

# *Predator-prey interactions*

## *Key concepts*

- Predator-prey cycles
- Phase portraits
- Stabilizing mechanisms
- Linear stability analysis
- Functional responses
- The paradox of enrichment

## *Predator-prey cycles*

All organisms use resources for growth, survival and reproduction. A large number of species obtain these resources by eating other species. Consequently, predator-prey interactions are common in nature and the goal of this chapter is to explore the ways in which predation can affect the fate of both species involved. The fact that so many predator-prey interactions exist suggests an enduring quality to the interaction, which may appear puzzling since it is such an asymmetrical interaction (the prey rarely turns the tables to become the predator). To help us consider why predator-prey interactions persist over very long time scales, let's first consider a motivating case study.

The temperate desert of Curlew Valley, Utah is home to a number of wild coyotes (*Canis latrans*). Although omnivorous, small mammals form an important part of their diet. The jackrabbit *Lepus californicus* is one of its most reliable sources of prey.

Abundance of both of these species has been estimated continuously in Curlew Valley from 1962-1986 (Figure 2). Clearly the abundances of these two species are connected. Specifically, we note

1. the jackrabbit population tends to increase when the coyote population size is low,

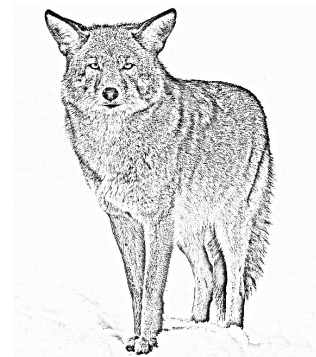


Figure 1: Coyote (*Canis latrans*).

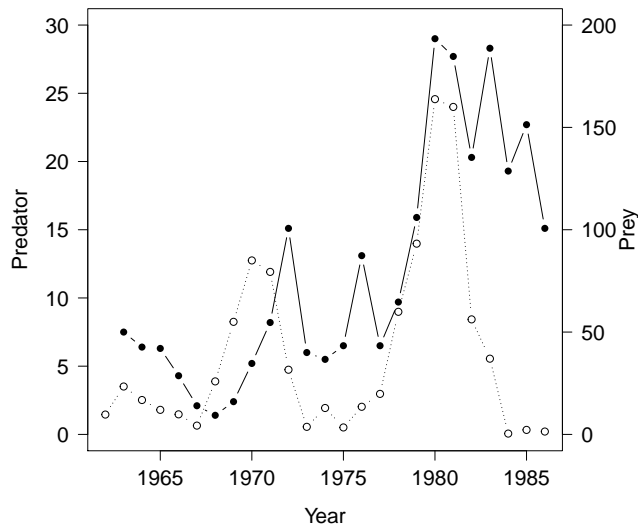


Figure 2: Abundances of coyotes (filled circles) and jackrabbits (open circles) in Curlew Valley, Utah (1962-1986).

2. decreases in the jackrabbit population are typically followed by decreases in the coyote population,
3. the jackrabbit population tends to decrease when the coyote population size is high,
4. increases in the jackrabbit populations are typically followed by increases in the coyote population.

Taken together, these pieces of evidence suggest that both the predator and prey populations are cycling between relatively low and high abundances. The cycling suggests that rather than the predator species consuming all the prey, its population drops when prey sources are scarce allowing the few remaining prey to escape predation and begin a period of prey population growth. In order to more formally consider interactions between predators and their prey, we can build a model describing their interaction.

### *Predator-prey models*

Let's consider a model of interacting prey ( $n$ ) and predator ( $p$ ) populations:

$$\begin{aligned}
 \frac{dn}{dt} &= rn - bnp \\
 \frac{dp}{dt} &= bcnp - ep.
 \end{aligned}
 \tag{1}$$

We are assuming that the prey population would undergo exponential growth (at rate  $r$ ) in the absence of the predator, and the predator population would undergo exponential decline (at rate  $e$ ) in the absence of the prey. The predation (modeled with  $-bnp$  and  $+bcnp$  terms) assumes that the per capita predation rate scales with prey population size (each individual predator eats more prey if more prey is available). The predation rate parameter  $b$  gets multiplied by another parameter  $c$  in the predator equation. This captures the idea that the correspondence between number of prey eaten and number of predator offspring born thanks to this resource is not necessarily one-to-one. We can think of parameter  $c$  as a conversion efficiency (conversion of prey into predator offspring).

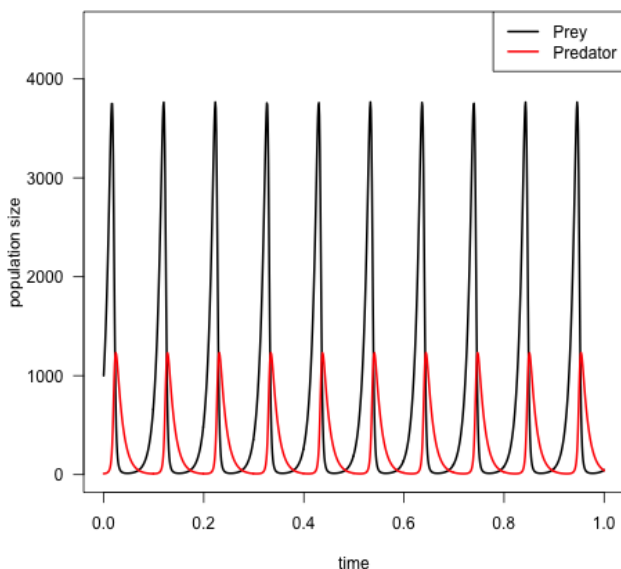


Figure 3: Predator-prey dynamics of equations 1 with parameters  $r = 100.0, b = 0.4, c = 0.3, e = 80.0$ .

We can solve this model by integrating both equations simultaneously (using a computer) and example solutions are shown in Fig. 3 (populations versus time) and Fig 4 (phase portrait). The phase portrait shows how the two populations change relative to one another. Each point in time is a specific part of the curve (e.g., on the blue loop in Fig. 4). We read down to the x-axis to find the prey population size at that time and left to the y-axis to find the predator population at that same time. Because the populations are cycling indefinitely at the same amplitudes, the phase portrait is a closed loop.

While these figures capture the essence of the cycling in the predator-prey data, both populations in the model experience troughs (Fig. 3 where the population size is so small, that they would, in reality, go

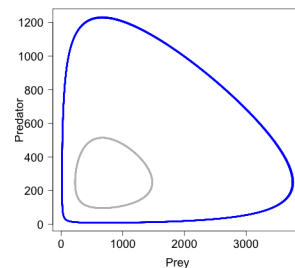


Figure 4: Phase portrait of predator-prey dynamics of equations 1 with parameters  $r = 100.0, b = 0.4, c = 0.3, e = 80.0$ . Two different set of initial conditions are used in the blue ( $n_0 = 1000, p_0 = 10$ ) and gray plots ( $n_0 = 500, p_0 = 500$ )

extinct (and this is true for almost all realistic choices of parameter values). Since many predator-prey interactions are enduring at the population level, this illustrative model requires additional features of real predator-prey systems.

### *Prey self-regulation*

While archetypal predators like rabbits are at least anecdotally fast reproducing, it is unrealistic to assume that their population would continue to grow exponentially. We can include density-dependent population growth by amending the model to

$$\begin{aligned} \frac{dn}{dt} &= rn \left(1 - \frac{n}{K}\right) - bnp \\ \frac{dp}{dt} &= bcnp - ep. \end{aligned} \quad (2)$$

By limiting prey population to a carrying capacity ( $K$ ) we may have made conditions worse for either species or possibly enabled coexistence. But how to tell? We can use a technique called *linear stability analysis* to study the long term behavior of interacting populations.

### *Linear stability analysis*

The following technique is a powerful tool for assessing the stability of equilibria associated with interacting populations. We'll illustrate it here with equations 2, but bear in mind that it can be used in many other interacting scenarios (competition, parasitism etc.).

Like in previous analyses of single species populations, we're asking what happens to populations if we "nudge" them away from their equilibria. Do they return to equilibria or does the nudge (technically: perturbation) grow? To answer this, we only need make small perturbations to the system.

We'll examine the stability of the coexistence equilibrium association with equations 2, which we find by setting the equations equal to zero, and solving for non-zero (co-existence) values of  $n$  and  $p$ :

$$n^* = \frac{e}{bc}, p^* = \frac{r}{b} \left(1 - \frac{e}{bcK}\right) \quad (3)$$

Because we're making arbitrarily small perturbations, we can *linearize* the system describing the dynamics of predator and prey. The basic concept is outlined in Fig. 5. We take derivatives of our (non-linear) equations and evaluate them at the equilibrium of the system.

We organize these derivatives into a matrix called a Jacobian matrix. For a system such as

From any initial conditions the system described by equations 1 forms a loop in the phase portrait (illustrated with the blue and gray curves as examples). This means the system is neutrally stable. Neither population moves to an equilibrium point, but neither of them wander from their trajectory on the loop. Assuming that during initial encounters, one or both populations would be small, then loops will always pass close to the axes where extinction becomes likely.

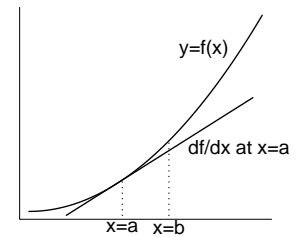


Figure 5: The concept of linearization. The non-linear function  $y = f(x)$  is linearized (by differentiation to get the slope) at the point  $x = a$ . Provided the point  $x = b$  is not too far from  $x = a$  we can approximate  $y$  at  $x = b$  as " $df/dx$  evaluated at  $x = a$ ". Then we would plug in  $x = b$  to this straight line equation to approximate the  $y$  value at this point.

Note that if we perturb, for example, the prey population by a small amount  $\epsilon$  away from its equilibrium  $n^*$  then  $n = n^* + \epsilon$ . The population (and the perturbation) will then change over time:  $n(t) = n^* + \epsilon(t)$  and the dynamics of  $n$  will be the same as the dynamics of  $\epsilon$  since  $dn/dt = d\epsilon/dt$ , with the constant,  $n^*$ , differentiating to zero.

$$\begin{aligned} dn_1/dt &= f_1(n_1, n_2) \\ dn_2/dt &= f_2(n_1, n_2) \end{aligned} \quad (4)$$

where the functions  $f_1$  and  $f_2$  describe the interaction between species 1 and 2, the Jacobian has the form

$$J = \begin{bmatrix} \frac{\partial f_1}{\partial n_1} & \frac{\partial f_1}{\partial n_2} \\ \frac{\partial f_2}{\partial n_1} & \frac{\partial f_2}{\partial n_2} \end{bmatrix} \quad (5)$$

where the (partial) derivatives are performed to linearize the system. This allows us approximate the dynamics of the system close to a point of interest (normally an equilibrium point)

$$\begin{bmatrix} dn_1/dt \\ dn_2/dt \end{bmatrix} = \begin{bmatrix} \frac{\partial f_1}{\partial n_1} & \frac{\partial f_1}{\partial n_2} \\ \frac{\partial f_2}{\partial n_1} & \frac{\partial f_2}{\partial n_2} \end{bmatrix} \begin{bmatrix} n_1 \\ n_2 \end{bmatrix} \quad (6)$$

Our Jacobian matrix has the form

$$J = \begin{bmatrix} r \left(1 - \frac{2n^*}{K}\right) - bp^* & -bn^* \\ bcp^* & bcn^* - e \end{bmatrix} \quad (7)$$

Before we work through the algebra further, let's briefly consider a more simple Jacobian matrix, so that we know what to look for in the following analysis

$$J = \begin{bmatrix} w & x \\ y & z \end{bmatrix} \quad (8)$$

This square matrix is similar to those we encountered in the age structure chapter, when we noted that eigenvalues gave information about population growth. Because we have linearized, the structure of the matrix is also very similar to the age-structured projection matrix. There, the linear nature (without density dependence) gave rise unbounded growth (or decline) according to the dominant eigenvalue. The eigenvalues of this generic Jacobian matrix are found from the characteristic equation

$$(w - \lambda)(z - \lambda) - xy = 0 \quad (9)$$

which is equivalent to

$$\lambda^2 - (w + z)\lambda + (wz - xy) = 0. \quad (10)$$

The eigenvalues give information on the growth (or decline) of the perturbation. The formula is quadratic in  $\lambda$  where  $(w + z)$  (also called the trace,  $T$ ) is the sum of the eigenvalues and  $(wz - xy)$  (also called the determinant,  $D$ ) is the product of the eigenvalues. For  $D$  to be  $>0$

then the eigenvalues must be of the same sign (either both positive or both negative), and for  $T$  to be  $<0$  then the eigenvalues must be negative. Therefore, if  $D > 0$  and  $T < 0$  then both eigenvalues are negative which means that perturbations are guaranteed to shrink over time. This would mean that the equilibrium in question is stable to perturbations.

### *Limited prey growth and predator-prey coexistence*

Now back to our coexistence equilibrium of predator and prey populations, with density-dependent prey population growth, equations (2). At the coexistence equilibrium, equation 3, the Jacobian can be written as

$$J = \begin{bmatrix} -\frac{e}{bcK} & -bn^* \\ bcp^* & 0 \end{bmatrix} \quad (11)$$

Note, we only care in the details so far as they let us know the sign of the trace,  $T$ , and determinant,  $D$ . Remember the parameters are all positive numbers (representing rates, conversion efficiency and carrying capacity) and the equilibrium values  $n^*$  and  $p^*$  are also both positive in the case of coexistence. Consequently, we see that  $T < 0$  and  $D > 0$  and conclude that coexistence is stable (Fig. 6).

### *Functional responses: handling times and satiation*

We've seen that adding density-dependence to the prey population stabilizes the interaction between predator and prey. But is that the only mechanism that can lead to coexistence? In the studies of coyotes and jackrabbits in Curlew Valley, functional feeding responses were measured. These measures (including number of predator scats found containing prey items such as hair and teeth) relate how much predation is occurring to how many prey are available (Fig. 7). These data are evidence that our earlier linear assumption about predation (doubling the amount of prey doubles the amount of predation, equation (1)) does not apply in the coyote-jackrabbit system. Rather, the implication is that the per capita predation rate is a saturating function of prey population size, meaning it increases initially then levels off - like the solid line shown in Fig. (7).

In this case the per capita predation rate can be modeled as

$$b(n) = \frac{an}{aT_H n + 1} \quad (12)$$

When  $n$  is small, the denominator of equation (12) is dominated by 1 (since  $1 > aT_H n$  for small  $n$ ). In this case, the expression is similar to our original scenario where per capita predation increases with

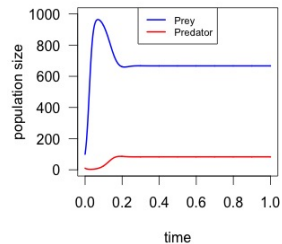


Figure 6: Example dynamics of predator and prey populations when the prey has density dependent population growth.

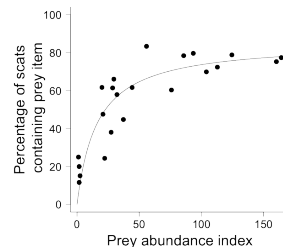


Figure 7: *C. latrans* functional feeding response to *L. californicus* abundance in Curlew Valley, Utah, 1977-1993. (Adapted from Bartel and Knowlton, 2005, *Canadian Journal of Zoology*)

prey population size. When  $n$  is large, the denominator of equation (12) is dominated by  $aT_H n$  in which case the overall predation rate is approximately  $1/T_H$ . We can think of  $T_H$  as the handling time associated with tracking, catching and eating prey. When this time is long, the maximum predation rate is relatively low. The original assumption in equation (1) (a straight line relationship between prey population size and per capita predation rate) is referred to as a type 1 functional response. This alternative assumption (supported by the coyote-jackrabbit data) is referred to as a type 2 functional response.

We can assess whether this mechanism is also stabilizing (when acting alone - i.e., without density-dependent prey population growth) by considering the following description of the predator-prey interaction

$$\begin{aligned} dn/dt &= rn - \frac{anp}{aT_H n + 1} \\ dp/dt &= \frac{acnp}{aT_H n + 1} - ep. \end{aligned} \quad (13)$$

Following the same methodology as earlier, we can calculate the co-existence equilibrium

$$n^* = \frac{e}{aT_H(c/T_H - e)}, p^* = \frac{rc}{aT_H(c/T_H - e)} \quad (14)$$

The trace ( $T$ ) for the coexistence equilibrium in this model evaluates to  $reT_H/c$  which is positive. This means that the type 2 functional response is a destabilizing mechanism. We can interpret this biologically by considering the per capita prey mortality (remember: predation is the only source of prey mortality considered in these models). The per capita prey mortality is given by

$$-\frac{ap}{aT_H n + 1} \quad (15)$$

The  $n$  in the denominator of equation (15) means that per capita prey mortality decreases with increasing prey population size (“*safety in numbers*”). This leads to a positive feedback and supports ever increasing predator populations.

### Functional responses: prey switching

Another important functional response applies to generalist predators (those that feed on several prey species). Because hunting prey is time consuming, predators are apt to target abundant host species (when they won’t have to spend as much time looking for their prey compared to hunting a relatively rare species). We can conceptualize this

Note: we’ve replaced  $rn(1 - n/K)$  with the original  $rN$

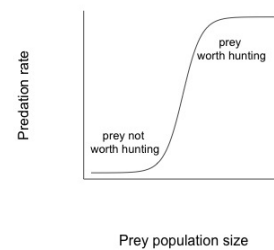


Figure 8: Type 3 functional response models prey switching, where a generalist predator prefers some other food source (not illustrated) when target prey population density is below some threshold.

as a predation rate that is maximal when prey populations are abundant and close to zero when prey are below some threshold population density. This is characterized by a type 3 functional response (Fig. 8).

While intuitively, this would appear to be a mechanism for coexistence (since the predators will leave small prey populations alone), the stability of the coexistence equilibrium in this case depends on the specific parameters of the model (including the parameters used to generate the type 3 functional response and initial conditions).

### *Explaining persistent cycles*

Already in this chapter we've encountered predator-prey models that are neutrally stable, stable and unstable. But what about our original motivating (and highly representative) dataset of coyotes and jackrabbits suggesting persistent cycles? Our modeling toolkit may have the answer since multiple mechanisms could be operating simultaneously. Importantly, stabilizing and destabilizing mechanisms could very likely be in operation in a broad array of predator-prey interactions.

With the right parameterization (choice of parameters), a predator-prey model that includes prey regulation and a type 2 functional response can generate persistent cycles (Fig. 9), though it can also lead to damped oscillations towards the coexistence equilibrium.

$$\begin{aligned} \frac{dn}{dt} &= rn \left(1 - \frac{n}{K}\right) - \frac{anp}{aT_H n + 1} \\ \frac{dp}{dt} &= \frac{acnp}{aT_H n + 1} - ep. \end{aligned} \quad (16)$$

### *The paradox of enrichment*

An interesting outcome from the model with stabilizing and destabilizing mechanisms present, equations (16) is that any enrichment of the environment with resources that increase the prey carrying capacity generate predator-prey cycles with more extreme amplitudes (Fig. 10). This means that in the population troughs, both predator and prey are more vulnerable to extinction. Rather than such additional resources helping the prey (and thereby helping their predator), they cause the system to exhibit dynamics that are detrimental to both species.

This idea was proposed by Rosenzweig, 1971 "The Paradox of Enrichment" Science Vol. 171: pp. 385-387



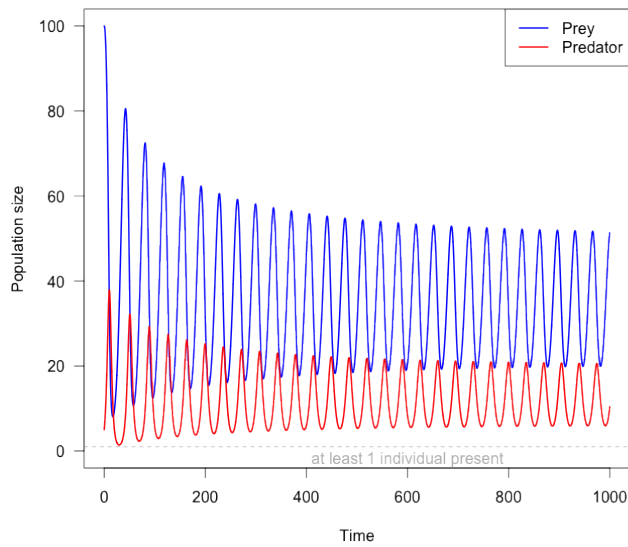


Figure 9: Dynamics of equations (16) giving rise to persistent cycling of predator and prey populations, with parameters  $r = 0.2, a = 0.02, c = 1, e = 0.4, K = 120, T_H = 1.0$

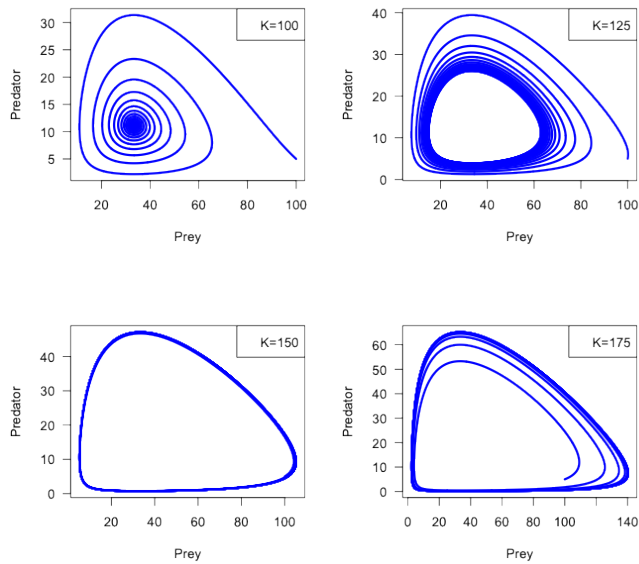


Figure 10: The paradox of enrichment: providing resources to the prey which increase its carrying capacity, leads to predator-prey cycles in which both species are more likely to go extinct in population troughs.

### *Important alternative/complementary mechanisms*

Although we've covered many of the important mechanisms to help understand the enduring nature of asymmetrical predator-prey interactions, there are some other mechanisms that can help to stabilize the dynamics. These mechanisms include

- Predator self regulation
- Spatially distributed prey refuges
- Predator immigration

These mechanisms may act independently or with other mechanisms already outlined. Together, this body of knowledge help us appreciate how one type of interspecific interaction can have so many outcomes.

### *Test yourself*

- Which of the functional feeding responses 1, 2 and 3 refer to density-dependent predation?
- What is the concept of linearization?
- What are possible outcomes of combining stabilizing and destabilizing mechanisms?
- What is a handling time?
- What is the paradox of enrichment?

### *Further reading*

- Bartel and Knowlton, 2005 "Functional feeding responses of coyotes, *Canis latrans*, to fluctuating prey abundance in the Curlew Valley, Utah, 1977-1993" Canadian Journal of Zoology Vol. 83: pp. 569-478
- Bartel, Knowlton and Stoddart, 2008 "Long term patterns in mammalian abundance in northern portions of the Great Basin" Journal of Mammalogy Vol. 89: pp. 1170-1183
- Rosenzweig, 1971 "The Paradox of Enrichment" Science Vol. 171: pp. 385-387

*Homework*

1. Use equations 2 to derive the coexistence equilibrium shown in equation 3.
2. Sketch an example of a predator-prey interaction exhibiting damped oscillations as both a regular plot (x-axis=time, y-axis=both population sizes) and a phase portrait. Label the initial conditions and any stable equilibria.
3. Write down a model with both predator and prey density-dependent growth, a type 2 functional response and predator immigration.
4. Draw coexistence (non-zero) nullclines for the 3 models given by equations 1, 2 and 13. Which models have density-dependence? What is the relationship between nullclines and density-dependence/independence?
5. By calculating diagonal elements of the Jacobian for the model represented by equations 2 show that the Trace for the coexistence equilibrium is  $-e/bcK$ .