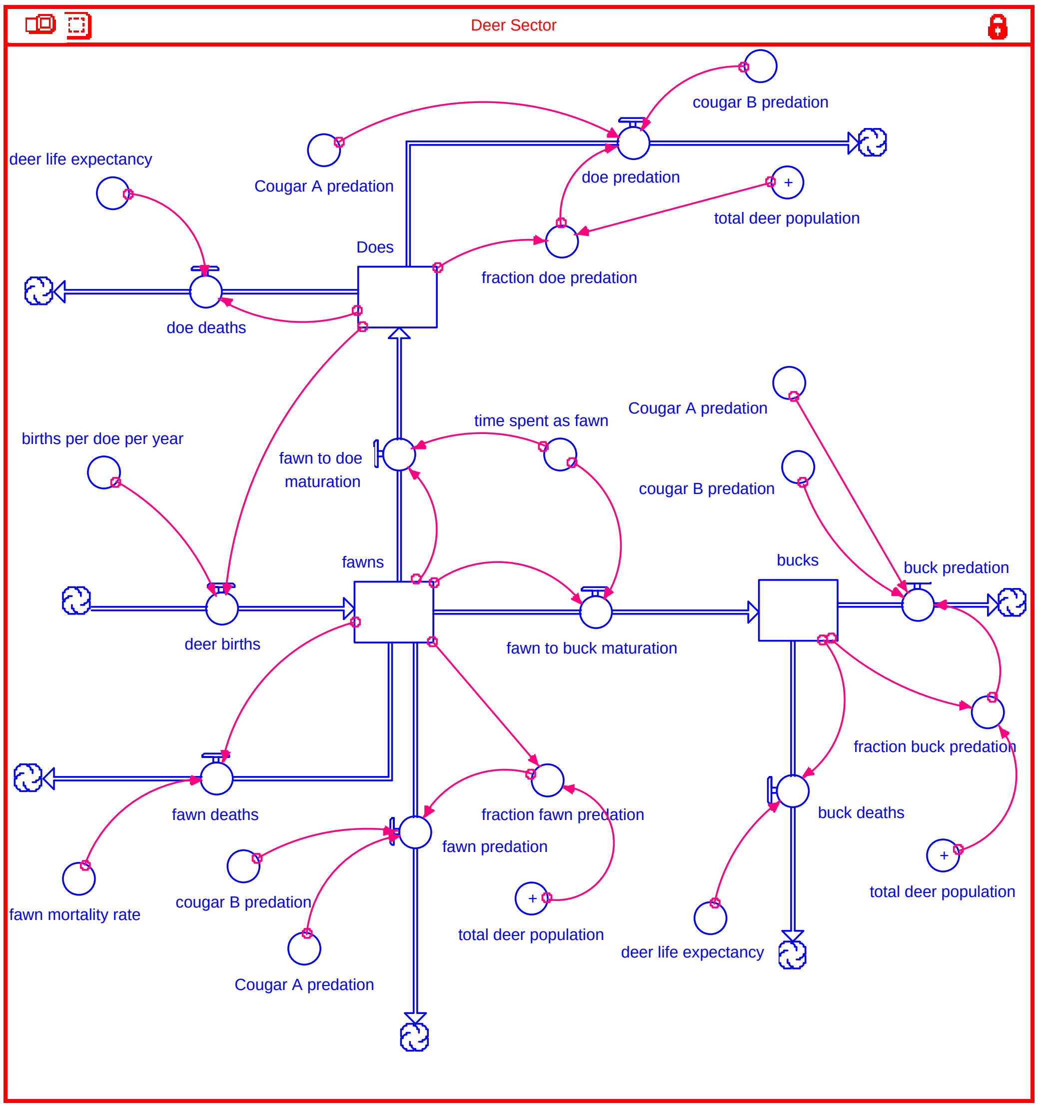

Figure 1. The deer sector of the expanded model.

We will assume births per doe per year is 1.5 (some have twins, but those without access to a good food source are more likely to have one.) The 1.5 represents an average over many years.) Fawn deaths represent death from causes other than predation; it depends on the number of fawns and the fawn mortality rate, which is 0.3. The does and the bucks have similar outflows that account for deaths from deaths due to “old age” (i.e., deaths other than predation). These depend on deer life expectancy. Let’s assume that bucks and does will live 12.5 years in the absence of predation.   Let’s also assume that the time spent as a fawn is 1.5 years. After 1.5 years, half the fawns move into the does, and the other half move into the bucks.

The predation flows are the focus of this exercise. There will be two cougar populations, known as Cougars A and Cougars B.   The total deer population (a summer variable) is located in the Cougar A Sector but is shown in the Deer Sector as a ghost variable. Total deer population is connected to fraction fawn predation variable, which is the fraction of the total population due to fawns. The equation for the fawn predation keeps track of the kills by both types of cougars:

fawn predation = cougar A predation*fraction fawn predation +
cougar B predation*fraction fawn predation.

In other words, the predation of fawns depends strictly on the prevalence of fawns in the deer population. At the start of the simulation, for example, the fawns comprise 50% of the population, so 50% of the deer kills from predation would be fawn kills.[2] A similar approach is used to allocate total predation among the doe and buck populations.

Expanding the Predator Sector

The cougar populations be identical to make the first model easy to understand. We expect two identical predators feeding on one prey population to find equilibrium and to co-exist indefinitely. But the competitive exclusion principle alerts us to a different result if one of the predators is more efficient at catching prey or has a larger litter size. In this situation, the more efficient predator will eventually drive the other out of the system.

We can test this principle by starting with two identical cougar populations, the populations shown in Fig. 2A,B. The initial value for the Cougar A population is 35. The Cougar A births is the product of the number of mature females, the litter size and the extra litter size multiplier. The Cougar A deaths is the population divided by the life span. To determine the number of mature female cougars, multiply the fraction of the population that is female (half) by the fraction of those females that are mature enough to give birth (2/3) and by the total number of cougars. The *extra litter size multiplier for cougar A* is a new variable with a slider to encourage experimentation. We will set this multiplier to 1.0 for now. (However, if we want to give these cougars a 5% advantage in reproduction, we can increase the multiplier to 1.05. If we want to impose a 5% disadvantage, we reduce the multiplier to 0.95.) The remaining variable in Fig. 2A is the Cougar A predation which is the product of the Cougar A population and the deer Cougar A kills per year.

[2] Students familiar with predation will know that the fawns tend to be somewhat more vulnerable than the older deer. This model does not account for that increased vulnerability.

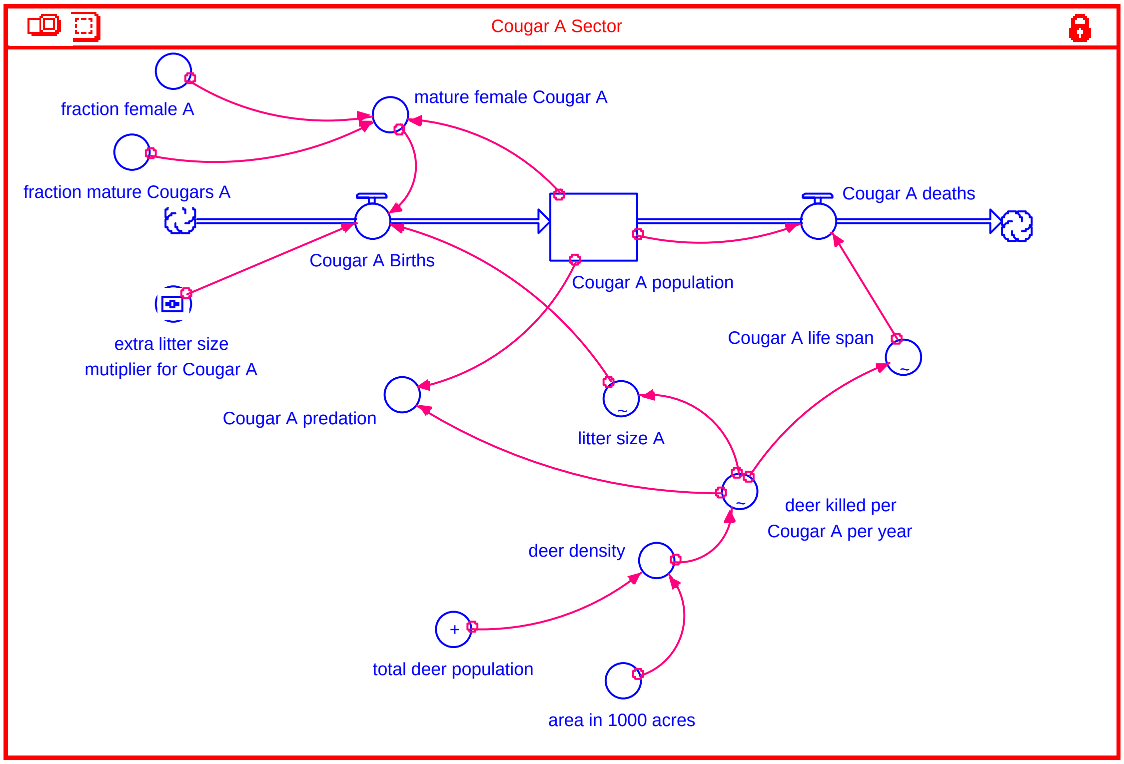

Fig. 2A. Diagram for the Cougar A population.

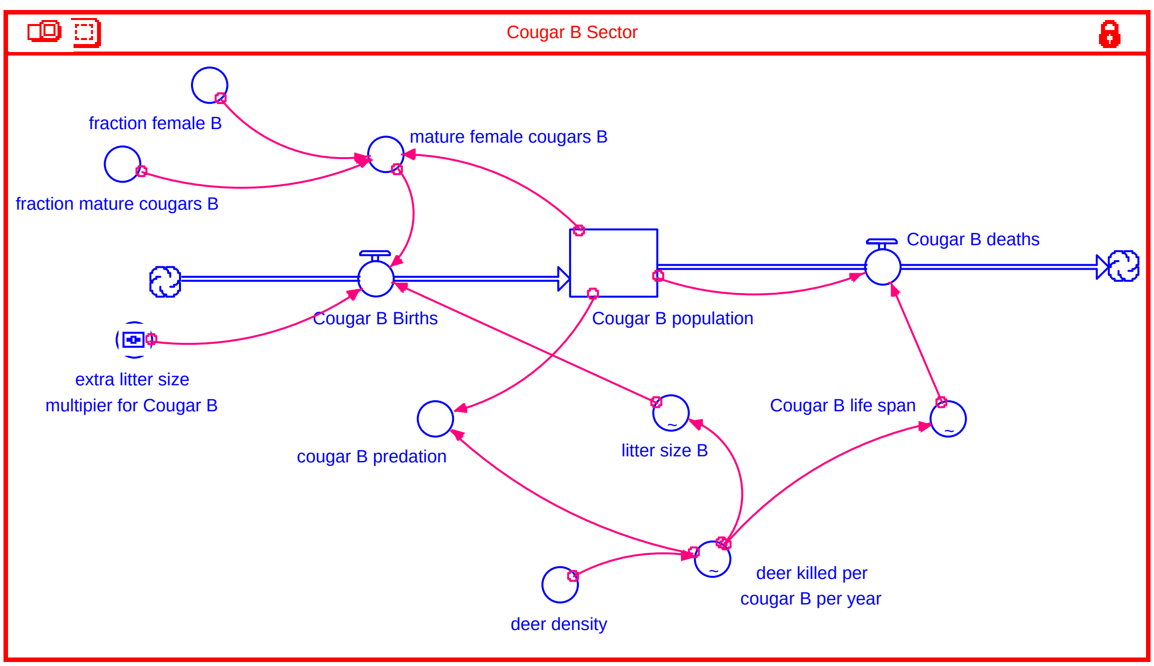

Fig. 2B. Diagram for the Cougar B population.

Fig 2B shows an identical treatment of the other cougar population. We adopt the identical assumptions for all the parameters – fraction female, fraction mature, litter size, and life span. And we set the extra litter size multiplier to 1.0. There were 50 cougars at the start of the simulations in the book. We'll start these simulations with 35 Cougars A and 15 Cougars B. We have 70% of the population as type A and 30% as type B. Since the two populations are identical in every other respect, we expect the simulations to show the 70%/30% mix to remain over time.

Exercises

1. Verify that 70%/30% Will Persist Forever:

Build the model shown in Figs. 1 and 2. Remember that the area is 800 thousand acres, and the deer density is measured in number of deer per thousand acres. The deer killed per cougar per year is a nonlinear function of the deer density. The two populations are assumed to have the identical success in predation, so you should use the 2nd shape (Table 20.1) for each population.

The cougar life span is used to control cougar deaths in Figs 2A,B. You know that the inverse of life span is the death rate (for example, a ten-year life span is a death rate of 0.1/year) Set the nonlinear relationship (~) for life spans to match the cougar death rates shown in Fig. 20.4 in the book.

The deer model in Fig 1 is more complicated than the deer portion of Fig. 1 since we now keep track of the does separately. The litter size should be controlled by a nonlinear graphical function (~) that corresponds to the short description of Fig 20.4 in the book.

Build the model and simulate for 20 years with DT set to 0.25 years. Your simulation should show damped oscillations in the deer and cougar populations. (The results should be similar to Fig 20.7 since you are using the 2nd predation function, but you should not expect to see identical results because of the many changes in the deer population.) Since the predators are identical in every respect, the simulations should show that 70% of the cougars will be type A and 30% will be type B during the entire simulation.

2. Test the Model with Different Starting Values

Rerun the model with the initial value of cougar A at 45 and the initial value of cougar B at 5. We still have 50 cougars at the start of the simulation, but with 90% as cougar A and only 10% as cougar B. Your simulation should show the identical results for the deer population as the previous exercise. And it should show the 90%/10% mix maintained during the entire simulation.

3. Simulate the Slow Exclusion of Cougar B

You know that two predator populations will not have identical attributes. One might have an advantage in predation; another might have an advantage in fertility or longevity. To test what happens when one population has an advantage, rerun the model in an 80 year simulation with cougar A given a 20% advantage in births after the 20th year of the simulation. This may be done by setting the pause interval to 20 years and changing the extra litter size multiplier for cougar A from 1.0 to 1.2 after the 20th year. You simulation should show that the Cougar A population will grow and Cougar B will fade to zero.

4. Simulate Rapid Exclusion of Cougar B

Rerun the model in an 80 year simulation with cougar A given a 100% advantage in births after the 20th year of the simulation. This may be done with a pause interval of 20 years and changing the extra litter size multiplier for cougar A from 1.0 to 2.0 after the 20th year. How long will it take for cougar B to be driven to extinction? What is the size of the cougar A population at the end of the simulation?

5. Simulate with Two Identical Prey Populations

Add a second deer population to the model, and split the population up between the two types (C and D). Give the two populations the identical assumptions and start the simulation with 2,000 of type C and 2,000 of type D. Simulate the model to verify that the 50%/50% mix of deer populations will persist forever.

6. Confirm Exclusion of a Weaker Prey Population

Introduce a multiplier for the deer populations that serves a purpose similar to the extra litter size multiplier for the cougar populations. Set the multipliers to 1.0 and simulate the model to see that you have a 50%/50% mix of deer populations. Then use the multiplier to give deer population C a slight advantage. Your simulation should show that deer population C will grow and that deer population D will fade to zero.

7. More Ambitious Exercise with Two Prey Populations

The previous exercises are for practice. Since you can anticipate the answers, you will know when you have done the modeling correctly. These exercises set the stage for more pragmatic modeling of competition among prey or among predators. If you are familiar with wildlife systems with two types of prey, adjust the model from exercises 5 and 6 to represent the two prey populations in a more descriptive manner. (In other words, get rid of the "extra multiplier" and use your own knowledge of the prey populations in the model. Perhaps one population is more vulnerable to predation, but the other population happens to have a smaller litter size. Then, before running the model, write down your expectations for which of the prey populations will emerge as the dominant population in the new model. (This step will not necessarily be easy. After all, how do we trade off differences in litter size against differences in vulnerability to predation? But take this step seriously before clicking on the run button.) Then simulate the new model and compare the results with your written explanation.

8. More Ambitious Exercise with Two Predator Populations

If you are familiar with wildlife systems with two types of predators, adjust the model from exercises 3 and 4 to represent the two predator populations in a more descriptive manner. (In other words, get rid of the "extra litter size multiplier" and use your own knowledge of the predator populations in the model. Perhaps one predator is more effective at tracking down the prey, but the other predator has a larger litter size.) Then, before running the model, write down your expectations for which of the predator populations will dominate in the new model. (This will not be easy, but take the time to write down your expectations anyway.) Then simulate the new model and compare the results with your written explanation.

Further Readings

Paul Colinvaux describes the competitive exclusion principle on page 337 of his Introduction to Ecology, John Wiley & Sons, 1973.

Eugene Odum describes the competitive exclusion principle on page 216 of Fundamentals of Ecology, Saunders College Publishing, third edition, 1971.

Odum credits Garret Hardin for naming the principle in "The competitive exclusion principle," *Science*, 131, pages 1292-1297.

Robert Ricklefs describes competitive exclusion on page 551 of Ecology, Chilton Press, second edition, 1973.