

Problem Set #5: Biomathematics, Spring 2001  
Discrete Time Predator-Prey Dynamics

1. -

- (a) In figure 1,  $\lambda = 2$  and  $a = 0.1$  and in figure 2,  $\lambda = 2$  and  $a = 0.5$ . We see that as  $a$  increases  $x(t+1)$  is less in the next generation for a given  $y(t)$ . As  $y(t)$  increases  $x(t+1)$  decreases exponentially such that as  $a$  increases, the decrease occurs at a greater rate. Larger values of  $\lambda$  cause  $x(t+1)$  to take on larger values for a given  $x(t)$ ,  $y(t)$  and  $a$ .
- (b) In figure 3,  $c = 10$  and  $a = 0.1$  and in figure 4,  $c = 10$  and  $a = 0.5$ . We see that as  $a$  increases  $y(t+1)$  takes on larger values for a given  $y(t)$  and  $x(t)$ , when  $y(t)$  and  $x(t)$  are small. Larger values of  $c$  cause  $y(t+1)$  to take on larger values for a given  $x(t)$ ,  $y(t)$  and  $a$ .
- (c) Equilibrium population sizes:

At equilibrium  $x(t+1) = x(t)$  and  $y(t+1) = y(t)$ , *simultaneously*.  
Let  $x(t+1) = x(t) = x$  and  $y(t+1) = y(t) = y$ , then  
 $x = \lambda x e^{-ay}$  and  $y = cx(1 - e^{-ay})$ .

We need to simultaneously solve for  $x$  and  $y$  such that the solutions satisfy the two previous equations. The first equation can easily be solved for  $y$  such that it is not a function of  $x$ .

$$x = \lambda x e^{-ay}$$

$$\frac{1}{\lambda} = e^{-ay} \text{ by dividing each side by } x \text{ and } \lambda$$

$-ay = -\ln \lambda$  by taking the natural logarithm of each side and simplifying

$$y = \frac{\ln \lambda}{a}$$

Since we have used the information provided by  $x = \lambda x e^{-ay}$  to solve for  $y$  we now substitute  $\frac{\ln \lambda}{a}$  for  $y$  into the equation  $y = cx(1 - e^{-ay})$  and solve for  $x$ .

$$\frac{\ln \lambda}{a} = cx(1 - \exp(-a \frac{\ln \lambda}{a}))$$

$$\frac{\ln \lambda}{a} = cx(1 - \frac{1}{\lambda})$$

$$x = \frac{\ln \lambda}{ca(1 - \frac{1}{\lambda})} = \frac{\lambda \ln \lambda}{ca(\lambda - 1)}$$

(d) -

$$F(x(t), y(t)) = \lambda x(t) e^{-ay(t)}$$

$$G(x(t), y(t)) = cx(t)(1 - e^{-ay(t)})$$

$$\frac{\partial F}{\partial x(t)} = \frac{\partial \lambda x(t) e^{-ay(t)}}{\partial x(t)} = \lambda e^{-ay(t)}$$

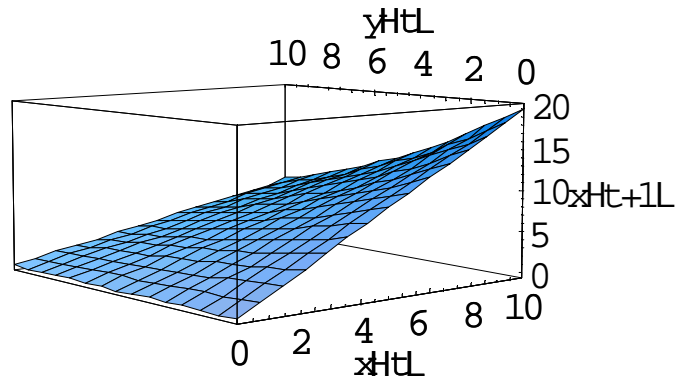


Figure 1:

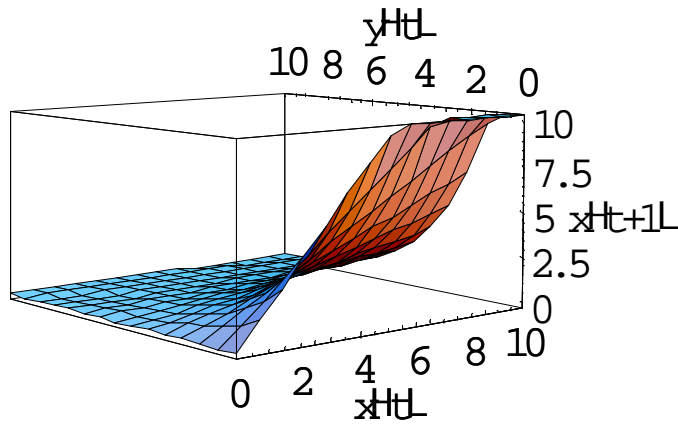


Figure 2:

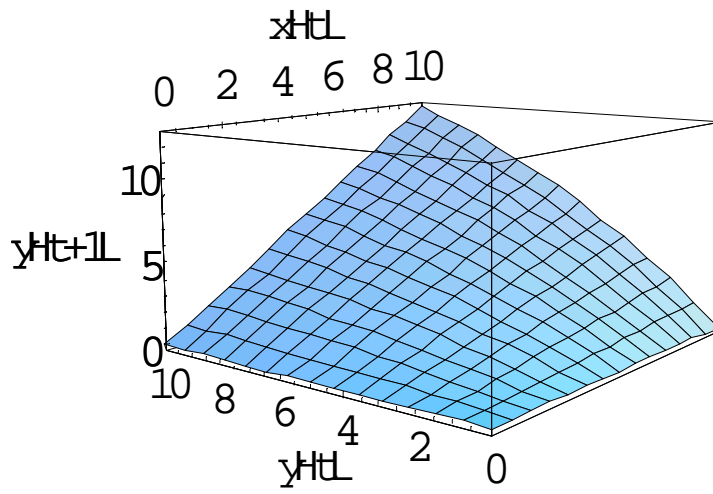


Figure 3:

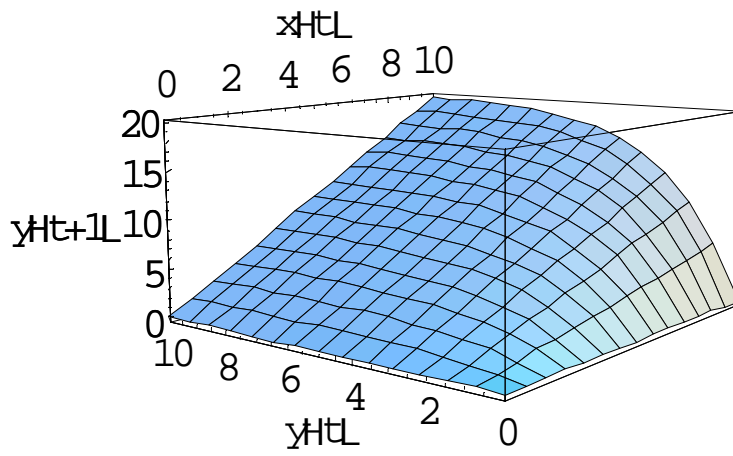


Figure 4:

$$\begin{aligned}\frac{\partial F}{\partial y(t)} &= \frac{\partial \lambda x(t) e^{-ay(t)}}{\partial y(t)} = \lambda x(t) e^{-ay(t)} \cdot (-a) = -a \lambda x(t) e^{-ay(t)} \\ \frac{\partial G}{\partial x(t)} &= \frac{\partial cx(t)(1 - e^{-ay(t)})}{\partial x(t)} = c(1 - e^{-ay(t)}) \\ \frac{\partial G}{\partial y(t)} &= \frac{\partial cx(t)(1 - e^{-ay(t)})}{\partial y(t)} = -cx(t) e^{-ay(t)} \cdot (-a) = acx(t) e^{-ay(t)}\end{aligned}$$

(e) -

$$\begin{aligned}\frac{\partial F}{\partial x(t)}(x, y) &= \frac{\partial F}{\partial x(t)}\left(\frac{\lambda \ln \lambda}{ca(\lambda - 1)}, \frac{\ln \lambda}{a}\right) = \lambda \exp\left(-a \frac{\ln \lambda}{a}\right) = \lambda \frac{1}{\lambda} = 1 \\ \frac{\partial F}{\partial y(t)}(x, y) &= \frac{\partial F}{\partial y(t)}\left(\frac{\lambda \ln \lambda}{ca(\lambda - 1)}, \frac{\ln \lambda}{a}\right) = -a \lambda \frac{\lambda \ln \lambda}{ca(\lambda - 1)} \exp\left(-a \frac{\ln \lambda}{a}\right) = \\ &= -a \lambda \frac{\lambda \ln \lambda}{ca(\lambda - 1)} \frac{1}{\lambda} = -\frac{\lambda \ln \lambda}{c(\lambda - 1)} \\ \frac{\partial G}{\partial x(t)}(x, y) &= \frac{\partial G}{\partial x(t)}\left(\frac{\lambda \ln \lambda}{ca(\lambda - 1)}, \frac{\ln \lambda}{a}\right) = c\left(1 - \exp\left(-a \frac{\ln \lambda}{a}\right)\right) = c\left(1 - \frac{1}{\lambda}\right) \\ \frac{\partial G}{\partial y(t)}(x, y) &= \frac{\partial G}{\partial y(t)}\left(\frac{\lambda \ln \lambda}{ca(\lambda - 1)}, \frac{\ln \lambda}{a}\right) = ac \frac{\lambda \ln \lambda}{ca(\lambda - 1)} \exp\left(-a \frac{\ln \lambda}{a}\right) = \\ &= \frac{\ln \lambda}{(\lambda - 1)} \\ \mathfrak{S} &= \begin{pmatrix} \frac{\partial F}{\partial x(t)}(x, y) & \frac{\partial F}{\partial y(t)}(x, y) \\ \frac{\partial G}{\partial x(t)}(x, y) & \frac{\partial G}{\partial y(t)}(x, y) \end{pmatrix} = \begin{pmatrix} 1 & -\frac{\lambda \ln \lambda}{c(\lambda - 1)} \\ c\left(1 - \frac{1}{\lambda}\right) & \frac{\ln \lambda}{(\lambda - 1)} \end{pmatrix}\end{aligned}$$

(f) -

Note that now  $x = x^*$  and  $y = y^*$ .

The equations for  $x(t+1) - x^*$  and  $y(t+1) - y^*$  are

$$x(t+1) - x^* = \frac{\partial F}{\partial x(t)}(x^*, y^*)(x(t) - x^*) + \frac{\partial F}{\partial y(t)}(x^*, y^*)(y(t) - y^*)$$

$$y(t+1) - y^* = \frac{\partial G}{\partial x(t)}(x^*, y^*)(x(t) - x^*) + \frac{\partial G}{\partial y(t)}(x^*, y^*)(y(t) - y^*).$$

Substituting for  $\frac{\partial F}{\partial x(t)}(x^*, y^*)$ ,  $\frac{\partial F}{\partial y(t)}(x^*, y^*)$ ,  $\frac{\partial G}{\partial x(t)}(x^*, y^*)$  and  $\frac{\partial G}{\partial y(t)}(x^*, y^*)$

based on the evaluated partial derivatives of our model (see 1e) yields,

$$x(t+1) - x^* = 1 \cdot (x(t) - x^*) - \frac{\lambda \ln \lambda}{c(\lambda - 1)}(y(t) - y^*)$$

$$y(t+1) - y^* = c\left(1 - \frac{1}{\lambda}\right)(x(t) - x^*) + \frac{\ln \lambda}{(\lambda - 1)}(y(t) - y^*).$$

In matrix form the previous system of equations can be represented as,

$$\begin{pmatrix} x(t+1) - x^* \\ y(t+1) - y^* \end{pmatrix} = \begin{pmatrix} 1 & -\frac{\lambda \ln \lambda}{c(\lambda - 1)} \\ c(1 - \frac{1}{\lambda}) & \frac{\ln \lambda}{(\lambda - 1)} \end{pmatrix} \begin{pmatrix} x(t) - x^* \\ y(t) - y^* \end{pmatrix} = \mathfrak{S} \begin{pmatrix} x(t) - x^* \\ y(t) - y^* \end{pmatrix}.$$

- (g) The previous system of equations described how the distance between a small perturbation and the equilibrium grows or decays with time. The model has a similar form as one that describes populations sizes of a single species divided into age classes. In that analysis we evaluated eigenvalues to determine whether the population grows or decays and whether it reaches a stable age distribution. Analogously, in our two species model, we can determine whether the small perturbation away from the equilibrium continues to grow or decay. If it continues to grow then the equilibrium is unstable and if it decays, the equilibrium is stable.

The eigenvalues of the Jacobian matrix are

$$\frac{1}{2} \frac{\lambda + \ln \lambda - 1 \pm \sqrt{\lambda^2 + \lambda 6 \ln \lambda - 2\lambda + \ln \lambda^2 - 2 \ln \lambda + 1 - \lambda^2 4 \ln \lambda}}{\lambda - 1}.$$

Both eigenvalues are independent of  $a$  and  $c$ , and are complex numbers for  $\lambda > 1$ . We can still evaluate the absolute value of each eigenvalue for  $\lambda > 1$ , and we see in figure 5 that for  $\lambda > 1$ , both eigenvalues take on the same value and each is greater than 1. Therefore, the equilibrium population size  $(x^*, y^*)$  of the basic Nicholson-Bailey model is always unstable, independent of the parameter values.

2. To reproduce the figures in the handout, we need to modify the program presented in Lab 5 by first exchanging the functions that describe the Nicholson-Bailey model with the Nicholson-Bailey model modified with Ricker density dependence. We then determine the parameters that were used to produce the figures. The only parameter that is not explicitly provided is  $a$ , but this can be inferred from equation 29a in the handout given  $r$ ,  $q$  and  $\bar{P}$ . Note that from equation 28b,  $c = 1$ . Applying this procedure to determine  $a$ , we find that for all the figures,  $a = 0.2$ .

3. -

- (a) In a refuge of size  $EK$ , in which  $K$  is the carrying capacity of the population and  $E$  is the probability an individual is in the refuge when the population is at its carrying capacity,  $EK$  is the maximum size of the refuge. If every individual is equally likely to enter the refuge, and  $EK \square x(t)$ , then  $EK/x(t)$  is the probability an individual is in the refuge.

- (b) If all individuals that are in the refuge escape parasitism, then the probability of escaping parasitism is 1. Of those that do not escape parasitism, the probability of being parasitized is  $\exp[-ay(t)]$ . Thus the expected probability an individual escapes parasitism is the probability it is in a refuge,  $(EK/x(t))$ , times the probability it escapes parasitism given it is in a refuge, (1), plus the probability it is outside a refuge,  $(1 - EK/x(t))$ , times the probability of escaping parasitism given it is outside a refuge,  $(\exp[-ay(t)])$ . Together this is

$$\left(\frac{EK}{x(t)}\right) + \left(1 - \left(\frac{EK}{x(t)}\right)\right) (\exp[-ay(t)]).$$

The concept can be visualized using a Venn Diagram as illustrated in figure 6. In figure 6 we see that the set of individuals that are in a refuge are also in the set that escapes parasitism, whereas only some of the individuals in the set of individuals outside the refuge also escape parasitism.

- (c)  $x(t+1) = \lambda x(t) \frac{EK}{x(t)} + \lambda x(t) \left(1 - \frac{EK}{x(t)}\right) \exp(-ay(t)) = \lambda EK + \lambda(x(t) - EK) \exp(-ay(t))$ . Written this way it is clear that if  $EK < x(t)$ , then on average  $EK$  individuals are in the refuge and escape parasitism and on average  $x(t) - EK$  individuals are outside the refuge and are vulnerable to parasitism at time  $t$ .
- (d) The probability of not escaping parasitism is 1 minus the probability of escaping parasitism or,

$$\begin{aligned} & 1 - \left(\left(\frac{EK}{x(t)}\right) + \left(1 - \left(\frac{EK}{x(t)}\right)\right) (\exp[-ay(t)])\right) \\ &= 1 - \left(\left(\frac{EK}{x(t)}\right) + (\exp[-ay(t)]) - \left(\frac{EK}{x(t)}\right) (\exp[-ay(t)])\right) \\ &= 1 - \left(\frac{EK}{x(t)}\right) - (\exp[-ay(t)]) + \left(\frac{EK}{x(t)}\right) (\exp[-ay(t)]) \\ &= \left(1 - \left(\frac{EK}{x(t)}\right)\right) (1 - (\exp[-ay(t)])) \end{aligned}$$

- (e) If  $\left(1 - \left(\frac{EK}{x(t)}\right)\right) (1 - (\exp[-ay(t)]))$  is the probability of being parasitized, and in the normal Nicholson Bailey model the term  $(1 - \exp(-ay(t)))$ , was the probability of being parasitized then,

$$y(t+1) = cx(t) \left(1 - \left(\frac{EK}{x(t)}\right)\right) (1 - (\exp[-ay(t)])) \text{ by substitution.}$$

Simplification yields,

$$\begin{aligned} y(t+1) &= cx(t) \left(1 - \left(\frac{EK}{x(t)}\right) - (\exp[-ay(t)]) + \left(\frac{EK}{x(t)}\right) (\exp[-ay(t)])\right) \\ &\text{by expanding } \left(1 - \left(\frac{EK}{x(t)}\right)\right) (1 - (\exp[-ay(t)])) \end{aligned}$$

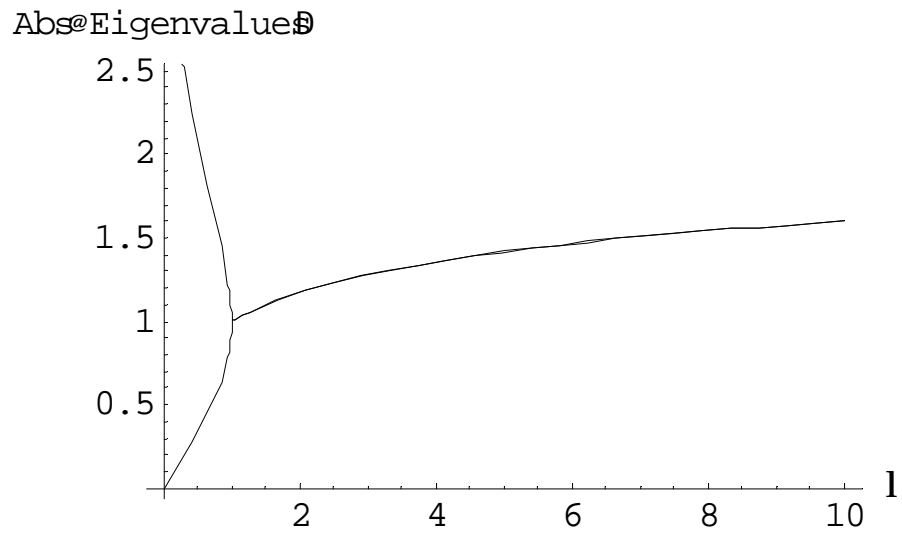


Figure 5:

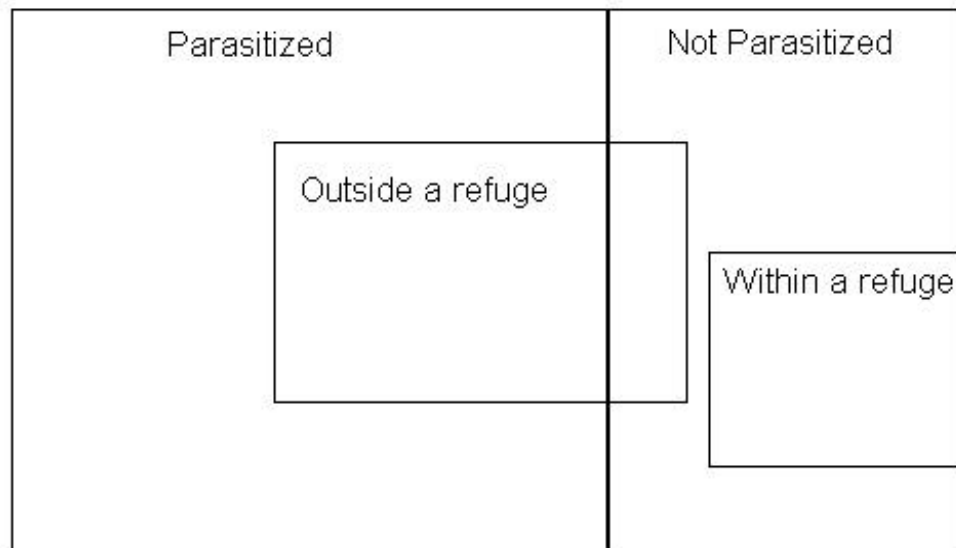


Figure 6:

$$y(t+1) = c(x(t) - EK - x(t) \exp[-ay(t)] + EK \exp[-ay(t)])$$

by multiplying through by  $x(t)$

$$y(t+1) = c(x(t) - EK)(1 - \exp[-ay(t)])$$

by factoring

4. It makes more sense to incorporate a refuge in the Nicholson-Bailey model that was modified with Ricker density dependence (Problem 3), then compare the effects of having a refuge with not having a refuge for the four sets of parameter values used to generate figures 3.5-3.8 in the handout.

Fig. 3.5 parameters: By adding a refuge of small to intermediate size say,  $E = 0.1 - 0.5$ , the equilibrium is approached more quickly. Refuges in which  $E > 0.65$ , essentially result in the parasitoid extinction because too many hosts can find refuge.

Fig. 3.6 parameters: A refuge of even small size  $E \approx 0.1$  results in a stable equilibrium instead of the limit cycle when there is no refuge. But having a refuge of size  $E > 0.20$  results in the rapid extinction of the parasitoid.

Fig. 3.7 parameters: By incorporating a refuge of only size  $E \approx 0.06$  results in a stable equilibrium. A refuge of about size  $E > 0.4$  results in the extinction of the parasitoid.

Fig. 3.8 parameters: A very small refuge of size  $E \approx 0.01$  results in a stable limit cycle instead of chaos. Increasing the refuge to  $E \approx 0.05$  results in a stable equilibrium. A refuge larger than about  $E \approx 0.20$  results in the rapid extinction of the parasitoid.

In general we see the small refuges general stabilize population dynamics in a host-parasitoid system. If refuges are too large - not surprisingly, the parasitoid goes extinct.

5. -

- (a) The parameter  $m$  should be between 0 and 1 because interference among parasitoids should decrease the expected number of hosts parasitized by the parasitoid population. As discussed in the lab, the term  $ay(t)$  in  $\exp(-ay(t))$  is the expected number of hosts parasitized by a parasitoid population of size  $y(t)$ . By raising  $ay(t)$  to a power between 0 and 1, this reduces this expected number.

(b)  $x(t+1) = \lambda x(t) \exp(-(ay(t))^{1-m})$

$$y(t+1) = cx(t)(1 - \exp(-(ay(t))^{1-m}))$$

- (c) Equilibrium states:

At equilibrium  $x(t+1) = x(t) = x$  and  $y(t+1) = y(t) = y$ , simultaneously.

$$x = \lambda x \exp(-(ay)^{1-m})$$



$$\frac{1}{\lambda} = \exp(-(ay)^{1-m})$$

$$(ay)^{1-m} = \ln \lambda$$

$$ay = (\ln \lambda)^{1/(1-m)}$$

$$y = \frac{(\ln \lambda)^{1/(1-m)}}{a}$$

Now solve for  $x$  using the equation  $y = cx(1 - \exp(-(ay)^{1-m}))$  :

$$\frac{(\ln \lambda)^{1/(1-m)}}{a} = cx(1 - \exp(-\left(a \frac{(\ln \lambda)^{1/(1-m)}}{a}\right)^{1-m}))$$

$$\frac{(\ln \lambda)^{1/(1-m)}}{a} = cx(1 - \exp(-\ln \lambda))$$

$$\frac{(\ln \lambda)^{1/(1-m)}}{a} = cx(1 - 1/\lambda)$$

$$x = \frac{\lambda(\ln \lambda)^{1/(1-m)}}{ca(\lambda - 1)}$$

For  $\lambda > e^1$  and  $0 < m < 1$ , the model with interference causes both the parasitoid and host to have higher equilibrium population sizes. For  $1 < \lambda \leq e^1$  and  $0 < m < 1$ , interference causes both the parasitoid and the host to have lower equilibrium population sizes.