Problems on Parasite and Disease Ecology

Solutions (detailed in some cases, just the results in other cases)

Problem PD1

Rabies is a serious microparasitic disease due to the transmission of a virus between hosts. One of the most important animal hosts is the red fox (*Vulpes vulpes*). Write down an SI model for this mammal assuming that demography is logistic, transmission is density-dependent and no infected animal can recover from the disease.

Use the following parameters:

- birth rate $\nu = 0.6$ year^{-1};
- natural death rate $\mu = 0.2$ year^{-1};
- carrying capacity $K = 5$ foxes km^{-2};
- disease-related death rate $\alpha = 5$ year^{-1};
- basic reproduction number of rabies $R_0 = 3$.

Compute:

(a) the transmission coefficient β of rabies in foxes;
(b) the endemic equilibrium densities of susceptible and infected foxes;
(c) the equilibrium prevalence of the disease.

Solution

$$\frac{dS}{dt} = rS\left(1 - \frac{S+I}{K}\right) - \beta IS$$

$$\frac{dI}{dt} = \beta IS - (\mu + \alpha)I$$

(a) Since $R_0 = \frac{\beta K}{\mu+\alpha}$ we get $\beta = \frac{R_0(\mu+\alpha)}{K}$ = 3.12 year^{-1}.

(b) $S_{eq} = \frac{\mu+\alpha}{\beta}$ =1.67 foxes km^{-2}

$$I_{eq} = \frac{r\left(1-\frac{S_{eq}}{K}\right)}{r/_{K}+\beta} = 0.083 \text{ foxes km}^{-2}$$

(c) Prevalence = $\frac{I_{eq}}{I_{eq}+S_{eq}}$ = 0.048

Problem PD2

The *gonorrhoea* of the fantasy population of striped kangaroos is a bacterial disease that strikes these kangaroos as a consequence of sexual contacts. The contact rate increases with the number of kangaroos and then saturates, because the maximum number of sexual contacts per unit time is obviously finite. The disease does not confer immunity. Describe the gonorrhoea dynamics in Marsupiumland by an SI model with saturating transmission and characterized by

- birth rate = 0.2 year^{-1};
- natural death rate = 0.05 year^{-1};
- carrying capacity = 50 kangaroos km^{-2};
- disease-related death rate = 0.01 year^{-1};
- infection rate = $\beta I/(\delta + N)$, with $\beta = 3\,\text{year}^{-1}$ and $\delta = 10\,\text{kangaroos}\,\text{km}^{-2}$ (with $N = S + I$);
- recovery rate = 2 year^{-1}.

Based on these data:

(i) write down the model for the gonorrhoea dynamics;
(ii) compute the basic reproduction number of the disease;
(iii) determine whether gonorrhoea can permanently establish within Marsupiumland kangaroos; and
(iv) compute the prevalence at the endemic equilibrium.

Solution

(i)

$$\begin{aligned} \dot{S} &= rS\left(1 - \frac{S+I}{K}\right) - \beta\frac{IS}{\delta+S+I} + \gamma I \\ \dot{I} &= \beta\frac{IS}{\delta+S+I} - (\mu + \alpha + \gamma)I \end{aligned}$$

(ii) $R_0 = \dfrac{\beta K}{(\delta+K)(\mu+\alpha+\gamma)} = 1.214$

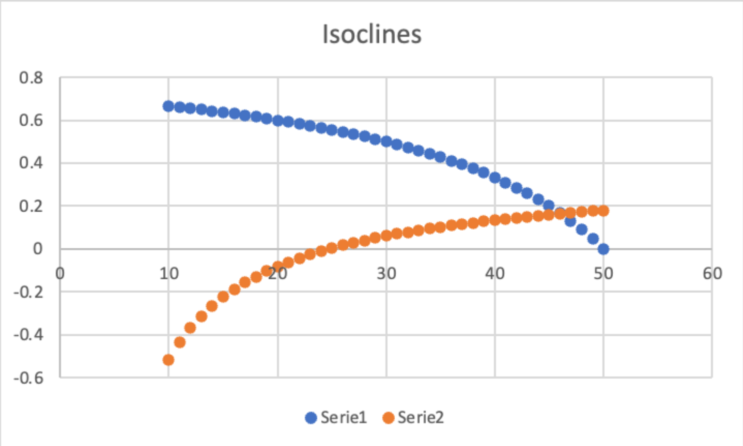
(iii) Since $R_0 > 1$ the disease can become endemic

(iv) The solution can be numerically found by changing variables from S and I to total numbers $N = S + I$ and prevalence of infected $x = I/N$. The corresponding isoclines are given by

$$\dot{N} = 0 \quad \Rightarrow \quad x = \frac{r\left(1 - \frac{N}{K}\right)}{\mu + \alpha + r\left(1 - \frac{N}{K}\right)}$$

$$\dot{x} = 0 \quad \Rightarrow \quad x = 1 - \frac{\gamma}{\beta\frac{N}{\delta+N} - r\left(1 - \frac{N}{K}\right) - (\mu + \alpha)}$$

The solution is found at the intersection of the two isoclines



Prevalence at equilibrium = 0.164

Problem PD3

In many microparasitic diseases a fraction of infected and infectious individuals is not symptomatic and thus can reproduce. For instance, *cholera* and *amoebiasis* are diseases with this peculiarity. Analyse the effect of asymptomatic individuals in an SI system without immunity, with density-dependent transmission and Malthusian demographics. Assume that:

- the birth rate of susceptibles and asymptomatics is $\nu = 0.7\,\text{year}^{-1}$;
- the natural death rate is $\mu = 0.2\,\text{year}^{-1}$;
- the disease-related death rate is $\alpha = 0.01\,\text{year}^{-1}$;

- S and I are measured as No. of individuals km^{-2};
- the transmission coefficient from infected to susceptible is $\beta = 2\,\text{year}^{-1}$ (No. of individuals $\text{km}^{-2})^{-1}$;
- the average recovery time from the disease is 15 days;
- a fraction σ of infected is symptomatic and cannot reproduce.

Write down the SI model equations and determine how the model equilibria vary for increasing σ. Find out the values of σ for which the disease can demographically regulate the Malthusian population.

Solution

$$\frac{dS}{dt} = \nu(S + (1-\sigma)I) - \mu S - \beta IS + \gamma I$$
$$\frac{dI}{dt} = \beta IS - (\mu + \gamma)I - \alpha\sigma I$$

The condition for regulation is $\sigma > \frac{\nu-\mu}{\nu+\alpha} = 0.704$.

Problem PD4

Selective culling is a method that can be employed to try to control wildlife diseases (e.g. *rabies*). Perform a simple analysis of the efficacy of this control method by using an SI model without immune response and with density-dependent transmission. Assume the following values for the parameters

- birth rate of susceptibles $\nu = 1.5\,\text{year}^{-1}$;
- natural death rate $\mu = 0.5\,\text{year}^{-1}$;
- disease-related death rate $\alpha = 1\,\text{year}^{-1}$;
- S and I are measured as No. of individuals km^{-2};
- carrying capacity $K = 13$ individuals km^{-2};
- transmission coefficient from infected to susceptible $\beta = 1\,\text{year}^{-1}$ (No. of individuals $\text{km}^{-2})^{-1}$;
- average recovery time from the disease = 2 months.

Find out whether the disease can establish in the population. If it can, analyse whether culling can eradicate the disease. Assume that hunters can distinguish and kill the infected animals only, inflicting a death rate h (year^{-1}). How big should h be to permanently eliminate the disease from the wildlife population?

Solution

The corresponding model is

$$\frac{dS}{dt} = rS\left(1 - \frac{S+I}{K}\right) - \beta IS + \gamma I$$

$$\frac{dI}{dt} = \beta IS - (\mu + \alpha + \gamma + h)I$$

Set h=0. The basic reproducion number is $R_0 = \frac{\beta K}{\mu+\alpha+\gamma}$=1.733. Thus the disease can establish.

If $h > 0$ the basic reproduction number is

$$R_0 = \frac{\beta K}{\mu + \alpha + \gamma + h}$$

and must be smaller than 1 to eradicate the disease. Therefore

$h > \beta K - (\mu + \alpha + \gamma) = 5.5\ \text{year}^{-1}$.

Problem PD5

Classical swine fever (CSF) is a viral disease with severe economic consequences for wild boars and domestic pigs. Domestic pigs as well as wild boars are highly susceptible to CSF infection. There are well documented reports that CSF may spill over from wild boar to domestic pigs. Transmission of the infection is by direct contact and the transmission is density-dependent.

Analyze the dynamics of *classical swine fever* in wild boars (*Sus scrofa*) using the information provided by Hone et al. (1992) who studied the disease in a Pakistan boar population. The demography is logistic with

- carrying capacity $K = 10.4$ ind. km^{-2};
- instantaneous intrinsic rate of demographic increase $r = 0.09$ year^{-1};
- natural mortality rate $\mu = 0.6$ year^{-1}.

The fever is very virulent with a quite high mortality rate due to the disease, namely $\alpha = 0.2$ day^{-1}. The recovery period for the few animals that survive is 15 days and the immunity is permanent. The estimated coefficient of disease transmission is $\beta = 0.044$ (ind. km^{-2})$^{-1}$ day^{-1}. Assume that the number of recovered boars can be approximately set to zero because mortality due to disease is very high.

Then

(a) Write a simple SI model for the disease;
(b) Calculate the basic reproduction number of CSF.

One of the possible methods for curbing the disease is by culling. Assume that both susceptible and infected boars are killed at a rate c (year^{-1}). Calculate then the value of c above which the disease cannot become endemic.

Solution

(a) The model with culling is

$$\frac{dS}{dt} = rS\left(1 - \frac{S+I}{K}\right) - \beta IS - cS$$

$$\frac{dI}{dt} = \beta IS - (\mu + \alpha + \gamma + c)I$$

(b) with $c = 0$, $R_0 = 1.71$ and the disease can become endemic.

If $c > 0$ the culling rate c must be > 0.037 year^{-1}.

Problem PD6

Vaccination is the most important means for preventing disease epidemics. Analyse its efficacy by considering a simple case of a city whose demography is described by a constant flow w of births and immigration and a mortality rate μ. Consider a microparasitic disease with density-dependent transmission that provides full immunity to people that recover. The population parameters are

- $w = 15000$ people year^{-1};
- μ = death rate of susceptible people = 0.015 year^{-1};
- α = additional mortality rate due to the disease = 0.005 year^{-1};
- β = coefficient of disease transmission = 0.0001 (number of people)$^{-1}$ year^{-1};
- recovery time = 0.5 months.

Assume that susceptible individuals are vaccinated at a rate V, where V is expressed as year^{-1}. Then

(a) Write down the SI model that governs the epidemiological dynamics;
(b) Calculate the basic reproduction number with no vaccination;
(c) Calculate how big the vaccination rate V should be in order to avoid that the disease establishes in the population;
(d) Calculate the number of susceptible people at equilibrium in the case of successful vaccination.

Solution

(a) Let ρ be the recovery rate = 1/0.5 month^{-1} = 24 year^{-1}. The model is

$$\frac{dS}{dt} = w - \mu S - \beta IS - VS$$
$$\frac{dI}{dt} = \beta IS - (\mu + \alpha + \rho)I$$

(b) If V=0, then the equilibrium population size of susceptibles is w/μ = 1 million. The basic reproduction number is

$R_0 = \frac{\beta w/\mu}{\mu+\alpha+\rho}$ = 4.16. The disease is obviously endemic without vaccination.

(c) With vaccination the equilibrium population size of susceptibles is $S_{eqV} = \frac{w}{\mu+V}$ and the corresponding basic reproduction number is

$$R_{0V} = \frac{\beta w/(\mu + V)}{\mu + \alpha + \rho}$$

Thus, the vaccination is successful if $R_{0V} < 1$, which implies $V > \frac{\beta w}{\mu+\alpha+\rho} - \mu = 0.0474$ year^{-1}.

(d) In case of successful vaccination $S_{eqV} = \frac{w}{\mu+V} < 240200$.

Problem PD7

Cholera is a microparasitic disease transmitted through exposure to water contaminated by the bacterium *Vibrio cholerae*. In the standard SIB model the rate at which one susceptible becomes infected is assumed to linearly increase with the bacterial concentration. A more realistic assumption is that it increases and saturates with the concentration in the following way:

$$\text{infection rate } = \beta B/(1+B)$$

where B is the normalized concentration of bacteria in the water (namely the concentration of bacteria divided by their carrying capacity). It is thus possible to better analyze the dynamics of *cholera* in a human community in which the recruitment of new susceptible individuals (due to either newborns or migration from nearby communities) is a constant flow w and the susceptible individuals have a mortality rate μ. For the modified SIB model assume that recovered people are permanently immune and parameters have the following values

- average life time of susceptibles: 70 years;
- constant flow $w = 5$ individuals day^{-1};
- infection rate = $\beta B/(1+B)$ with $\beta = 1$; [year^{-1}]
- recovery rate $\rho = 0.2$ day^{-1};
- contamination rate $\theta = 10^{-6}$ (No.infected)$^{-1}$ day^{-1};
- death rate of *V. cholerae* $\delta = 0.2$ day^{-1}.

Based on these data, write down the modified SIB model for the cholera dynamics. Then, consider a population that at the endemic equilibrium is characterized by 10,000 infected individuals. For this population

(a) Compute the equilibrium prevalence of the disease;
(b) Determine the disease-related death rate α.

Solution

$$\frac{dS}{dt} = w - \mu S - \frac{\beta BS}{1+B}$$
$$\frac{dI}{dt} = \frac{\beta BS}{1+B} - (\mu + \alpha + \rho)I$$
$$\frac{dB}{dt} = \theta I - \delta B$$

(a) The prevalence is $\frac{I_{eq}}{I_{eq}+S_{eq}} = 0.385$

(b) The disease-related death rate $\alpha = 0.2$ day^{-1}.

Problem PD8

Zika virus is an emerging mosquito-borne virus that infects and causes disease in humans. Although symptoms are usually mild, there is evidence that the infection of women during a critical part of pregnancy can lead to the development of microcephaly in the unborn child. The most important disease vector is the Yellow Fever mosquito, *Aedes aegypti*. Caminade et al. (2017) have studied the dynamics of the disease in relation to the climate of the countries hit by an epidemic of the virus. They estimated the following parameters for a country with an average temperature of 25 °C.

- a = number of bites per mosquito per unit time = 0.2 day^{-1}
- m = number of female mosquitoes per human host = 50
- b = probability of transmission of infection from infectious mosquitoes to humans per bite = 0.5
- ξ = mortality rates of mosquitoes = 0.19 day^{-1}
- recovery time from the disease = 7 days
- c = probability of transmission of infection from infectious humans to mosquitoes per bite = 0.1

You are required to:

(a) From the above parameters derive β, the mosquito-to-human transmission rate and ψ, the human-to-mosquito transmission rate.

(b) Write down a Ross model for the Zika virus describing the dynamics of the prevalence of infected humans (U) and that of infected mosquitoes (M).

(c) Calculate the basic reproduction number and assess whether the disease can establish in the country. If it can, calculate the prevalence of both humans and mosquitoes at equilibrium.

Solution

(a) $\beta = mab$ = 5 day^{-1}, $\psi = ac$ = 0.02 day^{-1}

(b)

$$\frac{dU}{dt} = \beta M(1-U) - \gamma U$$

$$\frac{dM}{dt} = \psi U(1-M) - \xi M$$

with γ = 1/70 = 0.0143 year^{-1}

(c) $R_0 = \frac{\beta\psi}{\gamma\xi}$ = 3.684

The disease can establish in the country and the two prevalences can be computed by setting the two derivatives to zero thus obtaining

$$\bar{U} = \frac{\beta\psi - \gamma\xi}{\psi(\beta + \gamma)}, \qquad \bar{M} = \frac{\beta\psi - \gamma\xi}{\beta(\psi + \xi)}$$

and finally U_{eq} = 0.708, M_{eq} = 0.069.

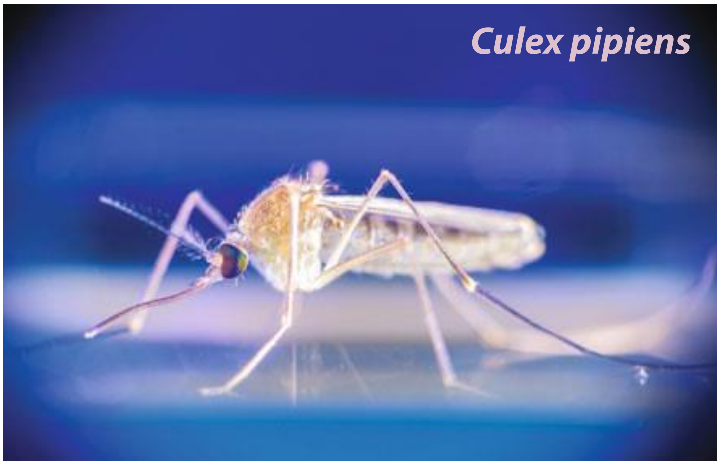
Problem PD9

West Nile virus (WNV) is a mosquito-borne flavivirus which has caused repeated outbreaks in humans in southern and central Europe. The main vector for WNV is the common mosquito *Culex pipiens*. Although the disease can be transmitted to humans the main virus reservoir is represented by birds. Vogels et al. (2017) have studied how the basic reproduction number of the disease varies with the average temperature of the country hosting mosquitoes and birds. They estimated the following parameters for countries with an average temperature of 23 °C and 28 °C, respectively.

- a = number of bites per mosquito per unit time = 0.14 day^{-1} at 23 °C and 0.2 day^{-1} at 28 °C
- m = number of female mosquitoes per bird host = 10
- b = probability of transmission of infection from infectious mosquitoes to birds per bite = 0.8
- average lifetime of mosquitoes = 33 days at 23 °C and 25 days at 28 °C
- bird recovery time from the disease = 5.5 days
- c = probability of transmission of infection from infectious birds to mosquitoes per bite = 0.04 at 23 °C and 0.34 at 28 °C

(A) From the above parameters derive β, the mosquito-to-bird transmission rate and ψ, the bird-to-mosquito transmission rate for both temperatures.
(B) Write down a Ross model for WNV describing the dynamics of the prevalence of infected birds (U) and that of infected mosquitoes (M).

Problem PD9 The common mosquito, the most important vector for West Nile Virus



(C) Calculate the basic reproduction number and establish whether the disease can establish at the two temperatures. If it can, calculate the prevalence of both birds and mosquitoes at equilibrium.

Solution

The solution is the same as that of the previous exercise.

Temperature	23°C	28°C
β	1.12 day^{-1}	1.6 day^{-1}
ψ	0.056 day^{-1}	0.068 day^{-1}
R_0	1.14	14.96
U_{eq}	0.105	0.838
M_{eq}	0.019	0.588

Problem PD10

Lyme disease, also known as Lyme borreliosis, is an infectious vector-borne disease caused by the *Borrelia spp.* bacterium. It is transmitted to humans and to many other mammals by the bites of infected ticks of the genus *Ixodes spp.* that leave a typical rash on the skin of bitten people, as shown in the Figure.

However, humans are not the main hosts of Lyme disease. A growing body of evidence implicates small mammals (e.g. mice, chipmunks, shrews) as key hosts of the disease. Moreover, a lot of other animals (e.g. deer) can be bitten by ticks but are not able to infect them, namely, even if they were bitten by infected ticks, they would not infect healthy ticks with borreliosis. This kind of hosts are called incompetent hosts and the phenomenon is termed dilution. In fact, if there are many incompetent hosts around, many of the ticks will make their blood meal on them and will not transmit the disease.

Study the effect of incompetent hosts by assuming the following realistic data for the small mammals (host) and ticks (vector) system:

- m_0 = mean number of ticks per small mammal when there are no incompetent hosts around = 0.15

Problem PD10 The rash due to Lyme disease on the leg of a person bitten by a tick of the species *Ixodes ricinus* (inset)

- a = mean number of bites per tick per day = 0.4 day^{-1}
- b = probability of transmission from tick to small mammal = 0.9
- c = probability of transmission from small mammal to tick = 0.8
- ξ = tick mortality = 0.015 day^{-1}
- γ = recovery rate of small mammals = 0.3 day^{-1}

When there are D [No. individuals km^{-2}] incompetent hosts in the environment, then the mean number of ticks per small mammal is lower and given by

$$m = \frac{m_0}{1 + \epsilon D}$$

with $\epsilon = 0.05$ (No. individuals km^{-2})$^{-1}$.

(i) calculate the basic reproduction number of the disease without incompetent hosts;
(ii) calculate the prevalence of ticks and hosts at equilibrium;
(iii) calculate the density D of incompetent hosts above which Lyme disease cannot establish in the small mammals.

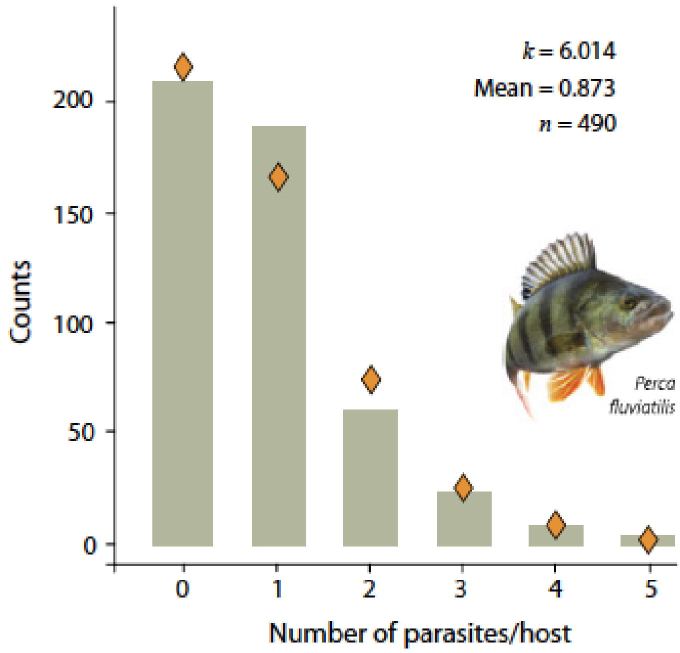
Solution

Without incompetent hosts, $R_0 = \frac{\beta\psi}{\gamma\xi} = 3.84$, prevalence of hosts $U_{eq} = 0.113$, prevalence of ticks $M_{eq} = 0.706$. Imposing R_0 with incompetent hosts to be < 1, one finds $D > 56.8$ No. of hosts km^{-2}.

Problem PD11

Fish populations can harbour several species of macroparasites. For instance the yellow perch (*Perca fluviatilis*) can be infected by the cestode worm *Triaenophorus nodulosus*. The characteristics of the parasite load distribution in the perch is shown in the Figure which reports the mean parasite load and the clumping parameter k. The yellow perch lives 5 years in the average. The mortality inflicted to the fish by the macroparasite is not easy to quantify, but one can approximately assume that a parasite load of 5 worms per fish inflicts a mortality which is about half the natural mortality of the perch. The estimated carrying capacity of the perch (e.g. in Lake Varese, northern Italy) is about 6,000 individuals km^{-2}. Its intrinsic instantaneous rate of increase is approximately 0.05 year^{-1}. The average life time of the adult *T. nodulosus* is not exactly known but can be assumed to be about 2 years.

Assume that the basic reproduction number of the disease is 1.2 and that the average parasite load reported in the Figure is the one that would establish at the equilibrium between hosts and parasites. By using the model by Anderson and May (1978), evaluate the abundance of hosts at equilibrium. Also, estimate the values of the two parameters λ and H_0 in the relationship $\lambda H/(H_0 + H)$ that links the fertility of one adult worm to the host density.



Problem PD11 Distribution of *Triaenophorus nodulosus* loads inside the yellow perch *Perca fluviatilis*

Solution

$$\frac{dH}{dt} = rH\left(1 - \frac{H}{K}\right) - \alpha P$$

$$\frac{dP}{dt} = \frac{\lambda PH}{H + H_0} - (m + \mu + \alpha)P - \alpha\frac{k+1}{k}\frac{P^2}{H}$$

(a) First determine the value of α as $5\alpha = 0.5\mu$, that is $\alpha = 0.02$ year^{-1}. The abundance of hosts at equilibrium can be found by setting $\frac{dH}{dt} = 0 = r\left(1 - \frac{H}{K}\right) - \alpha\frac{P}{H}$ and considering that P/H = 0.873. It turns out $H_{eq} = K\left(1 - \frac{\alpha}{r}(P/H)\right) = 3904.8$ individuals km^{-2}.

(b) First, set $\frac{dP}{dt} = 0$, which implies that $\frac{\lambda H}{H+H_0} - (m + \mu + \alpha) - \alpha\frac{k+1}{k}\frac{P}{H} = 0$. Second, remember that $R_0 = \frac{\lambda K}{H_0+K}\frac{1}{m+\mu+\alpha} = 1.2$. In this way we get a system of two equations in the two unknowns λ and H_0.
Solving the system we obtain $\lambda = 1.25$ and $H_0 = 2711.1$ individuals km^{-2}.

Problem PD12

The blue partridge of the Po valley (*Lagopus padanus*, a fantasy species) is often infested by nematode worms of the genus *Trichonicus*, which are not lethal, but have noxious effects on the bird fertility. When the partridge population is disease-free, the carrying capacity is $K = 40$ individuals km^{-2}, while the death rate is $\mu = 0.2$ year^{-1} and the intrinsic rate of demographic increase is $r = 0.1$ year^{-1}. Let L be the parasite load (i.e. the average number of adult worms inside the guts of each partridge); then the decrease of the per capita natality rate is εL with $\varepsilon = 0.05$ (No. of parasites/No. of partridges)$^{-1}$ year^{-1}. The death rate m of the parasite is 0.6 year^{-1}, while its reproduction rate (year^{-1}) is a function of the density H of partridges: $2H/(10 + H)$.

Find the coexistence equilibrium between parasites and hosts. Then graph the isoclines and determine the epidemiological dynamics.

Solution

$$\frac{dH}{dt} = rH\left(1 - \frac{H}{K}\right) - \varepsilon P$$

$$\frac{dP}{dt} = \frac{\lambda PH}{H + H_0} - (m + \mu)P$$

Setting $\frac{dP}{dt} = 0$ we obtain H_{eq} = 6.67 individuals km^{-2}. Then from the equation $\frac{dH}{dt} = 0$ one gets P_{eq} = 11.11 individuals km^{-2}. As $H_{eq} < K/2 = 20$ individuals km^{-2}, the isoclines are of the kind shown in Fig. 10.16b of the textbook, so that the equilibrium is unstable and the dynamics are self-sustained oscillations.