Modeling the fear effect in predator–prey interactions

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Motivation

The longstanding view is that predators only effect prey via predation. However, recent research shows that fear alone can reduce prey reproduction rates.

Fear can effect:

- Habitat Usage
- Foraging behaviors
- Vigilance
- Physiological changes

Recent experiment on songbirds

- sounds of predators
- protection from actual predation
- 40% birth rate reduction

Introduction

First, we begin with a basic logistic model.

$$\dot{x} = bx - dx - c_1 x^2$$

x	population of prey
b	birth rate of prey (natural)
d	death rate of prey (natural)
c_1	competition-related death rate of prey

Note, all parameters and variables are positive numbers.

Next, we multiply by a factor which reduces the birth rate due to fear effects.

$$\dot{x} = [f(k, y)b]x - dx - c_1 x^2$$

Here, k is a parameter which reflects the strength of the fear effect, and y is the population of the predator.

$$\dot{x} = [f(k,y)b]x - dx - c_1x^2$$

So, what sort of a function is $f(k,y)$? We'd like to think of it generally for now, but there are some things we can say for sure about it:

$f(0,y) = f(k,0) = 1$	No fear/predators, full birth.
$\frac{\partial f}{\partial k} < 0, \frac{\partial f}{\partial y} < 0$	More fear/pred, less birth.
$\lim_{y\to\infty} f(k,y) = \lim_{k\to\infty} f(k,y) = 0$	Maximum effect is 0 birth.

In short, $f : \mathbb{R}^+ \times \mathbb{R}^+ \to [0,1]$ is monotonically decreasing when thought of as a function of either k or y.

Next, we'll add in a predation function, $g(x)$, and include the predator population dynamics into our system.

$$\begin{aligned} \dot{x} &= [f(k,y)b]x - dx - c_1x^2 - g(x)y \\ \dot{y} &= [g(x)c_2]y - my \end{aligned}$$

Here, m is the mortality rate of predators, and c_2 is the conversion rate of prey's biomass to predator's biomass. That is, we are assuming that the predators' birth rate is directly proportional to predation.

Typically, the predation $g(x)$ is modeled in one of two ways:

- In a linear functional response,

$$g(x) = px,$$

  which assumes that predation is directly proportional to prey population.

- In a Holling Type II functional response,

$$g(x) = \frac{px}{1 + qx},$$

  which assumes that predation increases quickly as prey population increases, and then tapers off to approach $\frac{p}{q}$ asymptotically.

Linear Functional response

Let's explore the model, assuming a linear functional response for predation. So, $g(x) = px$, where p is a parameter that represents the predation rate.

$$\begin{aligned} \dot{x} &= [f(k,y)b]x - dx - c_1x^2 - pxy \\ \dot{y} &= pc_2xy - my \end{aligned}$$

Where are the fixed points? [1]

[1] Presenter: Write this system on the board.

Finding Fixed Points

There are (at most) 3 fixed points:

- $E_0 = (0, 0)$. This is a fixed point because

$$\begin{aligned}
\dot{x} &= [f(k,0)b](0) - d(0) - c_1(0)^2 - p(0) &= 0 \\
\dot{y} &= pc_2(0) - m(0) &= 0
\end{aligned}$$

- $E_1 = \left(\frac{(b-d)}{c_1}, 0\right)$, when $b > d$. To see that this is a fixed point,

$$\begin{aligned}
\dot{y} &= pc_2(0) - m(0) \\
&= 0 \\
\dot{x} &= [f(k,0)b]\left(\frac{(b-d)}{c_1}\right) - d\left(\frac{(b-d)}{c_1}\right) - c_1\left(\frac{(b-d)}{c_1}\right)^2 - p(0) \\
&= \frac{1}{c_1}\left[(1)b(b-d) - d(b-d) - (b-d)^2\right] \\
&= \frac{1}{c_1}\left[b^2 - 2bd + d^2 - (b-d)^2\right] \\
&= 0.
\end{aligned}$$

- E_2: If $\frac{(b-d)}{c_1} > \frac{m}{c_2 p}$, then $E_2 = \left(\frac{m}{c_2 p}, y^*\right)$, where y^* satisfies

$$b\,f(k, y^*) - d - c_1 x^* - p y^* = 0.$$

(This is $\frac{\dot{x}}{x} = 0$). To see that such a y^* exists, observe that this is equivalent to

$$\underbrace{b\,f(k, y^*) - p y^*}_{\text{decreasing}} = \underbrace{d + c_1 x^*}_{\text{increasing}},$$

and the LHS is b at $y = 0$, RHS is d at $x = 0$, and $b > d$.

- E_2 (continued):

  To see that E_2 is a fixed point:

$$\begin{aligned}\dot{x} &= [f(k,y^*)b]x^* - dx^* - c_1(x^*)^2 - px^*y^* \\ &= ([b\,f(k,y^*)] - d - c_1x^* - py^*)x^* \\ &= 0\end{aligned}$$

$$\begin{aligned}\dot{y} &= pc_2x^*y^* - my^* \\ &= pc_2\left(\frac{m}{c_2p}\right)y^* - my^* \\ &= my^* - my^* \\ &= 0\end{aligned}$$

Analyzing Stability

Thus, we have found 3 fixed points (or equilibria), E_0, E_1, and E_2. Let's analyze their stability.

Theorem (3.1)

0. *E_0 is stable if $(b-d)$ is negative, and unstable if positive.*
1. *E_1 is stable if $\frac{(b-d)}{c_1} < \frac{m}{c_2 p}$ (i.e. if E_2 does not exist) and is unstable if reversed.*
2. *E_2 is stable as long as it exists (when $\frac{(b-d)}{c_1} > \frac{m}{c_2 p}$).*

It should be intuitively obvious that if $(b-d) < 0$, then neither prey nor predator can survive. Observe:

$$\begin{aligned}
\dot{x} &= [f(k,y)b]x - dx - c_1x^2 - pxy \\
&= (f(k,y)b - d)x - c_1x^2 - pxy \\
&\leq (b-d)x - c_1x^2 - pxy \\
&< 0
\end{aligned}$$

$$\begin{aligned}
\dot{y} &= pc_2xy - my \\
&\to 0
\end{aligned}$$

Thus, E_0 is stable if $(b-d) < 0$.
The author omits the proof for stability of E_1, because the proof for E_2 is similar:

Claim: E_2 is stable. Recall that E_2 exists if $\frac{(b-d)}{c_1} > \frac{m}{c_2 p}$, and $E_2 = \left(\frac{m}{c_2 p}, y^*\right)$, where y^* satisfies

$$[f(k, y^*)b] - d - c_1 x^* - py^* = 0.$$

Proof.

We use the Jacobian:

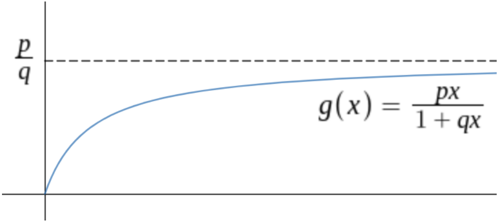
$$\begin{bmatrix} \frac{\partial \dot{x}}{\partial x} & \frac{\partial \dot{x}}{\partial y} \\ \frac{\partial \dot{y}}{\partial x} & \frac{\partial \dot{y}}{\partial y} \end{bmatrix}\Bigg|_{(x^*, y^*)} = \begin{bmatrix} [f(k, y^*)b] - d - 2c_1 x^* - py^* & bx^* \frac{\partial f}{\partial y} - px^* \\ pc_2 y^* & pc_2 x^* - m \end{bmatrix}$$

$$= \begin{bmatrix} -c_1 x^* & bx^* \frac{\partial f}{\partial y} - px^* \\ pc_2 y^* & m - m \end{bmatrix} = \begin{bmatrix} - & - \\ + & 0 \end{bmatrix}$$

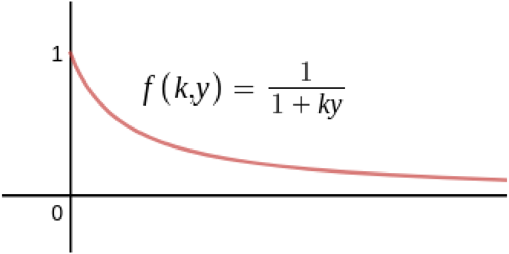
So since det > 0 and trace < 0, E_2 is stable. ∎

Holling Type II Functional Response

Now we've explored the dynamics assuming that the predation function $g(x)$ is a linear function, but it should agree with your intuition that in nature, predation levels with be roughly the same if the prey population is above a certain level. So in this section, we explore the dynamics when $g(x)$ is the following:



We also choose a particular form for $f(k, y)$, namely



Note that f still has the same general properties we've assumed so far.

So our model now takes this form:

$$\dot{x} = \frac{bx}{1+ky} - dx - c_1x^2 - \frac{pxy}{1+qx}$$
$$\dot{y} = \frac{pc_2xy}{1+qx} - my$$

Next, we find the fixed points. [2]

[2]Presenter: Write this system on the board.

There are two fixed points which are the same as we saw with the linear functional response:

- $E_0 = (0, 0)$,
- $E_1 = \left(\frac{b-d}{c_1}, 0\right)$ if $(b - d) > 0$.

The following can be confirmed as before using linearization:

- E_0 is unstable if E_1 exists.
- E_1 is stable if $(b - d)(c_2 p - mq) < c_1 m$,
- E_1 is unstable if $(b - d)(c_2 p - mq) > c_1 m$.

If E_1 is unstable, it turns out that there is another fixed point, E_2. The authors do not state its coordinates in closed-form, only that it exists when E_1 is unstable, and the give the following condition upon which E_2 is stable:

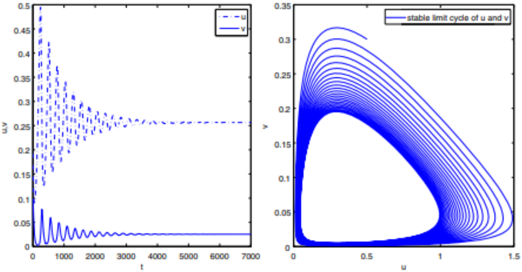
$$\begin{cases} b > d + \dfrac{c_1(c_2p + mq)}{q(c_2p - mq)} \\ k > \dfrac{q(c_2p - mq)^2((b-d)q(c_2p - mq) - a(c_2p + mq))}{c_2^2 p c_1(qd(c_2p - mq) + c_1(c_2p + mq))} \end{cases}$$

Gnarly.

The point here is that to maintain nonzero prey population, $b > d$. To maintain a stable predator population as well, the birth rate b needs to be high enough above the death rate d. In addition, the level of fear k must be above a certain amount as well.

Hopf Bifurcation

It turns out that under the right condition[3], E_2 is unstable and a stable limit cycle appears. Numerical exploration shows that this only happens if b is high enough above d.



(a) (b)

[3]That condition is $y^* < \frac{a_2 - 2a_5}{a_4 + 2a_5}$, where $a_2 = \frac{(b-d)q - c_1}{c_2 p - mq}$, $a_4 = \frac{dq + c_1}{c_2 p - mq}$, $a_5 = \frac{c_1 mq}{(c_2 p - mq)^2}$.

Conclusion

So we can see that when accounting for the cost of fear, assuming that the fear function is linear basically results in an effect which is the same as lowering the birth rate of the prey. But, if the parameters are right, the system can bifurcate, and where there was once a stable equilibrium between populations of prey and predator, now there exist oscillations. They can be supercritical or subcritical Hopf bifurcations as well, causing the population to either stabilize, or oscillate wildly until one of species is driven extinct.