

S1 Appendix: Proof of Theorem 1

The model is:

$$\frac{dS}{dt}(t) = D(t)(S^0(t) - S) - G(E, S) \quad (1)$$

$$\frac{dP}{dt}(t) = G(E, S) - \frac{1}{\gamma}(X_1 + X_2)F(P) - D(t)P \quad (2)$$

$$\frac{dE}{dt}(t) = (1 - q)X_1F(P) - D(t)E \quad (3)$$

$$\frac{dX_1}{dt}(t) = X_1(qF(P) - D(t)) \quad (4)$$

$$\frac{dX_2}{dt}(t) = X_2(F(P) - D(t)) \quad (5)$$

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

$$\begin{aligned} s &= S \\ p &= P \\ e &= \frac{E}{\gamma} \\ x_1 &= \frac{X_1}{\gamma} \\ x_2 &= \frac{X_2}{\gamma}, \end{aligned}$$

and introducing the rescaled functions

$$\begin{aligned} g(e, s) &:= G(\gamma e, s) \\ f(p) &:= F(P), \end{aligned}$$

we obtain the following scaled model:

$$\frac{ds}{dt}(t) = D(t)(S^0(t) - s) - g(e, s) \quad (6)$$

$$\frac{dp}{dt}(t) = g(e, s) - (x_1 + x_2)f(p) - D(t)p \quad (7)$$

$$\frac{de}{dt}(t) = (1 - q)x_1f(p) - D(t)e \quad (8)$$

$$\frac{dx_1}{dt}(t) = x_1(qf(p) - D(t)) \quad (9)$$

$$\frac{dx_2}{dt}(t) = x_2(f(p) - D(t)) \quad (10)$$

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:

$$\frac{dm}{dt}(t) = D(t)(S^0(t) - m), \quad (11)$$

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 $(p(t), e(t), x_1(t), x_2(t)) \rightarrow (0, 0, 0, 0)$ as $t \rightarrow \infty$.*

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 Ω_ϵ 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:

$$\begin{aligned} x_1(t) &= x_1(0) e^{\int_0^t qf(p(\tau)) - D(\tau) d\tau} \\ y_2(t) &= y_2(0) e^{\int_0^t qf(p(\tau)) - qD(\tau) d\tau} > 0, \text{ for all } t \text{ since } y_2(0) = x_2^q(0) > 0, \end{aligned}$$

Dividing the first by the second equation yields:

$$x_1(t) = y_2(t) \frac{x_1(0)}{y_2(0)} e^{-(1-q) \int_0^t D(\tau) d\tau} \leq B \frac{x_1(0)}{y_2(0)} e^{-(1-q)Dt},$$

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 $\lim_{t \rightarrow \infty} x_1(t) = 0$, where the

convergence is at least exponential with rate $(1 - q)\underline{D}$.

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 \underline{D} for $D(t)$ in **H2**, then implies that $z(t) \rightarrow 0$ at a rate which is at least exponential with rate \underline{D} . This fact, together with the convergence of $x_1(t)$ to zero established above, implies that $e(t) \rightarrow 0$ as well.

Next, consider the p -equation (7). There holds that for each $\tilde{\epsilon} > 0$:

$$\frac{dp}{dt}(t) \leq \tilde{\epsilon} - \underline{D}p, \text{ for all sufficiently large } t.$$

Notice that we used that $g(0, s) = 0$ for all $s \geq 0$, and the continuity of g , see **H1**, as well as **H2** for the lower bound of $D(t)$. It follows that $\limsup_{t \rightarrow \infty} p(t) \leq \tilde{\epsilon}/\underline{D}$, and since $\tilde{\epsilon} > 0$ was arbitrary, there follows that $p(t) \rightarrow 0$.

Finally, we consider the x_2 -equation (10). Since $p(t) \rightarrow 0$ and $f(0) = 0$ by **H1**, there holds that $f(p(t)) \leq \underline{D}/2$ for all t sufficiently large. Consequently,

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

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

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

$$x_1(t) = x_1(0) e^{\int_0^t qf(p(\tau)) - D(\tau)d\tau} \tag{12}$$

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

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:

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

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 $r(t) \rightarrow 0$, and hence also $x_1(t) \rightarrow 0$ 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 $x_1(t) \rightarrow 0$ and $x_2(t) \rightarrow 0$, because $0 < \underline{D} \leq D(t)$ for all t , by **H2**. Proof of convergence of $e(t)$ and $p(t)$ to zero now proceeds as in **Proof 1** as well.