

1. Let us consider the following system:

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K}\right) - \frac{cNP}{D + N} \quad (1)$$

$$\frac{dP}{dt} = sP \left(1 - \frac{P}{W}\right) \quad (2)$$

Claim. $(0, W)$ is a steady state of this system.

Proof.

$$\frac{dN}{dt} = r0 \left(1 - \frac{0}{K}\right) - \frac{0}{D + 0} = 0$$

$$\frac{dP}{dt} = sW \left(1 - \frac{W}{W}\right) = 0$$

Claim. $(K, 0)$ is a steady state of this system.

Proof.

$$\frac{dN}{dt} = rK \left(1 - \frac{K}{K}\right) - \frac{0}{D + K} = 0 - 0 = 0$$

$$\frac{dP}{dt} = 0 \cdot \left(1 - \frac{0}{W}\right) = 0$$

Claim. $(0, 0)$ is a steady state of this system.

Proof. This is trivial since all terms are 0.

The Jacobian of our system is

$$\mathbf{J} = \begin{bmatrix} r - \frac{2rN}{K} - \frac{cDP}{(D+N)^2} & \frac{-cN}{D+N} \\ 0 & s - \frac{sP}{W} \end{bmatrix}$$

Since it is upper triangular, the eigenvalues are the diagonal elements. Therefore, the point is stable if both diagonal elements are negative. Note that all parameters are positive.

$$\mathbf{J}(0, W) = \begin{bmatrix} r - \frac{c}{D} & 0 \\ 0 & -s \end{bmatrix}$$

Therefore, $(0, W)$ is stable when $r < \frac{cW}{D}$. That is, the rate of caribou growth has to be sufficiently small compared to the predation rate times the population cap of the wolves normalized to parameter D, which represents the scale of predation saturation. This can be interpreted as saying that the caribou growth rate has to be large enough to overcome predation if caribou are to coexist with wolves.

$$\mathbf{J}(K, 0) = \begin{bmatrix} -r & \frac{-cK}{D+K} \\ 0 & s \end{bmatrix}$$

This point is always a saddle point. If there are no wolves, none will appear; however, as soon as there is one wolf, the population will start growing.

$$\mathbf{J}(0, 0) = \begin{bmatrix} r & 0 \\ 0 & s \end{bmatrix}$$

This point is always unstable. Likewise to the above explanation extended to caribou and wolves.

2. Letting $\frac{dN}{dt} = rN \left(1 - \frac{N}{K}\right) - \frac{cNP}{D+N} = 0$ and assuming that $N \neq 0$, we get that

$$\begin{aligned} DrN - \frac{rN^2D}{K} - rN^2 - \frac{rN^3}{K} &= cNP \\ \iff \frac{-r}{K}N^2 + \left(r - \frac{rD}{K}\right)N + (Dr - cP) &= 0 \\ \iff N = \frac{(r - \frac{rD}{K}) \pm \sqrt{(r - \frac{rD}{K})^2 - 4\frac{-r}{K}(Dr - cP)}}{\frac{-2r}{K}} \end{aligned}$$

Therefore the N-nullcline is defined by the equation

$$N(P) = \frac{-(D - K) \pm \sqrt{(D + K)^2 - 4cKP/r}}{2} \quad (3)$$

Setting $\frac{dP}{dt} = 0$ gives us

$$sP = \frac{sP^2}{W}$$

Hence, $P = 0$ and $P = W$ are P-nullclines. The N-nullcline defined by equation (3) intersects the line $P = 0$ when

$$\begin{aligned} N &= \frac{-(D - K) \pm \sqrt{(D + K)^2}}{2} \\ \Rightarrow N_- &= -D \\ \Rightarrow N_+ &= K \end{aligned}$$

Here we get a new steady-state point $(-D, 0)$. However, this is non-biological since one cannot have negative population density and all parameters are positive. The N-nullcline intersects the line $P = W$ when

$$N = \frac{(K - D) \pm \sqrt{(D + K)^2 - 4cKW/r}}{2}$$

This gives us new steady-states under the condition

$$\frac{4cKW}{r} < (D + K)^2 \quad (4)$$

Furthermore,

$$\begin{aligned} K - D &< \sqrt{(K + D)^2 - 4cWK/r} \\ (K - D)^2 &< (K + D)^2 - 4cWK/r \\ K^2 - 2KD + D^2 &< K^2 + 2KD + D^2 - 4cWK/r \\ 4KD &> 4cWK/r \end{aligned}$$

Thus

$$N_- > 0 \iff rD > cW \quad (5)$$

This is the same criterion for our steady-state $(0, W)$ to change from a stable node to a saddle point. In fact, since no other steady-states can exist at $(0, W)$, the saddle-node bifurcation that occurs must be due to the collision between $(0, W)$ and (N_-, W) .

3. For our steady-state $(-D, 0)$ we get division by zero in the Jacobian, so there is a singularity in the system. Regardless, this point is non-biological. Therefore, let us consider only the points defined by

$$N_+ = \frac{-(D - K) + \sqrt{(D + K)^2 - 4cKW/r}}{2}$$

$$N_- = \frac{-(D - K) - \sqrt{(D + K)^2 - 4cKW/r}}{2}$$

We find that

$$\mathbf{J}(N_{\pm}, W) = \begin{bmatrix} r - \frac{2rN_{\pm}}{K} - \frac{cDW}{(D+N_{\pm})^2} & \frac{-cN_{\pm}}{D+N_{\pm}} \\ 0 & -s \end{bmatrix}$$

Therefore, the stability of these points depend upon the sign of the first element of the matrix. From this and the conclusion of the previous question, we conclude that (N_-, W) is a stable node for $rD < cW$ and is a saddle point for $rD > cW$. Now, consider the orthogonal projection of this system onto the one dimensional P-nullcline $P = W$. We have three steady-states defined by N_- , 0, and N_+ . Since all trajectories are monotonic in one dimension, when $N_- < 0$ is stable and 0 is unstable, $N_+ > 0$ must be stable. Conversely, when 0 is stable and $N_- > 0$ is unstable, $N_+ > N_-$ must be stable.

4. For simulations¹, the system was non-dimensionalized to the following:

$$\frac{d\bar{N}}{d\tau} = \bar{r}\bar{N}(1 - \bar{N}) - \frac{\bar{c}\bar{P}\bar{N}}{\bar{D} + \bar{N}} \quad (6)$$

$$\frac{d\bar{P}}{d\tau} = \bar{P}(1 - \bar{P}) \quad (7)$$

where $\bar{N} = \frac{N}{K}$, $\bar{P} = \frac{P}{W}$, $\tau = st$, $\bar{c} = \frac{cW}{sK}$, $\bar{D} = \frac{D}{K}$, and $\bar{r} = \frac{r}{s}$. Thus the criteria in equations (4) and (5) become

$$4\bar{c}/\bar{r} < (\bar{D} + 1)^2$$

and

$$\bar{r}\bar{D} > \bar{c}$$

respectively. Here, we consider three points in parameter space such that

- $4\bar{c}_3/\bar{r}_3 > (\bar{D}_3 + 1)^2$
- $4\bar{c}_2/\bar{r}_2 < (\bar{D}_2 + 1)^2$ and $\bar{r}_2\bar{D}_2 < \bar{c}_2$
- $4\bar{c}_1/\bar{r}_1 < (\bar{D}_1 + 1)^2$ and $\bar{r}_1\bar{D}_1 > \bar{c}_1$

That is, no additional steady states exist, one additional (biological) steady state exists, and two additional (biological) steady states exist, resp. Indeed this is what we observe numerically (see Figure 1).

5. Wolves do not depend on the density of caribou. This can be attributed to the abundance of other prey the wolves can predate on. Consequently, this allows wolves to prey on caribou until their extinction. In order for a population of caribou to survive, there needs to be a balance between the growth rate of caribou and the predation efficiency of wolves. In fact, if $4cKW/r > (D + K)^2$ the caribou population collapses. If the growth rate of caribou is

¹Code used to generate figures can be found on GitHub at <https://github.com/niklasbrake/HomeworkAssignments/tree/master/QLSC600/Module%206>

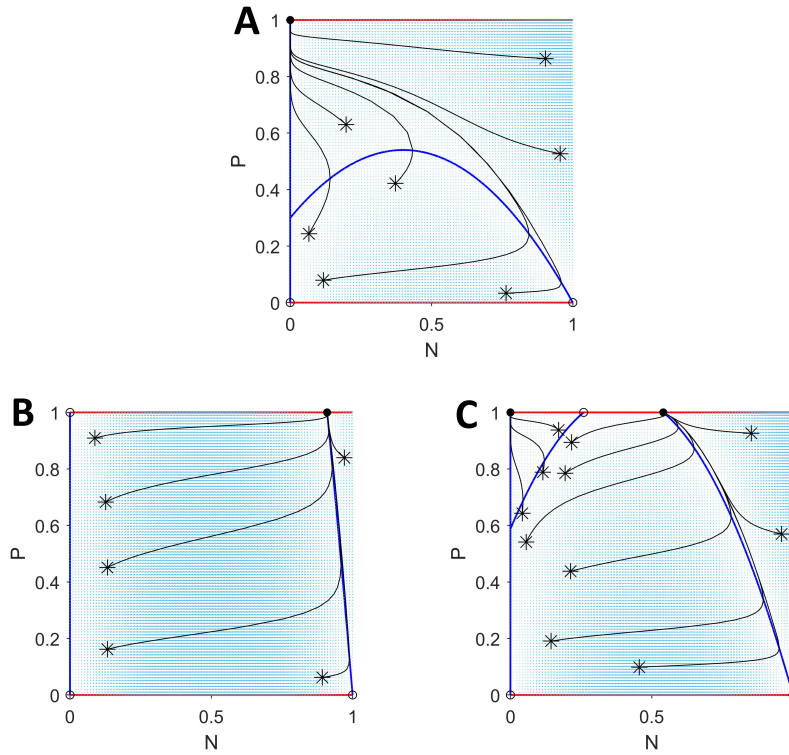


Figure 1: Phase plane portrait. Stars indicate initial conditions and black lines are trajectories of the system defined in equations (6) - (7). Solid blue lines indicate N -nullclines and solid red lines indicate P -nullclines. Closed circles are stable steady-states and open circles are unstable steady-states. **(A)** $\bar{D} = 0.2$, $\bar{c} = 0.33$, $\bar{r} = 0.5$. **(B)** $\bar{D} = 0.2$, $\bar{c} = 0.05$, $\bar{r} = 0.5$. **(C)** $\bar{D} = 0.2$, $\bar{c} = 0.33$, $\bar{r} = 0.98$.

too small and/or the predation efficiency of wolves on caribou is too large, the population of caribou will drop to zero. Interestingly, this system displays bi-stability as seen in Figure 1C. This means that there can be coexistence of wolves and caribou; however, if there were to be a disease or something that reduces the caribou population past the separatrix, the population would not be able to recover.