Chapter 4

Predator-Prey systems

Here we will consider a more realistic predator-prey model. We will start by building a fairly general set of equations to describe the predator-prey interactions, and later in the chapter we will solve the model with the functional responses for predator feeding rate as proposed by Holling.

In the first instance, we need to decide the kind of model for prey density in the absence of predation. As with the previous single species models (e.g. time-independent logistic equation), we will assume that in the absence of predation a positive prey density will reside at a globally stable steady population which we denote by $K$ (its carrying capacity): Thus for there to be a unique positive steady state we need

$$
\frac{dN}{dt} = N \rho(N), \text{ where } \rho(K) = 0,
$$

and $\rho(N) \neq 0$ if $N \neq K$. Moreover, we need $N = 0$ to be unstable if small prey populations are not to die out:

$$
\rho(0) > 0.
$$

Local stability of the steady state requires that $f(N) = N \rho(N)$ crosses the axis at $N = K$ with $f''(K) < 0$, since then $dN/dt < 0$ if $N$ is just larger than $K$ and $dN/dt > 0$ if $N$ is just less than $K$. But this means that $f'(K) = \rho(K) + K \rho'(K) = K \rho'(K) < 0$, and hence we require that $\rho'(K) < 0$ for local stability. In fact, if $\rho(K) = 0$, $\rho(N) \neq 0$ if $N \neq K$ and $\rho'(K) < 0$ then $K$ is globally stable on $(0, \infty)$, that is any $N(0) \in (0, \infty)$ will evolve to $K$. To summarise: We need

$$
\rho(0) > 0 \quad (4.1)
$$

$$
\rho(K) = 0, \text{ for some } K > 0 \quad (4.2)
$$

$$
\rho(N) \neq 0, \text{ for } 0 \leq N \neq K \quad (4.3)
$$

$$
(\Rightarrow \rho'(K) < 0). \quad (4.4)
$$

Now consider the situation for the predator when there is no prey present. We will assume that in the absence of food (prey) the predator population dies off exponentially at rate $\mu$; that is $P = -\mu P$ when $N = 0$. 

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The predator obviously has a detrimental effect on the per capita growth rate of prey, while the predator must sustain its entire net growth from eating prey. We will denote by \( \phi(N,P) \) the per-capita consumption rate of prey due to predation, so that adding to the growth rate \( \rho \) we obtain the net per-capita rate

\[
\frac{N}{N} = \rho(N) - \phi(N,P).
\]

For the predator, consumption of prey translates into growth, and we denote this per-capita rate by \( \sigma(N) \). Adding in the mortality term, this gives the net per-capita rate

\[
\frac{\dot{P}}{P} = \sigma(N) - \mu.
\]

We assume that both \( \phi \) and \( \sigma \) are smooth functions.

Hence the complete model is given by

\[
\begin{align*}
\frac{dN}{dt} &= N(\rho(N) - \phi(N,P)) = F(N,P) \\
\frac{dP}{dt} &= P(\sigma(N) - \mu) = G(N,P)
\end{align*}
\]  

(4.5)

Now to refine the model, we need to place sensible restrictions on the functions \( \phi, \sigma \). First, with no predator there can be no predation, no matter what the prey density is:

\[ \phi(N,0) = 0, \forall N > 0. \]

Moreover, for fixed prey density, we expect the predation to increase with predator density:

\[ \phi_P(N,P) > 0, \forall N, P > 0. \]

The next condition is not immediately obvious. It says that the more prey there are, the less the probability that any one of them will be consumed:

\[ \phi_N(N,P) \leq 0, \forall N, P > 0 \]

This completes the conditions on \( \phi \). Now we turn to \( \sigma \). If there are no prey then the predator is not consuming them:

\[ \sigma(0) = 0, \]

and the more prey there are, the more the predator consumes:

\[ \sigma'(N) > 0, \forall N > 0. \]

But notice that \( \sigma \) may still saturate for large \( N \).
2 Steady states

Let us first examine the possible steady states of (4.5). These are

\[(N, P) = (0, 0) \text{ and } (K, 0),\]

when \(P = 0\) is used; otherwise if \(N, P \neq 0\) we must have

\[
\begin{align*}
\rho(N) - \phi(N, P) &= 0 \\
\sigma(N) - \mu &= 0.
\end{align*}
\]

Now, \(\sigma(0) = 0\) and \(\sigma'(N) > 0\), so that for a given \(\mu > 0\), either \(\sigma\) saturates or it increases unbounded with increasing \(N\) (see figure 4.1). In the latter case there is a unique positive \(N^*\) such that \(\sigma(N^*) = \mu\). If \(\sigma\) saturates then either it saturates at a value less than \(\mu\), in which case there are no steady states \((N^*, P^*)\) with \(N^* > 0\), or \(\sigma\) saturates at a value greater than \(\mu\) and there is a unique \(N^* > 0\) such that \(\sigma(N^*) = \mu\).

Suppose that an \(N^*\) exists such that \(\sigma(N^*) = \mu\), so that it is then unique (recall that \(\sigma\) is smooth). We then seek \(P\) such that \(\rho(N^*) = \phi(N^*, P)\). First of all we certainly need that \(\rho(N^*) > 0\), that is

\[\rho(\sigma^{-1}(\mu)) > 0.\]

Since \(\rho\) can only be positive in \((0, K)\), this means that \(\sigma^{-1}(\mu) < K\), that is we require that

\[\mu < \sigma(K).\]
Hence there is no interior steady state if \( \sigma(K) \leq \mu \). Since \( \phi_p(N,P) > 0 \) and \( \phi(N,0) = 0 \), \( \phi(N^*,P) \) is increasing from zero. Again, \( \phi(N^*,\cdot) \) may saturate or increase unboundedly. If \( \phi(N^*,\cdot) \) saturates at a value less than \( \rho(N^*) \), then there is no interior steady state. Else there is a unique positive \( P^* \) such that \( \rho(N^*) = \phi(N^*,P^*) \).

We now consider the nullclines of (4.5). These are \( N = 0, P = 0, N = \sigma^{-1}(\mu) \) and the curve defined by \( \rho(N) = \phi(N,P) \). We can calculate the slope of the nullcline where \( \rho(N) - \phi(P,N) = 0 \). We find

\[
0 = \frac{d}{dN}[\rho(N) - \phi(N,P)] = \rho'(N) - \phi_N(N,P) - \phi_P(N,P) \frac{dP}{dN}
\]

and so

\[
\frac{dP}{dN} = \frac{\rho'(N) - \phi_N(N,P)}{\phi_P(N,P)}
\]

which is negative provided that \( \phi_N(N,P) \) is not too negative. We thus arrive at the nullclines illustrated in Figure 4.2. Note that if \( \phi(N^*,\cdot) \) saturates below \( \rho(N^*) \) then the \( \rho(N) = \phi(N,P) \) nullcline goes off to infinity before it can cross \( N = N^* \). We note that in:

**Region I**

\[
\frac{dN}{dt} < 0 \quad \text{and} \quad \frac{dP}{dt} > 0 \quad \Rightarrow \quad \frac{dP}{dN} < 0.
\]

Hence trajectories fall in this region.

**Region II**

\[
\frac{dN}{dt} < 0 \quad \text{and} \quad \frac{dP}{dt} < 0 \quad \Rightarrow \quad \frac{dP}{dN} > 0.
\]
Hence trajectories rise in this region.

Region III
\[ \frac{dN}{dt} > 0 \text{ and } \frac{dP}{dt} > 0 \Rightarrow \frac{dP}{dN} > 0. \]

Hence trajectories rise in this region.

Region IV
\[ \frac{dN}{dt} > 0 \text{ and } \frac{dP}{dt} < 0 \Rightarrow \frac{dP}{dN} > 0. \]

Hence trajectories fall in this region.

It is clear that trajectories encircle the steady state \( Q = (N^*, P^*) \) (so we expect spirals or limit cycles) but the precise picture cannot be determined without further analysis.

We therefore turn to linear stability analysis and consider the linear stability matrix:

\[
J(N,P) = \begin{pmatrix}
F_N(N,P) & F_P(N,P) \\
G_N(N,P) & G_P(N,P)
\end{pmatrix}
= \begin{pmatrix}
\rho(N) - \phi(N,P) + N\phi'(N) - N\Phi_N(N,P) & -N\Phi_P(N,P) \\
-\phi(K,0) + K\phi'(K) + K\Phi_N(K,0) & -K\Phi_P(K,0)
\end{pmatrix}
\]

We need to calculate the eigenvalues of \( J(N,P) \) at the steady states \((0,0), (K,0)\) and \((N^*, P^*)\).

1. \((N, P) = (0, 0)\).

\[
J(0,0) = \begin{pmatrix}
\rho(0) - \phi(0,0) & 0 \\
0 & \sigma(0) - \mu
\end{pmatrix}
= \begin{pmatrix}
\rho(0) & 0 \\
0 & -\mu
\end{pmatrix}
\]

Thus the eigenvalues are \( \rho(0) > 0 \) and \( -\mu < 0 \), which are opposite signs and hence we have a saddle - unstable.

2. \((N, P) = (K, 0)\).

\[
J(K,0) = \begin{pmatrix}
\rho(K) - \phi(K,0) + K\phi'(K) - K\Phi_N(K,0) & -K\Phi_P(K,0) \\
-\phi(K,0) + K(\phi'(K) - \phi_N(K,0)) & -K\Phi_P(K,0)
\end{pmatrix}
\]

Thus the eigenvalues are \( \lambda_1 = -\phi(K,0) + K(\phi'(K) - \phi_N(K,0)) < 0 = K\phi'(K) < 0 \) using (4.6) and \( \lambda_2 = \)
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\( \sigma(K) - \mu \). Hence if \( \sigma(K) < \mu \) then \((K,0)\) is a stable node, whereas if \( \sigma(K) > \mu \) \((K,0)\) is a saddle. In particular, if an interior steady state exists, so that \( \sigma(K) > \mu \) then \((K,0)\) is a saddle.

3. \((N,P) = (N^*,P^*)\).

\[
J(N^*,P^*) = \begin{pmatrix} p(N^*) - \phi(N^*,P^*) + N^*p'(N^*) - N^*\phi_N(N^*,P^*) - N^*\phi_p(N^*,P^*) & -N^*\phi_p(N^*,P^*) \\ P^*\sigma'(N^*) & -\mu \end{pmatrix}
\]

Since there is no simple structure to \( J \) (e.g. triangular), we turn to the trace and determinant of \( J \):

\[
\lambda_1 + \lambda_2 = \text{trace} \ J(N^*,P^*) = N^*(p'(N^*) - \phi_N(N^*,P^*))
\]
\[
\lambda_1\lambda_2 = \text{det} \ J(N^*,P^*) = N^*P^*\sigma'(N^*)\phi_p(N^*,P^*) > 0.
\]

That \( \lambda_1\lambda_2 > 0 \) rules out a saddle. Thus according to (4.6), if \( dP/dN < 0 \), from (4.7) it follows that \( \lambda_1 + \lambda_2 < 0 \) and so both eigenvalues have negative real part and positive real parts if \( dP/dN > 0 \).

When \( dP/dN = 0 \) the eigenvalues are purely imaginary. Hence if \( dP/dN < 0 \) the steady state \((N^*,P^*)\) is locally a stable spiral, and if \( dP/dN > 0 \) it is locally an unstable spiral.

There is still another possible feature of the phase plane that can occur if \((N^*,P^*)\) is unstable - an attracting periodic orbits which we call a stable limit cycle which can occur due to a Hopf bifurcation, which we now briefly explain.

4.1 Hopf Bifurcations

First we consider a toy system:

\[
\dot{x} = \mu x - y - x(x^2 + y^2)
\]
\[
\dot{y} = x + \mu y - y(x^2 + y^2).
\]

This system has a single steady state at the origin. The stability matrix at the origin is

\[
M = \begin{pmatrix} \mu & -1 \\ 1 & \mu \end{pmatrix}.
\]

\( M \) has eigenvalues \( \mu \pm i \). Linear stability analysis suggests that for \( \mu < 0 \) local to the origin we have a stable spiral, whereas for \( \mu > 0 \) we have an unstable spiral. For \( \mu = 0 \) the linear system has a centre. As we shall see this centre does not appear in the full nonlinear system. In fact, it is possible to rewrite these equations in polar coordinates \( r, \theta \) (Exercise). One finds that

\[
\dot{r} = r(\mu - r^2), \quad \dot{\theta} = 1.
\]
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Hence in polar coordinates, any solution moves around the origin with unit angular velocity, while changing radius. If $\mu \leq 0$ the solution spirals into the origin. If $\mu > 0$ and the solution starts with $r < \sqrt{\mu} > \sqrt{\mu}$, the solution spirals out(in) till it meets and asymptotically approaches the invariant circle $r = \sqrt{\mu}$ (see figure 4.3). Hence as $\mu$ increases from $\mu < 0$ to $\mu > 0$ the phase plane changes from a globally stable spiral to a locally unstable spiral at the origin with a periodic orbit surrounding it. The periodic orbit attracts all points except the origin. We call the periodic orbit a stable limit cycle. We notice that the limit cycle is created as the origin loses its stability. This toy model demonstrates a general phenomenon covered in the following theorem.

**Theorem 1 (Hopf Bifurcation)** Suppose we have the system

$$\frac{dx}{dt} = f(x, y, \mu), \quad \frac{dy}{dt} = g(x, y, \mu),$$

(4.9)

for $(x, y) \in \Omega \subset \mathbb{R}^2$ and $\mu \in (-\varepsilon, \varepsilon), \varepsilon > 0$. Let $x_0$ be a steady state of (4.9) and suppose that the Jacobian matrix

$$\begin{pmatrix} f_x & g_x \\ f_y & g_y \end{pmatrix}$$

has complex eigenvalues

$$\lambda = \sigma(\mu) \pm i\omega(\mu)$$

such that $\sigma(\mu) < 0$ for $\mu \in (-\varepsilon, 0)$ and $\sigma(\mu) > 0$ for $\mu \in (0, \varepsilon)$ and $\sigma(0) = 0$, but $\omega(0) \neq 0$. Suppose also that the following conditions also hold:

1. $f, g$ are analytic in $x, y$ and $\mu$;
2. $\frac{dg}{d\mu} > 0$ at $\mu = 0$;
3. $x_0$ is asymptotically stable;

Then: for sufficiently small $\mu > 0$ the unstable steady state $x_0$ is surrounded by a periodic attractor (limit cycle) which typically depends on $\mu$. The period of the cycle is approximately $2\pi/\omega(0)$.

Figure 4.3 show the movement of the eigenvalues, during a Hopf bifurcation, in the Argand plane. In the course you will not be expected to verify the 3 conditions of the theorem, but you will need to show that the change of stability leading to the possibility of a Hopf bifurcation can occur. (Exercise: Check the 3 conditions for the above toy system.)

Hence returning to our general Predator-Prey model, we see that a Hopf bifurcation, where a stable limit cycle appears around an unstable steady state, is possible if the eigenvalues pass from the left hand side of the Argand plane to the right hand side as parameters change. Note that the limit cycle may later disappear as parameters are changed further (see the Holling type 3 model, and in particular figure 4.6).

We will now consider specific Predator-Prey models by specifying the actual functional forms of $\phi, \sigma$.

### 4.2 Holling’s functional responses

Holling suggested three different types of functional forms for $\phi$ to model the predation rate. We will consider each of these in turn.
First, however, we argue that

\[
\frac{N \Phi(N,P)}{P} = \text{expected density of prey consumed per predator per unit time.}
\]

We thus identify

\[
\omega = \text{feeding rate} = \frac{N \Phi(N,P)}{P}.
\]

The three functional responses identified by Holling model the 3 different types of feeding rates.

1 **Holling Type 1: \( \omega = \gamma N \)**

Here the feeding rate does not saturate as the prey density increases. This is the response used in the classic predator-prey model of Lotka and Volterra, and we will add nothing to the story here. We do mention, though, that sometimes Holling type 1 is given as \( \omega = \min\{\gamma N, \gamma\} \) which saturates, but is not \( C^1 \).

2 **Holling Type 2 \( \omega = \frac{\gamma N}{A + N} \)**

Here the feeding rate saturates at the maximum feeding rate \( \gamma \). The feeding rate is half maximal at \( N = A \). This response models the fact that the consumption of prey is limited by satiation of predators, handling time (killing and eating) and time spent hunting prey. The curve of \( N \) against \( \omega \) is shown in figure 4.4. Such a functional response is known as *hyperbolic*. 
3 Holling Type 3 \( \omega = \frac{\gamma N^2}{A^2 + N^2} \)

Again the feeding rate saturates at the maximal feeding rate \( \gamma \). However there is a point of inflexion in the curve (see figure 4.4). This is intended to model that for small densities, prey are able to evade predators by taking refuge. Such a functional response is known as sigmoidal. We will now work through Holling type 2,3 for the general predator-prey models. In each case we will take \( \sigma(N) = \frac{\sigma N}{\partial N} \phi(N,P) \) (which is just a function of \( N \) as \( \phi \) is always linear in \( P \)).

4 Holling Type 2: Phase plane analysis

Here the model becomes:

\[
\begin{align*}
\dot{N} &= \rho N \left(1 - \frac{N}{K}\right) - \frac{\gamma NP}{A + N} \\
\dot{P} &= P \left(\frac{\sigma N}{A + N} - \mu\right).
\end{align*}
\]

There are steady states at \((0,0)\) and \((K,0)\). A third interior steady state \((N^*,P^*)\) exists if there is a positive solution to

\[
\begin{align*}
\rho \left(1 - \frac{N}{K}\right) - \frac{\gamma P}{A + N} &= 0 \quad (4.10) \\
\left(\frac{\sigma N}{A + N} - \mu\right) &= 0. \quad (4.11)
\end{align*}
\]

Figure 4.4: The three Holling functional responses
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The second equation yields
\[ N^* = \frac{\mu A}{\sigma - \mu}, \] (4.12)
which means that we require \( \sigma > \mu \). In fact inspection of the predator dynamics shows that if \( \sigma \leq \mu \), then \( \dot{P} < 0 \) for all \( P \neq 0 \) and so the predator would then die out. The corresponding value of \( P^* \) is
\[ P^* = \frac{\rho}{\gamma} (A + N^*) \left( 1 - \frac{N^*}{K} \right). \]
So we see that we also need \( N^* < K \). Hence for an interior steady state to exist we need
\[ A\mu < (\sigma - \mu)K, \]
which implies \( \sigma > \mu \). The stability matrix is calculated to be
\[ M = \begin{pmatrix} \rho \left(1 - \frac{N}{K}\right) - \frac{\gamma P}{A+N} & \frac{\gamma N P}{(A+N)^2} & -\frac{\gamma N}{A+N} \\ \frac{\rho N}{(A+N)^2} & -\frac{\gamma N}{A+N} - \mu \\ -\frac{\gamma N}{A+N} + \frac{\rho N}{(A+N)^2} & \frac{\rho N}{(A+N)^2} & -\mu \end{pmatrix}. \]
Hence at \((0,0)\) we have
\[ M = \begin{pmatrix} \rho & 0 \\ 0 & -\mu \end{pmatrix}, \]
so that the origin is a saddle. At \((K,0)\) we obtain
\[ M = \begin{pmatrix} -\rho & -\frac{\gamma K}{A+K} - \mu \\ 0 & \frac{\gamma K}{A+K} - \mu \end{pmatrix}. \]
If \( \sigma K < \mu (A + K) \) then there is no interior steady state and we see that \((K,0)\) has negative eigenvalues \(-\rho, \frac{\sigma K}{A+K} - \mu\) and so is a stable node. If \( \sigma K > \mu (A + K) \) then \((K,0)\) is a saddle.

Finally, when \( \sigma K > \mu (A + K) \) we need to examine the stability of the interior steady state \((N^*, P^*)\). Here the stability matrix becomes:
\[ M = \begin{pmatrix} -\frac{\rho N}{(A+N)^2} + \frac{\gamma N P}{(A+N)^2} & -\frac{\gamma N}{A+N} \\ \frac{\rho N}{(A+N)^2} & -\frac{\gamma N}{A+N} \end{pmatrix} \]
\((N^*, P^*)\)
If \( \lambda_1, \lambda_2 \) are the eigenvalues of \( M \) then
\[ \lambda_1 + \lambda_2 = \frac{\gamma N^* P^*}{(A+N^*)^2} - \frac{\rho N^*}{K} \]
\[ \lambda_1 \lambda_2 = \frac{\gamma N^* P^* \sigma P^* A}{A+N^* (A+N^*)^2} \]
We immediately see that \( \lambda_1 \lambda_2 > 0 \) so that the eigenvalues have real parts of the same sign. Now we tidy
up equation (4.13) using equation (4.10) to obtain

\[ \lambda_1 + \lambda_2 = \frac{\rho N^*}{K(A + N^*)} (K - A - 2N^*). \]

It is easy to show that the gradient of the \( N = 0 \) nullcline is \( P'(N) = \frac{\rho}{K} (K - A - 2N) \), which is negative if \( K < A \). Thus if \( K < A \) then the interior steady state is always stable, since the nullcline is decreasing. If \( K > A \), however, the nullcline as positive gradient at \( N = 0 \) and for some parameter values the trace may vanish and so a Hopf bifurcation is possible. Substituting \( N^* \) from (4.12) we have that \( (N^*, P^*) \) is stable if \( \delta = \sigma(K - A) - \mu(K + a) < 0 \) and unstable if \( \delta > 0 \). A Hopf bifurcation may appear if \( K > A \) and the parameters change so that \( \delta \) goes from being negative through zero and then positive. Figure 4.5 shows the phase plane changes for \( \delta = -1/2, 0, +1/2 \).

\[ \text{Figure 4.5: Phase plane for the type 2 Holling functional response. Going from top to bottom } \delta = -1/2, 0, +1/2. \]
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5 Holling Type 3: Phase plane analysis

Here the model becomes:

\[ N = ρN \left(1 - \frac{N}{K}\right) - \frac{γN^2P}{A^2 + N^2}, \]

\[ P = P \left(\frac{σN^2}{A^2 + N^2} - μ\right). \]

There are steady states at \((0,0)\) and \((K,0)\). A third interior steady state \((N^*, P^*)\) exists if there is a positive solution to

\[ ρ \left(1 - \frac{N}{K}\right) - \frac{γNP}{A^2 + N^2} = 0 \]  
\[ \left(\frac{σN^2}{A^2 + N^2} - μ\right) = 0. \]

The second equation yields

\[ N^* = A \sqrt{\frac{μ}{σ - μ}}, \]

so that as with type 2 we need \(σ > μ\) for an interior steady state. The corresponding value of \(P^*\) is

\[ P^* = \frac{ρ}{γN'}(A^2 + N^*) \left(1 - \frac{N^*}{K}\right). \]

So again we see that we need \(N^* < K\). Hence for an interior steady state to exist we need

\[ A \sqrt{μ} < \sqrt{σ - μ}K, \]

(which implies \(σ > μ\)). The stability matrix is calculated to be

\[ M = \begin{pmatrix} ρ \left(1 - \frac{N}{K}\right) - \frac{ρN}{K} & -\frac{2 γNP}{(A^2 + N^2)^2} + \frac{2 γγ^3 p}{(A^2 + N^2)^2} & -\frac{γ^2}{A^2 + N^2} \end{pmatrix} \left(\frac{σN^2}{A^2 + N^2} - μ\right) \]

Hence at \((0,0)\) we have

\[ M = \begin{pmatrix} ρ & 0 & 0 \\ 0 & -μ \end{pmatrix}, \]

so that the origin is a saddle. At \((K,0)\) we obtain

\[ M = \begin{pmatrix} -ρ & -\frac{γK^2}{A^2 + K^2} \\ 0 & -\frac{σK^2}{A^2 + K^2} - μ \end{pmatrix}. \]

If \(\sqrt{σK} < \sqrt{μ(A + K)}\) then there is no interior steady state and we see that \((K,0)\) has negative eigenvalues \(-ρ, \frac{σK^2}{A^2 + K^2} - μ\) and so is a stable node. If \(\sqrt{σK} > \sqrt{μ(A + K)}\) then \((K,0)\) is a saddle.
4.2. HOLLING’S FUNCTIONAL RESPONSES

Finally, when $\sigma K^2 > \mu (A^2 + K^2)$ we need to examine the stability of the interior steady state $(N^*, P^*)$. Here the stability matrix becomes:

$$M = \begin{pmatrix} -\frac{\rho N}{K} & -\frac{\gamma N P^*}{A^2 + N^2} + \frac{2\gamma N^2 P^*}{(A^2 + N^2)^2} - \frac{\gamma N^2}{A^2 + N^2} \\ 0 & 0 \end{pmatrix}_{(N^*, P^*)}$$

If $\lambda_1, \lambda_2$ are the eigenvalues of $M$ then

$$\begin{align*}
\lambda_1 + \lambda_2 &= -\frac{\rho N^*}{K} - \frac{\gamma N^* P^*}{A^2 + N^2} + \frac{2\gamma N^2 P^*}{(A^2 + N^2)^2} \\
\lambda_1 \lambda_2 &= \frac{\gamma N^2 P^*}{(A^2 + N^2)^2} - 2\rho N^* A^2
\end{align*}$$

We immediately see that $\lambda_1 \lambda_2 > 0$ so that the eigenvalues have real parts of the same sign. Now we tidy up equation (4.17) using equation (4.14) to obtain

$$\begin{align*}
\lambda_1 + \lambda_2 &= -\rho \left( \frac{N^*}{K} - \frac{\rho - \frac{\rho N^*}{K}}{1 - \frac{\rho N^*}{K}} \right) + 2\rho \frac{N^*}{K} \frac{N^2}{A^2 + N^2} \\
&= -\rho + 2\rho \left( 1 - \frac{N^*}{K} \right) \frac{N^2}{A^2 + N^2} \\
&= -\rho + 2\rho \left( 1 - \frac{N^*}{K} \right) \frac{\mu}{\sigma} \\
&= \rho \left( \frac{2\mu}{\sigma} - 1 - \frac{2\mu A}{\sigma K \sqrt{\sigma - \mu}} \right).
\end{align*}$$

Hence we see that for a Hopf bifurcation to be possible we need $2\mu > \sigma$. Now, we have established that

$$\lambda_1 + \lambda_2 = \rho \left( \frac{2\mu}{\sigma} - 1 - \frac{2\mu A}{\sigma K \sqrt{\sigma - \mu}} \right).$$

This is always negative if $\sigma \geq 2\mu$, but if $\sigma < 2\mu$, the above expression may go positive. Thus consider varying the mortality $\mu$ of the predator (see figure 4.6). When $\mu$ is small the gradient of the $N = 0$ nullcline is negative so the interior steady state is stable. As $\mu$ increases, the gradient becomes positive and a stable limit cycle appears around the interior steady state. As $\mu$ is increased further the gradient goes negative and the interior steady state returns to being (locally) stable. For large enough $\mu$ the oscillatory behaviour disappears. (This vanishing of the limit cycle for large $\mu$ cannot occur in the type 2 functional response model.)
CHAPTER 4. PREDATOR-PREY SYSTEMS

Figure 4.6: Phase plane for the type 3 Holling functional response. As the mortality \( \mu \) of the predator increases, the stable coexistence may become unstable leading to a stable limit cycle, but the limit cycle disappears for large enough \( \mu \), since the coexistence become stable again. (Plots running left to right, top to bottom as \( \mu \) increases.)

Figure 4.7: As the mortality \( \mu \) of the predator increases, \( \lambda_1 + \lambda_2 = \mu \left( \frac{2}{\alpha} - \frac{1}{\mu} - \frac{2A}{\alpha K} \sqrt{\frac{\mu}{\sigma - \mu}} \right) \) changes from negative to positive and back to negative. Thus the interior steady state goes from locally stable to unstable (for \( \mu \in (\mu_-, \mu_+) \)) to stable for \( \mu > \mu_+ \). The result is that a stable limit cycle appears in \( (\mu_-, \mu_+) \) but then disappears as \( \mu \) increases beyond \( \mu_+ \).