

4.11 The principle of competitive exclusion in population biology

- (a) Show that the change of coordinates $\beta_i y_i(t) = x_i(t/\alpha_i \beta_i)$ reduces this system of equations to

$$\dot{y}_1 = y_1(1 - y_1) + a_1 y_1 y_2, \quad \dot{y}_2 = y_2(1 - y_2) - a_2 y_1 y_2$$

where $a_1 = \gamma_1 \beta_2 / \alpha_1 \beta_1$ and $a_2 = \gamma_2 \beta_1 / \alpha_2 \beta_2$.

- (b) What are the stable equilibrium populations when (i) $0 < a_2 < 1$, (ii) $a_2 > 1$?
 (c) It is observed that $a_1 = 3a_2$ (a_2 is a measure of the aggressiveness of the predator). What is the value of a_2 if the predator's instinct is to maximize its stable equilibrium population?
 6. (a) Let $x(t)$ be a solution of $\dot{x} = ax - M\sqrt{x}$, with $M > a\sqrt{x(t_0)}$. Show that
- $$a\sqrt{x} = M - (M - a\sqrt{x(t_0)})e^{a(t-t_0)/2}.$$
- (b) Conclude from (a) that $x(t)$ approaches zero in finite time.
 (c) Let $x(t), y(t)$ be a solution of (7), with $by(t_0) > a\sqrt{x(t_0)}$. Show that $x(t)$ reaches zero in finite time. *Hint:* Observe that $y(t)$ is increasing for $t > t_0$.
 (d) It can be shown that $by(t)$ will eventually exceed $a\sqrt{x(t)}$ for every solution $x(t), y(t)$ of (7) with $x(t_0)$ and $y(t_0)$ positive. Conclude, therefore, that all solutions $x(t), y(t)$ of (7) achieve $x=0$ in finite time.

4.11 The principle of competitive exclusion in population biology

It is often observed, in nature, that the struggle for existence between two similar species competing for the same limited food supply and living space nearly always ends in the complete extinction of one of the species. This phenomenon is known as the "principle of competitive exclusion." It was first enunciated, in a slightly different form, by Darwin in 1859. In his paper 'The origin of species by natural selection' he writes: "As the species of the same genus usually have, though by no means invariably, much similarity in habits and constitutions and always in structure, the struggle will generally be more severe between them, if they come into competition with each other, than between the species of distinct genera."

There is a very interesting biological explanation of the principle of competitive exclusion. The cornerstone of this theory is the idea of a "niche." A niche indicates what place a given species occupies in a community; i.e., what are its habits, food and mode of life. It has been observed that as a result of competition two similar species rarely occupy the same niche. Rather, each species takes possession of those kinds of food and modes of life in which it has an advantage over its competitor. If the two species tend to occupy the same niche then the struggle for existence between them will be very intense and result in the extinction of the weaker species.

An excellent illustration of this theory is the colony of terns inhabiting the island of Jorilgatch in the Black Sea. This colony consists of four different species of terns: sandwich-tern, common-tern, blackbeak-tern, and lit-

ξ, η respectively, as t approaches infinity. Lemma 2 of Section 4.8 implies that (ξ, η) is an equilibrium point of (4). Now, the only equilibrium points of (4) are $(0, 0)$, $(K_1, 0)$, and $(0, K_2)$, and (ξ, η) obviously cannot equal any of these three points. We conclude therefore, that any solution $N_1(t), N_2(t)$ of (4) which starts in region I must leave this region at a later time. \square

Lemma 2. Any solution $N_1(t), N_2(t)$ of (4) which starts in region II at time $t = t_0$ will remain in this region for all future time $t \geq t_0$, and ultimately approach the equilibrium solution $N_1 = K_1, N_2 = 0$.

PROOF. Suppose that a solution $N_1(t), N_2(t)$ of (4) leaves region II at time $t = t^*$. Then, either $\dot{N}_1(t^*)$ or $\dot{N}_2(t^*)$ is zero, since the only way a solution of (4) can leave region II is by crossing l_1 or l_2 . Assume that $N_1(t^*) = 0$. Differentiating both sides of the first equation of (4) with respect to t and setting $t = t^*$ gives

$$\frac{d^2 N_1(t^*)}{dt^2} = \frac{-a_1 N_1(t^*)}{K_1} \frac{dN_2(t^*)}{dt}.$$

This quantity is positive. Hence, $N_1(t)$ has a minimum at $t = t^*$. But this is impossible, since $N_1(t)$ is increasing whenever a solution $N_1(t), N_2(t)$ of (4) is in region II. Similarly, if $\dot{N}_2(t^*) = 0$, then

$$\frac{d^2 N_2(t^*)}{dt^2} = \frac{-a_2 N_2(t^*)}{K_2} \frac{dN_1(t^*)}{dt}.$$

This quantity is negative, implying that $N_2(t)$ has a maximum at $t = t^*$. But this is impossible, since $N_2(t)$ is decreasing whenever a solution $N_1(t), N_2(t)$ of (4) is in region II.

The previous argument shows that any solution $N_1(t), N_2(t)$ of (4) which starts in region II at time $t = t_0$ will remain in region II for all future time $t \geq t_0$. This implies that $N_1(t)$ is monotonic increasing and $N_2(t)$ is monotonic decreasing for $t \geq t_0$, with $N_1(t) < K_1$ and $N_2(t) > K_2$. Consequently, by Lemma 1 of Section 4.8, both $N_1(t)$ and $N_2(t)$ have limits ξ, η respectively, as t approaches infinity. Lemma 2 of Section 4.8 implies that (ξ, η) is an equilibrium point of (4). Now, (ξ, η) obviously cannot equal $(0, 0)$ or $(0, K_2)$. Consequently, $(\xi, \eta) = (K_1, 0)$, and this proves Lemma 2. \square

Lemma 3. Any solution $N_1(t), N_2(t)$ of (4) which starts in region III at time $t = t_0$ and remains there for all future time must approach the equilibrium solution $N_1(t) = K_1, N_2(t) = 0$ as t approaches infinity.

PROOF. If a solution $N_1(t), N_2(t)$ of (4) remains in region III for $t \geq t_0$, then both $N_1(t)$ and $N_2(t)$ are monotonic decreasing functions of time for $t \geq t_0$, with $N_1(t) > 0$ and $N_2(t) > 0$. Consequently, by Lemma 1 of Section 4.8, both $N_1(t)$ and $N_2(t)$ have limits ξ, η respectively, as t approaches infinity. Lemma 2 of Section 4.8 implies that (ξ, η) is an equilibrium point of (4). Now, (ξ, η) obviously cannot equal $(0, 0)$ or $(0, K_2)$. Consequently, $(\xi, \eta) = (K_1, 0)$. \square

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PROOF OF THEOREM 6. Lemmas 1 and 2 above state that every solution $N_1(t), N_2(t)$ of (4) which starts in regions I or II at time $t = t_0$ must approach the equilibrium solution $N_1 = K_1, N_2 = 0$ as t approaches infinity. Similarly, Lemma 3 shows that every solution $N_1(t), N_2(t)$ of (4) which starts in region III at time $t = t_0$ and remains there for all future time must also approach the equilibrium solution $N_1 = K_1, N_2 = 0$. Next, observe that any solution $N_1(t), N_2(t)$ of (4) which starts on l_1 or l_2 must immediately afterwards enter region II. Finally, if a solution $N_1(t), N_2(t)$ of (4) leaves region III, then it must cross the line l_1 and immediately afterwards enter region II. Lemma 2 then forces this solution to approach the equilibrium solution $N_1 = K_1, N_2 = 0$. \square

Theorem 6 deals with the case of identical species; i.e., $\alpha = \beta = 1$. By a similar analysis (see Exercises 4–6) we can predict the outcome of the struggle for existence for all values of α and β .

Reference

Gause, G. F., 'The Struggle for Existence,' Dover Publications, New York, 1964.

EXERCISES

1. Rewrite the system of equations (4) in the form

$$\frac{K_1}{a_1 N_1} \frac{dN_1}{dt} = K_1 - N_1 - N_2, \quad \frac{K_2}{a_2 N_2} \frac{dN_2}{dt} = K_2 - N_1 - N_2.$$

Then, subtract these two equations and integrate to obtain directly that $N_2(t)$ approaches zero for all solutions $N_1(t), N_2(t)$ of (4) with $N_1(t_0) > 0$.

2. The system of differential equations

$$\begin{aligned} \frac{dN_1}{dt} &= N_1 [-a_1 + c_1(1 - b_1 N_1 - b_2 N_2)] \\ \frac{dN_2}{dt} &= N_2 [-a_2 + c_2(1 - b_1 N_1 - b_2 N_2)] \end{aligned} \quad (*)$$

is a model of two species competing for the same limited resource. Suppose that $c_1 > a_1$ and $c_2 > a_2$. Deduce from Theorem 6 that $N_1(t)$ ultimately approaches zero if $a_1 c_2 > a_2 c_1$, and $N_2(t)$ ultimately approaches zero if $a_1 c_2 < a_2 c_1$.

3. In 1926, Volterra presented the following model of two species competing for the same limited food supply:

$$\begin{aligned} \frac{dN_1}{dt} &= [b_1 - \lambda_1(h_1 N_1 + h_2 N_2)] N_1 \\ \frac{dN_2}{dt} &= [b_2 - \lambda_2(h_1 N_1 + h_2 N_2)] N_2. \end{aligned}$$

Suppose that $b_1/\lambda_1 > b_2/\lambda_2$. (The coefficient b_i/λ_i is called the susceptibility of species i to food shortages.) Prove that species 2 will ultimately become extinct if $N_1(t_0) > 0$.

Problems 4–6 are concerned with the system of equations

$$\frac{dN_1}{dt} = \frac{a_1 N_1}{K_1} (K_1 - N_1 - \alpha N_2), \quad \frac{dN_2}{dt} = \frac{a_2 N_2}{K_2} (K_2 - N_2 - \beta N_1). \quad (*)$$

4. (a) Assume that $K_1/\alpha > K_2$ and $K_2/\beta < K_1$. Show that $N_2(t)$ approaches zero as t approaches infinity for every solution $N_1(t), N_2(t)$ of $(*)$ with $N_1(t_0) > 0$.
 (b) Assume that $K_1/\alpha < K_2$ and $K_2/\beta > K_1$. Show that $N_1(t)$ approaches zero as t approaches infinity for every solution $N_1(t), N_2(t)$ of $(*)$ with $N_1 N_2(t_0) > 0$.
Hint: Draw the lines $l_1: N_1 + \alpha N_2 = K_1$ and $l_2: N_2 + \beta N_1 = K_2$, and follow the proof of Theorem 6.
5. Assume that $K_1/\alpha > K_2$ and $K_2/\beta > K_1$. Prove that all solutions $N_1(t), N_2(t)$ of $(*)$, with both $N_1(t_0)$ and $N_2(t_0)$ positive, ultimately approach the equilibrium solution

$$N_1 = N_1^0 = \frac{K_1 - \alpha K_2}{1 - \alpha\beta}, \quad N_2 = N_2^0 = \frac{K_2 - \beta K_1}{1 - \alpha\beta}.$$

Hint:

- (a) Draw the lines $l_1: N_1 + \alpha N_2 = K_1$ and $l_2: N_2 + \beta N_1 = K_2$. The two lines divide the first quadrant into four regions (see Figure 2) in which both \dot{N}_1 and \dot{N}_2 have fixed signs.

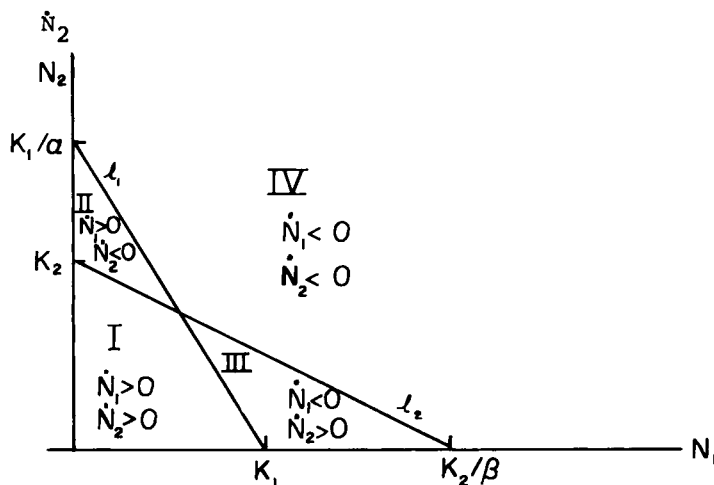


Figure 2

- (b) Show that all solutions $N_1(t), N_2(t)$ of $(*)$ which start in either region II or III must remain in these regions and ultimately approach the equilibrium solution $N_1 = N_1^0, N_2 = N_2^0$.
- (c) Show that all solutions $N_1(t), N_2(t)$ of $(*)$ which remain exclusively in region I or region IV for all time $t \geq t_0$ must ultimately approach the equilibrium solution $N_1 = N_1^0, N_2 = N_2^0$.

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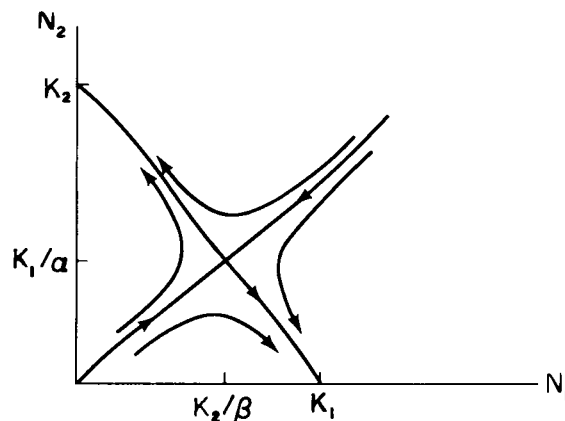


Figure 3

6. Assume that $K_1/\alpha < K_2$ and $K_2/\beta < K_1$.
 - (a) Show that the equilibrium solution $N_1=0, N_2=0$ of (*) is unstable.
 - (b) Show that the equilibrium solutions $N_1=K_1, N_2=0$ and $N_1=0, N_2=K_2$ of (*) are asymptotically stable.
 - (c) Show that the equilibrium solution $N_1=N_1^0, N_2=N_2^0$ (see Exercise 5) of (*) is a saddle point. (This calculation is very cumbersome.)
 - (d) It is not too difficult to see that the phase portrait of (*) must have the form described in Figure 3.

4.12 The Threshold Theorem of epidemiology

Consider the situation where a small group of people having an infectious disease is inserted into a large population which is capable of catching the disease. What happens as time evolves? Will the disease die out rapidly, or will an epidemic occur? How many people will ultimately catch the disease? To answer these questions we will derive a system of differential equations which govern the spread of an infectious disease within a population, and analyze the behavior of its solutions. This approach will also lead us to the famous Threshold Theorem of epidemiology which states that an epidemic will occur only if the number of people who are susceptible to the disease exceeds a certain threshold value.

We begin with the assumptions that the disease under consideration confers permanent immunity upon any individual who has completely recovered from it, and that it has a negligibly short incubation period. This latter assumption implies that an individual who contracts the disease becomes infective immediately afterwards. In this case we can divide the population into three classes of individuals: the infective class (I), the susceptible class (S) and the removed class (R). The infective class consists of those individuals who are capable of transmitting the disease to others.

The susceptible class consists of those individuals who are not infective, but who are capable of catching the disease and becoming infective. The removed class consists of those individuals who have had the disease and are dead, or have recovered and are permanently immune, or are isolated until recovery and permanent immunity occur.

The spread of the disease is presumed to be governed by the following rules.

Rule 1: The population remains at a fixed level N in the time interval under consideration. This means, of course, that we neglect births, deaths from causes unrelated to the disease under consideration, immigration and emigration.

Rule 2: The rate of change of the susceptible population is proportional to the product of the number of members of (S) and the number of members of (I).

Rule 3: Individuals are removed from the infectious class (I) at a rate proportional to the size of (I).

Let $S(t)$, $I(t)$, and $R(t)$ denote the number of individuals in classes (S), (I), and (R), respectively, at time t . It follows immediately from Rules 1–3 that $S(t)$, $I(t)$, $R(t)$ satisfies the system of differential equations

$$\begin{aligned}\frac{dS}{dt} &= -rSI \\ \frac{dI}{dt} &= rSI - \gamma I \\ \frac{dR}{dt} &= \gamma I\end{aligned}\tag{1}$$

for some positive constants r and γ . The proportionality constant r is called the infection rate, and the proportionality constant γ is called the removal rate.

The first two equations of (1) do not depend on R . Thus, we need only consider the system of equations

$$\frac{dS}{dt} = -rSI, \quad \frac{dI}{dt} = rSI - \gamma I\tag{2}$$

for the two unknown functions $S(t)$ and $I(t)$. Once $S(t)$ and $I(t)$ are known, we can solve for $R(t)$ from the third equation of (1). Alternately, observe that $d(S + I + R)/dt = 0$. Thus,

$$S(t) + I(t) + R(t) = \text{constant} = N$$

so that $R(t) = N - S(t) - I(t)$.

The orbits of (2) are the solution curves of the first-order equation

$$\frac{dI}{dS} = \frac{rSI - \gamma I}{-rSI} = -1 + \frac{\gamma}{rS}.\tag{3}$$

Integrating this differential equation gives

$$I(S) = I_0 + S_0 - S + \rho \ln \frac{S}{S_0},\tag{4}$$

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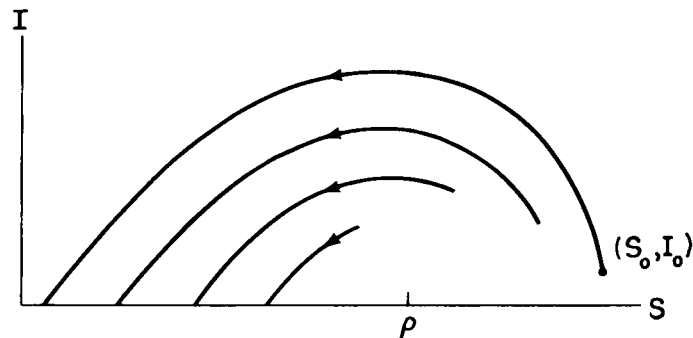


Figure 1. The orbits of (2)

where S_0 and I_0 are the number of susceptibles and infectives at the initial time $t = t_0$, and $\rho = \gamma/r$. To analyze the behavior of the curves (4), we compute $I'(S) = -1 + \rho/S$. The quantity $-1 + \rho/S$ is negative for $S > \rho$, and positive for $S < \rho$. Hence, $I(S)$ is an increasing function of S for $S < \rho$, and a decreasing function of S for $S > \rho$.

Next, observe that $I(0) = -\infty$ and $I(S_0) = I_0 > 0$. Consequently, there exists a unique point S_∞ , with $0 < S_\infty < S_0$, such that $I(S_\infty) = 0$, and $I(S) > 0$ for $S_\infty < S \leq S_0$. The point $(S_\infty, 0)$ is an equilibrium point of (2) since both dS/dt and dI/dt vanish when $I = 0$. Thus, the orbits of (2), for $t_0 \leq t < \infty$, have the form described in Figure 1.

Let us see what all this implies about the spread of the disease within the population. As t runs from t_0 to ∞ , the point $(S(t), I(t))$ travels along the curve (4), and it moves along the curve in the direction of decreasing S , since $S(t)$ decreases monotonically with time. Consequently, if S_0 is less than ρ , then $I(t)$ decreases monotonically to zero, and $S(t)$ decreases monotonically to S_∞ . Thus, if a small group of infectives I_0 is inserted into a group of susceptibles S_0 , with $S_0 < \rho$, then the disease will die out rapidly. On the other hand, if S_0 is greater than ρ , then $I(t)$ increases as $S(t)$ decreases to ρ , and it achieves a maximum value when $S = \rho$. It only starts decreasing when the number of susceptibles falls below the threshold value ρ . From these results we may draw the following conclusions.

Conclusion 1: An epidemic will occur only if the number of susceptibles in a population exceeds the threshold value $\rho = \gamma/r$.

Conclusion 2: The spread of the disease does not stop for lack of a susceptible population; it stops only for lack of infectives. In particular, some individuals will escape the disease altogether.

Conclusion 1 corresponds to the general observation that epidemics tend to build up more rapidly when the density of susceptibles is high due to overcrowding, and the removal rate is low because of ignorance, inadequate isolation and inadequate medical care. On the other hand, outbreaks tend to be of only limited extent when good social conditions entail lower

densities of susceptibles, and when removal rates are high because of good public health vigilance and control.

If the number of susceptibles S_0 is initially greater than, but close to, the threshold value ρ , then we can estimate the number of individuals who ultimately contract the disease. Specifically, if $S_0 - \rho$ is small compared to ρ , then the number of individuals who ultimately contract the disease is approximately $2(S_0 - \rho)$. This is the famous Threshold Theorem of epidemiology, which was first proven in 1927 by the mathematical biologists Kermack and McKendrick.

Theorem 7 (Threshold Theorem of epidemiology). *Let $S_0 = \rho + v$ and assume that v/ρ is very small compared to one. Assume moreover, that the number of initial infectives I_0 is very small. Then, the number of individuals who ultimately contract the disease is $2v$. In other words, the level of susceptibles is reduced to a point as far below the threshold as it originally was above it.*

PROOF. Letting t approach infinity in (4) gives

$$0 = I_0 + S_0 - S_\infty + \rho \ln \frac{S_\infty}{S_0}.$$

If I_0 is very small compared to S_0 , then we can neglect it, and write

$$\begin{aligned} 0 &= S_0 - S_\infty + \rho \ln \frac{S_\infty}{S_0} \\ &= S_0 - S_\infty + \rho \ln \left[\frac{S_0 - (S_0 - S_\infty)}{S_0} \right] \\ &= S_0 - S_\infty + \rho \ln \left[1 - \left(\frac{S_0 - S_\infty}{S_0} \right) \right]. \end{aligned}$$

Now, if $S_0 - \rho$ is small compared to ρ , then $S_0 - S_\infty$ will be small compared to S_0 . Consequently, we can truncate the Taylor series

$$\ln \left[1 - \left(\frac{S_0 - S_\infty}{S_0} \right) \right] = - \left(\frac{S_0 - S_\infty}{S_0} \right) - \frac{1}{2} \left(\frac{S_0 - S_\infty}{S_0} \right)^2 + \dots$$

after two terms. Then,

$$\begin{aligned} 0 &= S_0 - S_\infty - \rho \left(\frac{S_0 - S_\infty}{S_0} \right) - \frac{\rho}{2} \left(\frac{S_0 - S_\infty}{S_0} \right)^2 \\ &= (S_0 - S_\infty) \left[1 - \frac{\rho}{S_0} - \frac{\rho}{2S_0^2} (S_0 - S_\infty) \right]. \end{aligned}$$

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Solving for $S_0 - S_\infty$, we see that

$$\begin{aligned} S_0 - S_\infty &= 2S_0 \left(\frac{S_0}{\rho} - 1 \right) = 2(\rho + \nu) \left[\frac{\rho + \nu}{\rho} - 1 \right] \\ &= 2(\rho + \nu) \frac{\nu}{\rho} = 2\rho \left(1 + \frac{\nu}{\rho} \right) \frac{\nu}{\rho} \cong 2\nu. \end{aligned} \quad \square$$

During the course of an epidemic it is impossible to accurately ascertain the number of new infectives each day or week, since the only infectives who can be recognized and removed from circulation are those who seek medical aid. Public health statistics thus record only the number of new removals each day or week, not the number of new infectives. Therefore, in order to compare the results predicted by our model with data from actual epidemics, we must find the quantity dR/dt as a function of time. This is accomplished in the following manner. Observe first that

$$\frac{dR}{dt} = \gamma I = \gamma(N - R - S).$$

Second, observe that

$$\frac{dS}{dR} = \frac{dS/dt}{dR/dt} = \frac{-rSI}{\gamma I} = \frac{-S}{\rho}.$$

Hence, $S(R) = S_0 e^{-R/\rho}$ and

$$\frac{dR}{dt} = \gamma(N - R - S_0 e^{-R/\rho}). \quad (5)$$

Equation (5) is separable, but cannot be solved explicitly. However, if the epidemic is not very large, then R/ρ is small and we can truncate the Taylor series

$$e^{-R/\rho} = 1 - \frac{R}{\rho} + \frac{1}{2} \left(\frac{R}{\rho} \right)^2 + \dots$$

after three terms. With this approximation,

$$\begin{aligned} \frac{dR}{dt} &= \gamma \left[N - R - S_0 \left[1 - R/\rho + \frac{1}{2} (R/\rho)^2 \right] \right] \\ &= \gamma \left[N - S_0 + \left(\frac{S_0}{\rho} - 1 \right) R - \frac{S_0}{2} \left(\frac{R}{\rho} \right)^2 \right]. \end{aligned}$$

The solution of this equation is

$$R(t) = \frac{\rho^2}{S_0} \left[\frac{S_0}{\rho} - 1 + \alpha \tanh \left(\frac{1}{2} \alpha \gamma t - \phi \right) \right] \quad (6)$$

where

$$\alpha = \left[\left(\frac{S_0}{\rho} - 1 \right)^2 + \frac{2S_0(N - S_0)}{\rho^2} \right]^{1/2}, \quad \phi = \tanh^{-1} \frac{1}{\alpha} \left(\frac{S_0}{\rho} - 1 \right)$$

and the hyperbolic tangent function $\tanh z$ is defined by

$$\tanh z = \frac{e^z - e^{-z}}{e^z + e^{-z}}.$$

It is easily verified that

$$\frac{d}{dz} \tanh z = \operatorname{sech}^2 z = \frac{4}{(e^z + e^{-z})^2}.$$

Hence,

$$\frac{dR}{dt} = \frac{\gamma \alpha^2 \rho^2}{2S_0} \operatorname{sech}^2 \left(\frac{1}{2} \alpha \gamma t - \phi \right). \quad (7)$$

Equation (7) defines a symmetric bell shaped curve in the t - dR/dt plane (see Figure 2). This curve is called the epidemic curve of the disease. It illustrates very well the common observation that in many actual epidemics, the number of new cases reported each day climbs to a peak value and then dies away again.

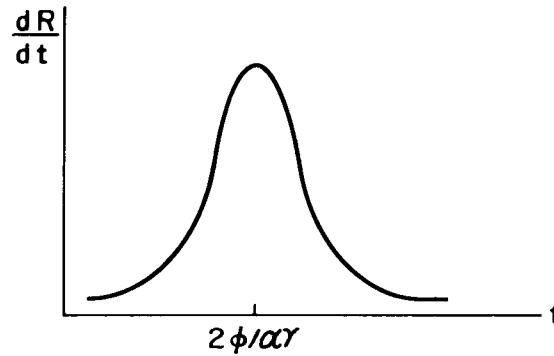


Figure 2

Kermack and McKendrick compared the values predicted for dR/dt from (7) with data from an actual plague in Bombay which spanned the last half of 1905 and the first half of 1906. They set

$$\frac{dR}{dt} = 890 \operatorname{sech}^2(0.2t - 3.4)$$

with t measured in weeks, and compared these values with the number of deaths per week from the plague. This quantity is a very good approximation of dR/dt , since almost all cases terminated fatally. As can be seen from Figure 3, there is excellent agreement between the actual values of

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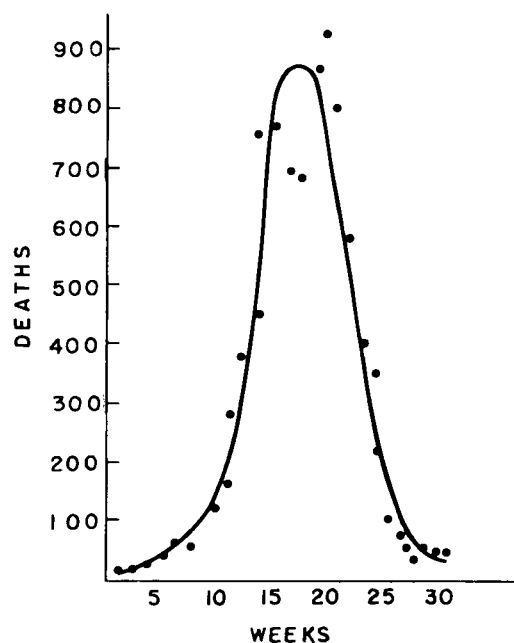


Figure 3

dR/dt , denoted by •, and the values predicted by (7). This indicates, of course, that the system of differential equations (1) is an accurate and reliable model of the spread of an infectious disease within a population of fixed size.

References

- Bailey, N. T. J., 'The mathematical theory of epidemics,' 1957, New York.
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 Waltman, P., 'Deterministic threshold models in the theory of epidemics,' Springer-Verlag, New York, 1974.

EXERCISES

1. Derive Equation (6).
2. Suppose that the members of (S) are vaccinated against the disease at a rate λ proportional to their number. Then,

$$\frac{dS}{dt} = -rSI - \lambda S, \quad \frac{dI}{dt} = rSI - \gamma I. \quad (*)$$

- (a) Find the orbits of (*).
- (b) Conclude from (a) that $S(t)$ approaches zero as t approaches infinity, for every solution $S(t)$, $I(t)$ of (*).

3. Suppose that the members of (S) are vaccinated against the disease at a rate λ proportional to the product of their numbers and the square of the members of (I). Then,

$$\frac{dS}{dt} = -rSI - \lambda SI^2, \quad \frac{dI}{dt} = I(rS - \gamma). \quad (*)$$

- (a) Find the orbits of (*).
 (b) Will any susceptibles remain after the disease dies out?
4. The *intensity* i of an epidemic is the proportion of the total number of susceptibles that finally contracts the disease. Show that

$$i = \frac{I_0 + S_0 - S_\infty}{S_0}$$

where S_∞ is a root of the equation

$$S = S_0 e^{(S - S_0 - I_0)/\rho}.$$

5. Compute the intensity of the epidemic if $\rho = 1000$, $I_0 = 10$, and (a) $S_0 = 1100$, (b) $S_0 = 1200$, (c) $S_0 = 1300$, (d) $S_0 = 1500$, (e) $S_0 = 1800$, (f) $S_0 = 1900$. (This cannot be done analytically.)
6. Let R_∞ denote the total number of individuals who contract the disease.
 (a) Show that $R_\infty = I_0 + S_0 - S_\infty$.
 (b) Let R_1 denote the members of (R) who are removed from the population prior to the peak of the epidemic. Compute R_1/R_∞ for each of the values of S_0 in 5a–5f. Notice that most of the removals occur after the peak. This type of asymmetry is often found in actual notifications of infectious diseases.
7. It was observed in London during the early 1900's, that large outbreaks of measles epidemics recurred about once every two years. The mathematical biologist H. E. Soper tried to explain this phenomenon by assuming that the stock of susceptibles is constantly replenished by new recruits to the population. Thus, he assumed that

$$\frac{dS}{dt} = -rSI + \mu, \quad \frac{dI}{dt} = rSI - \gamma I \quad (*)$$

for some positive constants r , γ , and μ .

- (a) Show that $S = \gamma/r$, $I = \mu/\gamma$ is the only equilibrium solution of (*).
 (b) Show that every solution $S(t)$, $I(t)$ of (*) which starts sufficiently close to this equilibrium point must ultimately approach it as t approaches infinity.
 (c) It can be shown that every solution $S(t)$, $I(t)$ of (*) approaches the equilibrium solution $S = \gamma/r$, $I = \mu/\gamma$ as t approaches infinity. Conclude, therefore, that the system (*) does not predict recurrent outbreaks of measles epidemics. Rather, it predicts that the disease will ultimately approach a steady state.

4.13 A model for the spread of gonorrhea

Gonorrhea ranks first today among reportable communicable diseases in the United States. There are more reported cases of gonorrhea every year than the combined totals for syphilis, measles, mumps, and infectious hepatitis. Public health officials estimate that more than 2,500,000 Ameri-

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cans contract gonorrhea every year. This painful and dangerous disease, which is caused by the gonococcus germ, is spread from person to person by sexual contact. A few days after the infection there is usually itching and burning of the genital area, particularly while urinating. About the same time a discharge develops which males will notice, but which females may not notice. Infected women may have no easily recognizable symptoms, even while the disease does substantial internal damage. Gonorrhea can only be cured by antibiotics (usually penicillin). However, treatment must be given early if the disease is to be stopped from doing serious damage to the body. If untreated, gonorrhea can result in blindness, sterility, arthritis, heart failure, and ultimately, death.

In this section we construct a mathematical model of the spread of gonorrhea. Our work is greatly simplified by the fact that the incubation period of gonorrhea is very short (3–7 days) compared to the often quite long period of active infectiousness. Thus, we will assume in our model that an individual becomes infective immediately after contracting gonorrhea. In addition, gonorrhea does not confer even partial immunity to those individuals who have recovered from it. Immediately after recovery, an individual is again susceptible. Thus, we can split the sexually active and promiscuous portion of the population into two groups, susceptibles and infectives. Let $c_1(t)$ be the total number of promiscuous males, $c_2(t)$ the total number of promiscuous females, $x(t)$ the total number of infective males, and $y(t)$ the total number of infective females, at time t . Then, the total numbers of susceptible males and susceptible females are $c_1(t) - x(t)$ and $c_2(t) - y(t)$ respectively. The spread of gonorrhea is presumed to be governed by the following rules:

1. Male infectives are cured at a rate a_1 proportional to their total number, and female infectives are cured at a rate a_2 proportional to their total number. The constant a_1 is larger than a_2 since infective males quickly develop painful symptoms and therefore seek prompt medical attention. Female infectives, on the other hand, are usually asymptomatic, and therefore are infectious for much longer periods.

2. New infectives are added to the male population at a rate b_1 proportional to the total number of male susceptibles and female infectives. Similarly, new infectives are added to the female population at a rate b_2 proportional to the total number of female susceptibles and male infectives.

3. The total numbers of promiscuous males and promiscuous females remain at constant levels c_1 and c_2 , respectively.

It follows immediately from rules 1–3 that

$$\begin{aligned}\frac{dx}{dt} &= -a_1x + b_1(c_1 - x)y \\ \frac{dy}{dt} &= -a_2y + b_2(c_2 - y)x.\end{aligned}\tag{1}$$

Remark. The system of equations (1) treats only those cases of gonorrhea which arise from heterosexual contacts; the case of homosexual contacts (assuming no interaction between heterosexuals and homosexuals) is treated in Exercises 5 and 6. The number of cases of gonorrhea which arise from homosexual encounters is a small percentage of the total number of incidents of gonorrhea. Interestingly enough, this situation is completely reversed in the case of syphilis. Indeed, more than 90% of all cases of syphilis reported in the state of Rhode Island during 1973 resulted from homosexual encounters. (This statistic is not as startling as it first appears. Within ten to ninety days after being infected with syphilis, an individual usually develops a chancre sore at the spot where the germs entered the body. A homosexual who contracts syphilis as a result of anal intercourse with an infective will develop a chancre sore on his rectum. This individual, naturally, will be reluctant to seek medical attention, since he will then have to reveal his identity as a homosexual. Moreover, he feels no sense of urgency, since the chancre sore is usually painless and disappears after several days. With gonorrhea, on the other hand, the symptoms are so painful and unmistakable that a homosexual will seek prompt medical attention. Moreover, he need not reveal his identity as a homosexual since the symptoms of gonorrhea appear in the genital area.)

Our first step in analyzing the system of differential equations (1) is to show that they are realistic. Specifically, we must show that $x(t)$ and $y(t)$ can never become negative, and can never exceed c_1 and c_2 , respectively. This is the content of Lemmas 1 and 2.

Lemma 1. *If $x(t_0)$ and $y(t_0)$ are positive, then $x(t)$ and $y(t)$ are positive for all $t \geq t_0$.*

Lemma 2. *If $x(t_0)$ is less than c_1 and $y(t_0)$ is less than c_2 , then $x(t)$ is less than c_1 and $y(t)$ is less than c_2 for all $t \geq t_0$.*

PROOF OF LEMMA 1. Suppose that Lemma 1 is false. Let $t^* > t_0$ be the first time at which either x or y is zero. Assume that x is zero first. Then, evaluating the first equation of (1) at $t = t^*$ gives $\dot{x}(t^*) = b_1 c_1 y(t^*)$. This quantity is positive. (Note that $y(t^*)$ cannot equal zero since $x = 0, y = 0$ is an equilibrium solution of (1).) Hence, $x(t)$ is less than zero for t close to, and less than t^* . But this contradicts our assumption that t^* is the first time at which $x(t)$ equals zero. We run into the same contradiction if $y(t^*) = 0$. Thus, both $x(t)$ and $y(t)$ are positive for $t \geq t_0$. \square

PROOF OF LEMMA 2. Suppose that Lemma 2 is false. Let $t^* > t_0$ be the first time at which either $x = c_1$, or $y = c_2$. Suppose that $x(t^*) = c_1$. Evaluating the first equation of (1) at $t = t^*$ gives $\dot{x}(t^*) = -a_1 c_1$. This quantity is negative. Hence, $x(t)$ is greater than c_1 for t close to, and less than t^* . But this

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contradicts our assumption that t^* is the first time at which $x(t)$ equals c_1 . We run into the same contradiction if $y(t^*) = c_2$. Thus, $x(t)$ is less than c_1 and $y(t)$ is less than c_2 for $t \geq t_0$. \square

Having shown that the system of equations (1) is a realistic model of gonorrhea, we now see what predictions it makes concerning the future course of this disease. Will gonorrhea continue to spread rapidly and uncontrollably as the data in Figure 1 seems to suggest, or will it level off eventually? The following extremely important theorem of epidemiology provides the answer to this question.

Theorem 8.

(a) Suppose that a_1a_2 is less than $b_1b_2c_1c_2$. Then, every solution $x(t)$, $y(t)$ of (1) with $0 < x(t_0) < c_1$ and $0 < y(t_0) < c_2$, approaches the equilibrium solution

$$x = \frac{b_1b_2c_1c_2 - a_1a_2}{a_1b_2 + b_1b_2c_2}, \quad y = \frac{b_1b_2c_1c_2 - a_1a_2}{a_2b_1 + b_1b_2c_1}$$

as t approaches infinity. In other words, the total numbers of infective males and infective females will ultimately level off.

(b) Suppose that a_1a_2 is greater than $b_1b_2c_1c_2$. Then every solution $x(t)$, $y(t)$ of (1) with $0 < x(t_0) < c_1$ and $0 < y(t_0) < c_2$, approaches zero as t approaches infinity. In other words, gonorrhea will ultimately die out.

Our first step in proving part (a) of Theorem 8 is to split the rectangle $0 < x < c_1$, $0 < y < c_2$ into regions in which both dx/dt and dy/dt have fixed signs. This is accomplished in the following manner. Setting $dx/dt = 0$ in (1), and solving for y as a function of x gives

$$y = \frac{a_1x}{b_1(c_1 - x)} \equiv \phi_1(x).$$

Similarly, setting $dy/dt = 0$ in (1) gives

$$x = \frac{a_2y}{b_2(c_2 - y)}, \quad \text{or} \quad y = \frac{b_2c_2x}{a_2 + b_2x} \equiv \phi_2(x).$$

Observe first that $\phi_1(x)$ and $\phi_2(x)$ are monotonic increasing functions of x ; $\phi_1(x)$ approaches infinity as x approaches c_1 , and $\phi_2(x)$ approaches c_2 as x approaches infinity. Second, observe that the curves $y = \phi_1(x)$ and $y = \phi_2(x)$ intersect at $(0, 0)$ and at (x_0, y_0) where

$$x_0 = \frac{b_1b_2c_1c_2 - a_1a_2}{a_1b_2 + b_1b_2c_2}, \quad y_0 = \frac{b_1b_2c_1c_2 - a_1a_2}{a_2b_1 + b_1b_2c_1}.$$

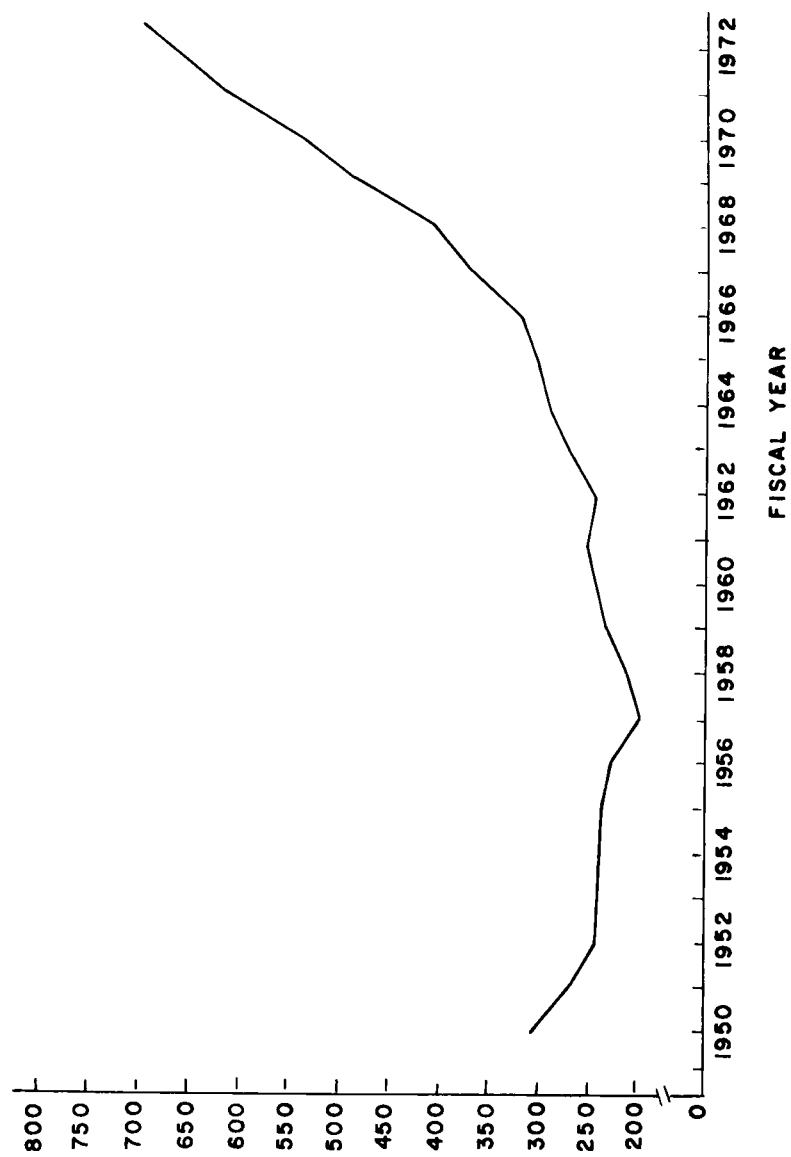


Figure 1. Reported cases of gonorrhea, in thousands, for 1950–1973.

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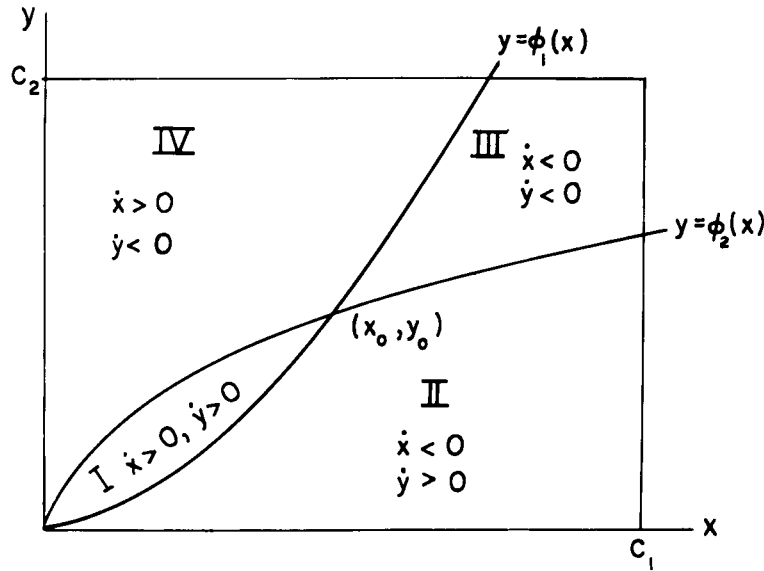


Figure 2

Third, observe that $\phi_2(x)$ is increasing faster than $\phi_1(x)$ at $x=0$, since

$$\phi_2'(0) = \frac{b_2 c_2}{a_2} > \frac{a_1}{b_1 c_1} = \phi_1'(0).$$

Hence, $\phi_2(x)$ lies above $\phi_1(x)$ for $0 < x < x_0$, and $\phi_2(x)$ lies below $\phi_1(x)$ for $x_0 < x < c_1$, as shown in Figure 2. The point (x_0, y_0) is an equilibrium point of (1) since both dx/dt and dy/dt are zero when $x = x_0$ and $y = y_0$.

Finally, observe that dx/dt is positive at any point (x, y) above the curve $y = \phi_1(x)$, and negative at any point (x, y) below this curve. Similarly, dy/dt is positive at any point (x, y) below the curve $y = \phi_2(x)$, and negative at any point (x, y) above this curve. Thus, the curves $y = \phi_1(x)$ and $y = \phi_2(x)$ split the rectangle $0 < x < c_1$, $0 < y < c_2$ into four regions in which dx/dt and dy/dt have fixed signs (see Figure 2).

Next, we require the following four simple lemmas.

Lemma 3. Any solution $x(t), y(t)$ of (1) which starts in region I at time $t = t_0$ will remain in this region for all future time $t \geq t_0$ and approach the equilibrium solution $x = x_0, y = y_0$ as t approaches infinity.

PROOF. Suppose that a solution $x(t), y(t)$ of (1) leaves region I at time $t = t^*$. Then, either $\dot{x}(t^*)$ or $\dot{y}(t^*)$ is zero, since the only way a solution of (1) can leave region I is by crossing the curve $y = \phi_1(x)$ or $y = \phi_2(x)$. Assume that $\dot{x}(t^*) = 0$. Differentiating both sides of the first equation of (1) with re-

spect to t and setting $t = t^*$ gives

$$\frac{d^2x(t^*)}{dt^2} = b_1(c_1 - x(t^*)) \frac{dy(t^*)}{dt}.$$

This quantity is positive, since $x(t^*)$ is less than c_1 , and dy/dt is positive on the curve $y = \phi_1(x)$, $0 < x < x_0$. Hence, $x(t)$ has a minimum at $t = t^*$. But this is impossible, since $x(t)$ is increasing whenever the solution $x(t), y(t)$ is in region I. Similarly, if $\dot{y}(t^*) = 0$, then

$$\frac{d^2y(t^*)}{dt^2} = b_2(c_2 - y(t^*)) \frac{dx(t^*)}{dt}.$$

This quantity is positive, since $y(t^*)$ is less than c_2 , and dx/dt is positive on the curve $y = \phi_2(x)$, $0 < x < x_0$. Hence, $y(t)$ has a minimum at $t = t^*$. But this is impossible, since $y(t)$ is increasing whenever the solution $x(t), y(t)$ is in region I.

The previous argument shows that any solution $x(t), y(t)$ of (1) which starts in region I at time $t = t_0$ will remain in region I for all future time $t \geq t_0$. This implies that $x(t)$ and $y(t)$ are monotonic increasing functions of time for $t \geq t_0$, with $x(t) < x_0$ and $y(t) < y_0$. Consequently, by Lemma 1 of Section 4.8, both $x(t)$ and $y(t)$ have limits ξ, η , respectively, as t approaches infinity. Lemma 2 of Section 4.8 implies that (ξ, η) is an equilibrium point of (1). Now, it is easily seen from Figure 2 that the only equilibrium points of (1) are $(0, 0)$ and (x_0, y_0) . But (ξ, η) cannot equal $(0, 0)$ since both $x(t)$ and $y(t)$ are increasing functions of time. Hence, $(\xi, \eta) = (x_0, y_0)$, and this proves Lemma 3. \square

Lemma 4. Any solution $x(t), y(t)$ of (1) which starts in region III at time $t = t_0$ will remain in this region for all future time and ultimately approach the equilibrium solution $x = x_0, y = y_0$.

PROOF. Exactly the same as Lemma 3 (see Exercise 1). \square

Lemma 5. Any solution $x(t), y(t)$ of (1) which starts in region II at time $t = t_0$, and remains in region II for all future time, must approach the equilibrium solution $x = x_0, y = y_0$ as t approaches infinity.

PROOF. If a solution $x(t), y(t)$ of (1) remains in region II for $t \geq t_0$, then $x(t)$ is monotonic decreasing and $y(t)$ is monotonic increasing for $t \geq t_0$. Moreover, $x(t)$ is positive and $y(t)$ is less than c_2 , for $t \geq t_0$. Consequently, by Lemma 1 of Section 4.8, both $x(t)$ and $y(t)$ have limits ξ, η respectively, as t approaches infinity. Lemma 2 of Section 4.8 implies that (ξ, η) is an equilibrium point of (1). Now, (ξ, η) cannot equal $(0, 0)$ since $y(t)$ is increasing for $t \geq t_0$. Therefore, $(\xi, \eta) = (x_0, y_0)$, and this proves Lemma 5. \square

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Lemma 6. Any solution $x(t), y(t)$ of (1) which starts in region IV at time $t = t_0$ and remains in region IV for all future time, must approach the equilibrium solution $x = x_0, y = y_0$ as t approaches infinity.

PROOF. Exactly the same as Lemma 5 (see Exercise 2). \square

We are now in a position to prove Theorem 8.

PROOF OF THEOREM 8. (a) Lemmas 3 and 4 state that every solution $x(t), y(t)$ of (1) which starts in region I or III at time $t = t_0$ must approach the equilibrium solution $x = x_0, y = y_0$ as t approaches infinity. Similarly, Lemmas 5 and 6 state that every solution $x(t), y(t)$ of (1) which starts in region II or IV and which remains in these regions for all future time, must also approach the equilibrium solution $x = x_0, y = y_0$. Now, observe that if a solution $x(t), y(t)$ of (1) leaves region II or IV, then it must cross the curve $y = \phi_1(x)$ or $y = \phi_2(x)$, and immediately afterwards enter region I or region III. Consequently, all solutions $x(t), y(t)$ of (1) which start in regions II and IV or on the curves $y = \phi_1(x)$ and $y = \phi_2(x)$, must also approach the equilibrium solution $x(t) = x_0, y(t) = y_0$. \square

(b) PROOF #1. If $a_1 a_2$ is greater than $b_1 b_2 c_1 c_2$, then the curves $y = \phi_1(x)$ and $y = \phi_2(x)$ have the form described in Figure 3 below. In region I, dx/dt is positive and dy/dt is negative; in region II, both dx/dt and dy/dt are negative; and in region III, dx/dt is negative and dy/dt is positive. It is a simple matter to show (see Exercise 3) that every solution $x(t), y(t)$ of (1) which starts in region II at time $t = t_0$ must remain in this region for all

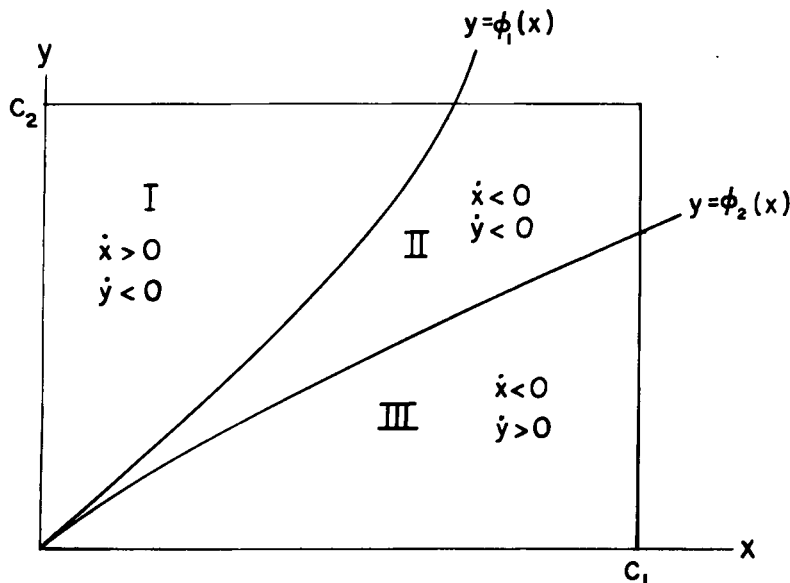


Figure 3

future time, and approach the equilibrium solution $x=0, y=0$ as t approaches infinity. It is also trivial to show that every solution $x(t), y(t)$ of (1) which starts in region I or region III at time $t=t_0$ must cross the curve $y=\phi_1(x)$ or $y=\phi_2(x)$, and immediately afterwards enter region II (see Exercise 4). Consequently, every solution $x(t), y(t)$ of (1), with $0 < x(t_0) < c_1$ and $0 < y(t_0) < c_2$, approaches the equilibrium solution $x=0, y=0$ as t approaches infinity. \square

PROOF #2. We would now like to show how we can use the Poincaré–Bendixson theorem to give an elegant proof of part (b) of Theorem 8. Observe that the system of differential equations (1) can be written in the form

$$\frac{d}{dt} \begin{pmatrix} x \\ y \end{pmatrix} = \begin{pmatrix} -a_1 & b_1 c_1 \\ b_2 c_2 & -a_2 \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix} - \begin{pmatrix} b_1 x y \\ b_2 x y \end{pmatrix}. \quad (2)$$

Thus, by Theorem 2 of Section 4.3, the stability of the solution $x=0, y=0$ of (2) is determined by the stability of the equilibrium solution $x=0, y=0$ of the linearized system

$$\frac{d}{dt} \begin{pmatrix} x \\ y \end{pmatrix} = \mathbf{A} \begin{pmatrix} x \\ y \end{pmatrix} = \begin{pmatrix} -a_1 & b_1 c_1 \\ b_2 c_2 & -a_2 \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix}.$$

The characteristic polynomial of the matrix \mathbf{A} is

$$\lambda^2 + (a_1 + a_2)\lambda + a_1 a_2 - b_1 b_2 c_1 c_2$$

whose roots are

$$\lambda = \frac{-(a_1 + a_2) \pm [(a_1 + a_2)^2 - 4(a_1 a_2 - b_1 b_2 c_1 c_2)]^{1/2}}{2}.$$

It is easily verified that both these roots are real and negative. Hence, the equilibrium solution $x=0, y=0$ of (2) is asymptotically stable. This implies that any solution $x(t), y(t)$ of (1) which starts sufficiently close to the origin $x=y=0$ will approach the origin as t approaches infinity. Now, suppose that a solution $x(t), y(t)$ of (1), with $0 < x(t_0) < c_1$ and $0 < y(t_0) < c_2$, does not approach the origin as t approaches infinity. By the previous remark, this solution must always remain a minimum distance from the origin. Consequently, its orbit for $t \geq t_0$ lies in a bounded region in the $x-y$ plane which contains no equilibrium points of (1). By the Poincaré–Bendixson Theorem, therefore, its orbit must spiral into the orbit of a periodic solution of (1). But the system of differential equations (1) has no periodic solution in the first quadrant $x \geq 0, y \geq 0$. This follows immediately from Exercise 11, Section 4.8, and the fact that

$$\begin{aligned} \frac{\partial}{\partial x} [-a_1 x + b_1(c_1 - x)y] + \frac{\partial}{\partial y} [-a_2 y + b_2(c_2 - y)x] \\ = -(a_1 + a_2 + b_1 y + b_2 x) \end{aligned}$$

is strictly negative if both x and y are nonnegative. Consequently, every

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solution $x(t), y(t)$ of (1), with $0 < x(t_0) < c_1$ and $0 < y(t_0) < c_2$ approaches the equilibrium solution $x=0, y=0$ as t approaches infinity. \square

Now, it is quite difficult to evaluate the coefficients a_1, a_2, b_1, b_2, c_1 , and c_2 . Indeed, it is impossible to obtain even a crude estimate of a_2 , which should be interpreted as the average amount of time that a female remains infective. (Similarly, a_1 should be interpreted as the average amount of time that a male remains infective.) This is because most females do not exhibit symptoms. Thus, a female can be infective for an amount of time varying from just one day to well over a year. Nevertheless, it is still possible to ascertain from public health data that $a_1 a_2$ is less than $b_1 b_2 c_1 c_2$, as we now show. Observe that the condition $a_1 a_2 < b_1 b_2 c_1 c_2$ is equivalent to

$$1 < \left(\frac{b_1 c_1}{a_2} \right) \left(\frac{b_2 c_2}{a_1} \right).$$

The quantity $b_1 c_1 / a_2$ can be interpreted as the average number of males that one female infective contacts during her infectious period, if every male is susceptible. Similarly, the quantity $b_2 c_2 / a_1$ can be interpreted as the average number of females that one male infective contacts during his infectious period, if every female is susceptible. The quantities $b_1 c_1 / a_2$ and $b_2 c_2 / a_1$ are called the maximal female and male contact rates, respectively. Theorem 8 can now be interpreted in the following manner.

- (a) If the product of the maximal male and female contact rates is greater than one, then gonorrhea will approach a nonzero steady state.
- (b) If the product of the maximal male and female contact rates is less than one, then gonorrhea will die out eventually.

In 1973, the average number of female contacts named by a male infective during his period of infectiousness was 0.98, while the average number of male contacts named by a female infective during her period of infectiousness was 1.15. These numbers are very good approximations of the maximal male and female contact rates, respectively, and their product does not exceed the product of the maximal male and female contact rates. (The number of contacts of a male or female infective during their period of infectiousness is slightly less than the maximal male or female contact rates. However, the *actual* number of contacts is often greater than the number of contacts named by an infective.) The product of 1.15 with 0.98 is 1.0682. Thus, gonorrhea will ultimately approach a nonzero steady state.

Remark. Our model of gonorrhea is rather crude since it lumps all promiscuous males and all promiscuous females together, regardless of age. A more accurate model can be obtained by separating the male and female populations into different age groups and then computing the rate of change of infectives in each age group. This has been done recently, but the analysis is too difficult to present here. We just mention that a result

completely analogous to Theorem 8 is obtained: either gonorrhea dies out in each age group, or it approaches a constant, positive level in each age group.

EXERCISES

In Problems 1 and 2, we assume that $a_1 a_2 < b_1 b_2 c_1 c_2$.

1. (a) Suppose that a solution $x(t), y(t)$ of (1) leaves region III of Figure 2 at time $t = t^*$ by crossing the curve $y = \phi_1(x)$ or $y = \phi_2(x)$. Conclude that either $x(t)$ or $y(t)$ has a maximum at $t = t^*$. Then, show that this is impossible. Conclude, therefore, that any solution $x(t), y(t)$ of (1) which starts in region III at time $t = t_0$ must remain in region III for all future time $t > t_0$.
 (b) Conclude from (a) that any solution $x(t), y(t)$ of (1) which starts in region III has a limit ξ, η as t approaches infinity. Then, show that (ξ, η) must equal (x_0, y_0) .
2. Suppose that a solution $x(t), y(t)$ of (1) remains in region IV of Figure 2 for all time $t > t_0$. Prove that $x(t)$ and $y(t)$ have limits ξ, η respectively, as t approaches infinity. Then conclude that (ξ, η) must equal (x_0, y_0) .

In Problems 3 and 4, we assume that $a_1 a_2 > b_1 b_2 c_1 c_2$.

3. Suppose that a solution $x(t), y(t)$ of (1) leaves region II of Figure 3 at time $t = t^*$ by crossing the curve $y = \phi_1(x)$ or $y = \phi_2(x)$. Show that either $x(t)$ or $y(t)$ has a maximum at $t = t^*$. Then, show that this is impossible. Conclude, therefore, that every solution $x(t), y(t)$ of (1) which starts in region II at time $t = t_0$ must remain in region II for all future time $t \geq t_0$.
4. (a) Suppose that a solution $x(t), y(t)$ of (1) remains in either region I or III of Figure 3 for all time $t \geq t_0$. Show that $x(t)$ and $y(t)$ have limits ξ, η respectively, as t approaches infinity.
 (b) Conclude from Lemma 1 of Section 4.8 that $(\xi, \eta) = (0, 0)$.
 (c) Show that (ξ, η) cannot equal $(0, 0)$ if $x(t), y(t)$ remains in region I or region III for all time $t \geq t_0$.
 (d) Show that any solution $x(t), y(t)$ of (1) which starts on either $y = \phi_1(x)$ or $y = \phi_2(x)$ will immediately afterwards enter region II.
5. Assume that $a_1 a_2 < b_1 b_2 c_1 c_2$. Prove directly, using Theorem 2 of Section 4.3, that the equilibrium solution $x = x_0, y = y_0$ of (1) is asymptotically stable. *Warning:* The calculations are extremely tedious.
6. Assume that the number of homosexuals remains constant in time. Call this constant c . Let $x(t)$ denote the number of homosexuals who have gonorrhea at time t . Assume that homosexuals are cured of gonorrhea at a rate α_1 , and that new infectives are added at a rate $\beta_1(c - x)x$.
 (a) Show that $\dot{x} = -\alpha_1 x + \beta_1 x(c - x)$.
 (b) What happens to $x(t)$ as t approaches infinity?
7. Suppose that the number of homosexuals $c(t)$ grows according to the logistic law $\dot{c} = c(a - bc)$, for some positive constants a and b . Let $x(t)$ denote the number of homosexuals who have gonorrhea at time t , and assume (see Problem 6) that $\dot{x} = -\alpha_1 x + \beta_1 x(c - x)$. What happens to $x(t)$ as t approaches infinity?