S1 Appendix: Proof of Theorem 1

The model is:

\[
\frac{dS}{dt}(t) = D(t)(S^0(t) - S) - G(E, S) \tag{1}
\]
\[
\frac{dP}{dt}(t) = G(E, S) - \frac{1}{\gamma} (X_1 + X_2) F(P) - D(t)P \tag{2}
\]
\[
\frac{dE}{dt}(t) = (1 - q)X_1 F(P) - D(t)E \tag{3}
\]
\[
\frac{dX_1}{dt}(t) = X_1 (qF(P) - D(t)) \tag{4}
\]
\[
\frac{dX_2}{dt}(t) = X_2 (F(P) - D(t)) \tag{5}
\]

By scaling the state variables of system (1) – (5) as follows:

\[
s = S \\
p = P \\
e = \frac{E}{\gamma} \\
x_1 = \frac{X_1}{\gamma} \\
x_2 = \frac{X_2}{\gamma},
\]

and introducing the rescaled functions

\[
g(e, s) := G(\gamma e, s) \tag{6}
\]
\[
f(p) := F(P) \tag{7}
\]

we obtain the following scaled model:

\[
\frac{ds}{dt}(t) = D(t)(S^0(t) - s) - g(e, s) \tag{6}
\]
\[
\frac{dp}{dt}(t) = g(e, s) - (x_1 + x_2)f(p) - D(t)p \tag{7}
\]
\[
\frac{de}{dt}(t) = (1 - q)x_1 f(p) - D(t)e \tag{8}
\]
\[
\frac{dx_1}{dt}(t) = x_1 (qf(p) - D(t)) \tag{9}
\]
\[
\frac{dx_2}{dt}(t) = x_2 (f(p) - D(t)) \tag{10}
\]
Notice that \( H1 \), which holds for the rate functions \( G(E, S) \) and \( F(P) \), is also valid for the scaled rate functions \( g(e, s) \) and \( f(p) \).

The total mass of this scaled model,

\[
m = s + p + e + x_1 + x_2,
\]
satisfies a linear equation:

\[
\frac{dm}{dt}(t) = D(t)(S^0(t) - m),
\]
which is easily verified by adding all the equations of the scaled model. This equation, and the upper bound for \( S^0(t) \) in \( H2 \) imply that the following family of compact sets

\[
\Omega_{\epsilon} = \{(s, p, e, x_1, x_2) \mid s \geq 0, p \geq 0, e \geq 0, x_1 \geq 0, x_2 \geq 0, m \leq \bar{S}^0 + \epsilon\};
\]
are forward invariant sets of the scaled model, for all \( \epsilon \geq 0 \).

The Main Result, Theorem 1, is an immediate Corollary of the following result, which is the tragedy of the commons for the scaled model:

**Theorem 1.** Assume that \( H1 \) and \( H2 \) hold, and assume that the initial condition of \((6) - (10)\) is such that \( x_2(0) > 0 \); that is, the cheater is present initially. Then \((p(t), e(t), x_1(t), x_2(t)) \to (0,0,0,0) \) as \( t \to \infty \).

**Proof**

Given the initial condition, we can find an \( \epsilon \geq 0 \) such that the solution \((s(t), p(t), e(t), x_1(t), x_2(t))\) is contained in the compact set \( \Omega_{\epsilon} \) for all \( t \geq 0 \). We shall present two proofs. The first involves a (biologically nontrivial) transformation of one of the system’s variables. The second considers the ratio of cooperators and cheaters, a biologically natural measure, and reveals that this ratio does not increase.

**Proof 1:** Consider the variable \( y_2 = x_2^q \). Then

\[
\frac{dy_2}{dt}(t) = y_2(qf(p) - qD(t))
\]

Equation (9), and the above equation can be integrated:

\[
x_1(t) = x_1(0) e^{\int_0^t qf(p(\tau)) - D(\tau)d\tau}
\]
\[
y_2(t) = y_2(0) e^{\int_0^t qf(p(\tau)) - qD(\tau)d\tau} > 0, \text{ for all } t \text{ since } y_2(0) = x_2^q(0) > 0,
\]
Dividing the first by the second equation yields:

\[
x_1(t) = y_2(t) \frac{x_1(0)}{y_2(0)} e^{-(1-q)\int_0^t D(\tau)d\tau} \leq B \frac{x_1(0)}{y_2(0)} e^{-(1-q)D_t},
\]
where we have used the lower bound for \( D(t) \), see \( H2 \), to establish the last inequality, and the positive bound \( B \) for \( y_2(t) \) which exists because the solution, and therefore also \( x_2(t) \), is bounded. From this follows that \( \lim_{t \to \infty} x_1(t) = 0 \), where the
convergence is at least exponential with rate \((1-q)D\).
Next we consider the dynamics of the variable \(z = Qx_1 - e\), where \(Q = (1-q)/q\):

\[
\dot{z} = -D(t)z,
\]

which is solvable, yielding \(z(t) = z(0) e^{-\int_0^t D(\tau)d\tau}\). The lower bound \(D\) for \(D(t)\) in \(\textbf{H2}\), then implies that \(z(t) \to 0\) at a rate which is at least exponential with rate \(D\).
This fact, together with the convergence of \(x_1(t)\) to zero established above, implies that \(e(t) \to 0\) as well.
Next, consider the \(p\)-equation (7). There holds that for each \(\tilde{\epsilon} > 0\):

\[
\frac{dp}{dt}(t) \leq \tilde{\epsilon} - Dp, \quad \text{for all sufficiently large } t.
\]

Notice that we used that \(g(0,s) = 0\) for all \(s \geq 0\), and the continuity of \(g\), see \(\textbf{H1}\), as well as \(\textbf{H2}\) for the lower bound of \(D(t)\). It follows that \(\limsup_{t \to \infty} p(t) \leq \tilde{\epsilon}/D\), and since \(\tilde{\epsilon} > 0\) was arbitrary, there follows that \(p(t) \to 0\).
Finally, we consider the \(x_2\)-equation (10). Since \(p(t) \to 0\) and \(f(0) = 0\) by \(\textbf{H1}\), there holds that \(f(p(t)) \leq D/2\) for all \(t\) sufficiently large. Consequently,

\[
\frac{dx_2}{dt}(t) \leq -\frac{D}{2} x_2, \quad \text{for all sufficiently large } t,
\]

and thus \(x_2(t) \to 0\), concluding the proof in this case.

**Proof 2:** Equations (9) and (10) can be integrated:

\[
x_1(t) = x_1(0) e^{\int_0^t qf(p(\tau)) - D(\tau)d\tau}, \quad (12)
\]

\[
x_2(t) = x_2(0) e^{\int_0^t f(p(\tau)) - D(\tau)d\tau} > 0, \quad \text{for all } t \text{ since } x_2(0) > 0. \quad (13)
\]

Thus, the ratio \(r(t) = x_1(t)/x_2(t)\) is well-defined and satisfies the differential equation:

\[
\frac{dr}{dt}(t) = -(1-q)f(p)r,
\]

which shows that the ratio does not increase. The solution of this equation is:

\[
r(t) = r(0) e^{-(1-q)\int_0^t f(p(\tau))d\tau} \quad (14)
\]

We distinguish two cases depending on the integrability of the function \(f(p(t))\):

**Case 1:** \(\int_0^\infty f(p(\tau))d\tau = \infty\).
It follows from (14) that \(r(t) \to 0\), and hence also \(x_1(t) \to 0\) because \(x_2(t)\) is bounded. Proof of convergence of \(e(t), p(t)\) and \(x_2(t)\) to zero now proceeds as in **Proof 1**.

**Case 2:** \(\int_0^\infty f(p(\tau))d\tau < \infty\).
It follows from (12)−(13) that both \(x_1(t) \to 0\) and \(x_2(t) \to 0\), because \(0 < D \leq D(t)\) for all \(t\), by \(\textbf{H2}\). Proof of convergence of \(e(t)\) and \(p(t)\) to zero now proceeds as in **Proof 1** as well.