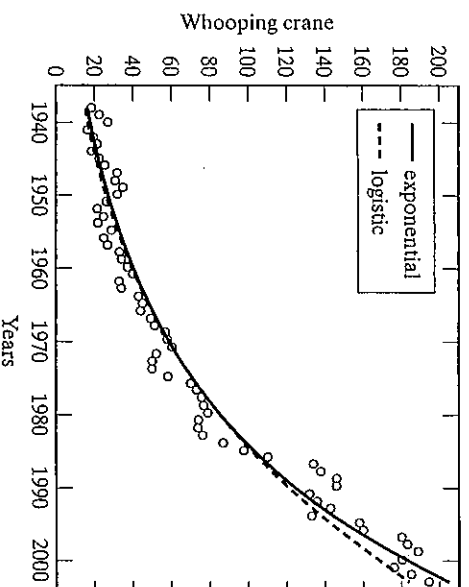


Figure 3.2 Whooping crane population data from 1938 to 1998. The data are fitted to the exponential curve (solid line) and the Beverton-Holt curve (dashed line).



whooping cranes in North America breeds in Wood Buffalo National Park in northern Canada and spends the winter in Aransas National Wildlife Refuge on the Texas coast. Data from the Wood Buffalo/Aransas (WBA) winter population are graphed in Figure 3.2 (U.S. Fish & Wildlife Service, 2005). (See the Appendix to Chapter 3.) An exponential curve,  $N_t = N_0\lambda^t$ , and the Beverton-Holt curve are fit to the whooping crane population data ( $t$ ,  $N_t$ ) using a least squares approximation.

For the exponential curve, let  $y_t = \ln(N_t) = \ln(N_0) + t \ln(\lambda)$ . The command *polyfit* in MATLAB finds the least squares estimates for the parameters. The estimate for  $N_0 \approx 15.88$  and for  $\lambda \approx 1.040$ .

The Beverton-Holt difference equation has an explicit solution which is given in Exercise 10 in Chapter 2 and equals

$$N_t = \frac{N_0 K \lambda^t}{K + N_0 (\lambda^t - 1)}.$$

If we assume  $K$  is known, then we can make a change of variable and fit a linear curve. Making the change of variable

$$y_t = \ln\left(\frac{1}{N_t} - \frac{1}{K}\right)$$

in the Beverton-Holt solution leads to

$$y_t = \ln\left(\frac{1}{N_0} - \frac{1}{K}\right) - t \ln \lambda.$$

A least squares approximation is used to fit the whooping crane data to the normalized logistic curve  $y_t$  with  $K = 500$ . Estimates for the other parameters are  $N_0 \approx 14.71$  and  $\lambda = 1.046$ . The estimate for  $K$  is used only for illustration purposes; an estimate for  $K$  is not known. For both models, the parameter estimates for  $\lambda$  show that the whooping crane population is increasing on the average about 4% per year. See Figure 3.2. ■

### 3.3 Nicholson-Bailey Model

One of the earliest applications of a discrete-time model to a biological system involved two insects, a parasitoid and its host. The model is named after the two researchers, Nicholson and Bailey, who developed the model and applied

it to the parasitoid, *Encarsia formosa*, and the host, *Trioletodes vaporariorum* (1935). The term "parasitoid" means a parasite which is free living as an adult but lays eggs in the larvae or pupae of the host. Hosts that are not parasitized give rise to their own progeny. Hosts that are successfully parasitized die but the eggs laid by the parasitoid may survive to be the next generation of parasitoids.

Parasitoids are frequently used as biological control agents to control insect pests. Introduction of a parasitoid led to a successful biological control program involving the California citrus industry. In the late 1800s citrus crops in California were being ruined by the insect pest, cottony cushion scale insect. A parasitoid fly and a predatory insect, the vedalia beetle, were introduced from Australia (Hoffmann and Frodsham, 1993). Within a few years, the pest was under control.

The following derivation for the host-parasitoid model of Nicholson-Bailey is based on the discussion presented by Edelstein-Keshet (1988). The basic variables and parameters are defined as follows:

$N_t$  = density of host species in generation  $t$ .

$P_t$  = density of parasitoid species in generation  $t$ .

$f(N_t, P_t)$  = fraction of hosts not parasitized.

$r$  = number of eggs laid by a host that survive through the larvae, pupae and adult stages.

$e$  = number of eggs laid by a parasitoid on a single host that survive through larvae, pupae, and adult stages.

The parameters  $r$  and  $e$  are positive. Applying these definitions, the general host-parasitoid model has the following form:

$$\begin{aligned} N_{t+1} &= rN_t f(N_t, P_t), \\ P_{t+1} &= eN_t(1 - f(N_t, P_t)). \end{aligned}$$

Note that if  $N_t = 0$ , then  $P_{t+1} = 0$ . The parasitoid cannot survive without the host. This is one reason why parasitoids are good biological control agents.

The Nicholson-Bailey model assumes a simple functional form for  $f(N_t, P_t)$ . The function  $f$  depends on the searching behavior of the parasitoid. The number of encounters of the parasitoids,  $P_t$ , with the hosts,  $N_t$ , is in direct proportion to host density  $N_t$ , that is, it follows the law of mass action,

$$aN_tP_t,$$

where the constant  $a$  is referred to as the *searching efficiency*, the probability that a given parasitoid will encounter a given host during its searching lifetime. Nicholson and Bailey assumed that  $a$  was a constant. The number of encounters are distributed randomly among the available hosts and assumed to follow the Poisson distribution,

$$p(n) = \frac{\exp(-\mu)\mu^n}{n!}, \quad n = 0, 1, 2, \dots,$$

where  $n$  is the number of encounters and  $\mu$  is the average number of encounters per host in one generation. Once a host is parasitized, it cannot be parasitized again. Therefore, only the first encounter between parasitoid and host is important. Hosts with no encounters  $p(0)$  are separated from those with more than one encounter,  $1 - p(0)$ .

Now, we estimate the fraction of hosts not parasitized,  $f(N_t, P_t)$ . The probability of no encounters of the host by the parasitoid represents the fraction of hosts that are not parasitized, that is,

$$p(0) = \frac{\exp(-\mu)\mu^0}{0!} = \exp(-\mu).$$

The parameter  $\mu$  can be estimated from the number of encounters:

$$\mu = \frac{\# \text{ encounters}}{N_t} = \frac{aN_t P_t}{N_t} = aP_t.$$

Thus,

$$p(0) = \exp(-aP_t) = f(N_t, P_t).$$

It follows from the preceding discussion that the Nicholson-Bailey model has the following form:

$$\begin{aligned} N_{t+1} &= rN_t \exp(-aP_t) = F(N_t, P_t), \\ P_{t+1} &= eN_t(1 - \exp(-aP_t)) = G(N_t, P_t). \end{aligned} \quad (3.1)$$

The equilibrium solutions and the local asymptotic stability of model (3.1) are analyzed. The equilibrium solutions of the Nicholson-Bailey model are found by solving the following equations simultaneously for  $\bar{N}$  and  $\bar{P}$ ,

$$\begin{aligned} \bar{N} &= r\bar{N} \exp(-a\bar{P}), \\ \bar{P} &= e\bar{N}(1 - \exp(-a\bar{P})). \end{aligned}$$

There are two equilibria. One equilibrium is the zero equilibrium, where  $\bar{N} = 0$  and  $\bar{P} = 0$ . The other equilibrium is

$$\bar{P} = \frac{\ln r}{a}, \quad \text{and} \quad \bar{N} = \frac{r \ln r}{(r-1)ae}.$$

Note that the latter equilibrium is positive if  $r > 1$ .

To analyze the local asymptotic stability, the Jacobian matrix is calculated and evaluated at an equilibrium. Computer algebra systems can be used to simplify calculations. In the Appendix to Chapter 3, commands in Maple are given for setting up and evaluating the Jacobian matrix. The partial derivatives of  $F(N, P) = rN \exp(-aP)$  and  $G(N, P) = eN(1 - \exp(-aP))$  are calculated below for the Jacobian matrix,

$$J(N, P) = \begin{pmatrix} r \exp(-aP) & -arN \exp(-aP) \\ e(1 - \exp(-aP)) & aeN \exp(-aP) \end{pmatrix}.$$

At the zero equilibrium  $J$  is given by

$$J(0, 0) = \begin{pmatrix} r & 0 \\ 0 & 0 \end{pmatrix}.$$

Since the eigenvalues are  $\lambda_{1,2} = r, 0$ , the zero equilibrium is locally asymptotically stable if  $|r| < 1$  and unstable if  $|r| > 1$ . Since  $r > 0$ , the zero equilibrium is locally asymptotically stable if  $0 < r < 1$  and unstable if  $r > 1$ .

The Jacobian matrix at the positive equilibrium,  $\bar{P} = \ln(r)/a$  and  $\bar{N} = r \ln r / [(r-1)ae]$ ,  $r > 1$ , can be simplified by noting  $r \exp(-a\bar{P}) = 1$ . Thus,

$$J(\bar{N}, \bar{P}) = \begin{pmatrix} 1 & \frac{-r \ln r}{(r-1)e} \\ \frac{(r-1)e}{r} & \frac{\ln r}{(r-1)} \end{pmatrix}.$$

The equilibrium is locally asymptotically stable if

$$\left| 1 + \frac{\ln r}{(r-1)} \right| < 1 + \frac{\ln r}{(r-1)} + \ln r < 2. \quad (3.2)$$

The first inequality is satisfied when  $r > 1$ . It will be shown by the following theorem that the second inequality is *not* satisfied, which implies that the positive equilibrium is unstable. There exist eigenvalues of the Jacobian matrix satisfying  $|\lambda_i| > 1$ .

### Theorem 3.1

The positive equilibrium in the Nicholson-Bailey model (3.1), where

$$\bar{P} = \frac{\ln r}{a}, \quad \text{and} \quad \bar{N} = \frac{r \ln r}{(r-1)ae}$$

for  $r > 1$ , is unstable.

**Proof** Consider the second inequality in (3.2) and define  $s(r) = (r-1)[1 + \ln(r)/(r-1) + \ln(r) - 2] = 1 - r + r \ln(r)$ . If  $s(r) < 0$ , then the second inequality is satisfied. However, it will be shown that  $s(r) > 0$ , which implies the equilibrium is unstable.

First, note that  $s(1) = 1 - 1 - \ln 1 = 0$  and  $s'(r) = -1 + \ln r + 1 = \ln r$ . Thus,  $s'(r) > 0$  for  $r > 1$ ;  $s$  is strictly increasing for  $r > 1$ . Thus,  $s(r) > 0$  for  $r > 1$ . The equilibrium is unstable.  $\square$

Figure 3.3 illustrates the dynamics of the Nicholson-Bailey model (3.1) when  $r < 1$  and  $r > 1$ . When  $r > 1$ , the oscillations increase in amplitude, but they also get very close to zero so that numerically the values are set to zero; population extinction occurs even in this case.

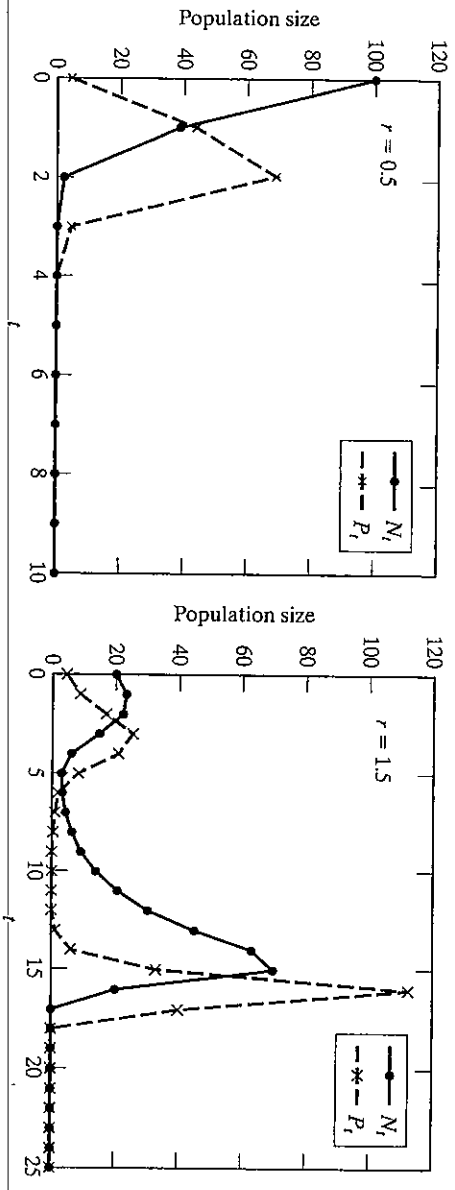


Figure 3.3 Some simulations of the Nicholson-Bailey model when  $r < 1$  and  $r > 1$  ( $a = 0.05$  and  $e = 2$ ).

### 3.4 Other Host-Parasitoid Models

There are a number of unrealistic assumptions in the Nicholson-Bailey model. For example, a constant reproductive rate of the host, a constant searching efficiency, and a homogeneous environment are unrealistic assumptions. With additional realistic assumptions, the positive equilibrium can be locally asymptotically stable. Some of these more realistic assumptions are discussed next.

Suppose the reproductive rate  $r$  in the host equation is replaced by a density-dependent factor,  $g(N_t)$ ,

$$\begin{aligned} N_{t+1} &= N_t g(N_t) \exp(-aP_t), \\ P_{t+1} &= eN_t(1 - \exp(-aP_t)). \end{aligned}$$

Some forms for the density-dependent factor  $g$  that have been studied include

$$\frac{r}{N_t^b}, \quad \exp\left(r\left(1 - \frac{N_t}{K}\right)\right) \quad \text{and} \quad \frac{r}{(1 + cN_t)^b}.$$

For some parameter values the density-dependent factor has a stabilizing influence. If the host population does not grow too fast (the value of  $r$  in the density-dependent factor should not be too large), then there exists a locally asymptotically stable equilibrium. See Figure 3.4 when  $g(N_t) = \exp(1.5(1 - N_t/25))$ .

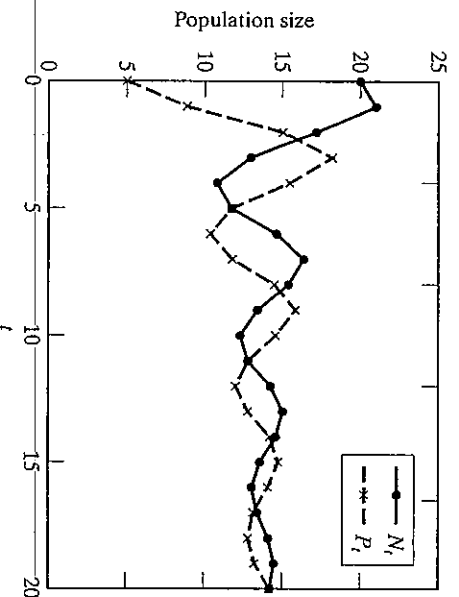
Suppose the environment is not homogeneous. Suppose the environment is patchy, so that a proportion of the host population may find a refuge and be safe from attack by parasitoids. Let  $\gamma$  be the proportion of hosts that are not safe from attack by parasitoids and  $1 - \gamma$  be the proportion of hosts that are safe within a refuge. In this case, the model has the form

$$\begin{aligned} N_{t+1} &= r(1 - \gamma)N_t + r\gamma N_t \exp(-aP_t), \\ P_{t+1} &= \gamma eN_t[1 - \exp(-aP_t)]. \end{aligned}$$

Another way to model the effect of a refuge is to assume there is a constant number of hosts  $N_0$  in a refuge. The hosts,  $N_0$ , are safe from attack by parasitoids. The model has the form

$$\begin{aligned} N_{t+1} &= rN_0 + r(N_t - N_0) \exp(-aP_t), \\ P_{t+1} &= e(N_t - N_0)[1 - \exp(-aP_t)]. \end{aligned}$$

Modified  
Bailey model with  
dependent factor  
 $\exp(1.5(1 - N_t/25))$   
and  $e = 2$ .



Another generalization of the Nicholson-Bailey host-parasitoid model is to include more than one parasitoid. Suppose there is one host and two parasitoids which parasitize the same host. Suppose the host density is denoted by  $N$ , and the two parasitoid densities are denoted by  $P$  and  $Q$ . In addition, suppose the parasitoid  $P$  acts first, followed by  $Q$  that acts on the surviving hosts. For example, the host species may be attacked in different developmental stages by a range of parasitoids. Hassell (1978) discusses a winter moth that is parasitized by egg, larval, and pupal parasitoids. A model with this form is

$$\begin{aligned}N_{t+1} &= rN_t f_1(P_t) f_2(Q_t), \\P_{t+1} &= e_1 N_t [1 - f_1(P_t)], \\Q_{t+1} &= e_2 N_t f_1(P_t) [1 - f_2(Q_t)].\end{aligned}$$

If the proportion of hosts not parasitized by the parasitoids takes the same form as in the Nicholson-Bailey model [i.e.,  $f_i(x) \equiv \exp(-a_i x)$ ], then the positive equilibrium will be unstable. However, for some other forms, there are regions in parameter space that give rise to a stable positive equilibrium.

A model in which a parasitoid parasitizes another parasitoid is referred to as a host-parasitoid-hyperparasitoid system. In this case,  $N$  is the host,  $P$  is the primary parasitoid, and  $Q$  is the hyperparasitoid which only parasitizes hosts first parasitized by  $P$ . The function  $f_1$  is the fraction of hosts  $N$  not parasitized by  $P$  and  $f_2$  is the fraction of parasitoids  $P$  not parasitized by  $Q$ . The model has the form

$$\begin{aligned}N_{t+1} &= rN_t f_1(P_t), \\P_{t+1} &= e_1 N_t [1 - f_1(P_t)] f_2(Q_t), \\Q_{t+1} &= e_2 N_t [1 - f_1(P_t)] [1 - f_2(Q_t)].\end{aligned}$$

Hassell (1978) studies this host-parasitoid-hyperparasitoid model when

$$f_i(x) = \left(1 + \frac{a_i x}{k_i}\right)^{-k_i}, \quad a_i, k_i > 0, \quad i = 1, 2.$$

These particular forms are derived from a negative binomial distribution rather than a Poisson distribution. The search for hosts by parasitoids is not random. For example, parasitoids may aggregate in patches where there is high prey density. The parameter  $k_i$  is related to parasitoid aggregation. Aggregation is strongest when  $k_i \rightarrow 0$ ,

$$\lim_{k_i \rightarrow 0} \left(1 + \frac{a_i x}{k_i}\right)^{-k_i} = 1,$$

and weakest when  $k_i \rightarrow \infty$ ,

$$\lim_{k_i \rightarrow \infty} \left(1 + \frac{a_i x}{k_i}\right)^{-k_i} = \exp(-a_i x).$$

In this latter case, the form of  $f$  is the one in Nicholson-Bailey's model (3.1). Some extensions and applications to biological control in host-parasitoid systems can be found in the references (Barlow et al., 2004; Hassell, et al., 1991; King and Hastings, 2003; Lynch et al., 2002; Várkonyi et al., 2002).

### 3.5 Host-Parasite Models

Host-parasite models are similar to host-parasitoid models, except that the parasite does not necessarily kill the host. A host-parasite model was formulated by Leslie and Gower in 1960 and has a particularly simple form. Let  $H_t$  denote the host and  $P_t$  the parasite populations at time  $t$ . Then the host-parasite model is defined as follows:

$$\begin{aligned} H_{t+1} &= \frac{\alpha_1 H_t}{1 + \gamma_1 P_t}, \\ P_{t+1} &= \frac{\alpha_2 P_t}{1 + \gamma_2 P_t/H_t}, \end{aligned} \quad (3.3)$$

where  $H_0 > 0$ ,  $P_0 > 0$ ,  $\alpha_i > 0$ , and  $\gamma_i > 0$ ,  $i = 1, 2$ . The parameters  $\alpha_i$  are growth rates of the host and parasite populations in the absence of the other population. The larger the quantity  $\gamma_1 P_t$ , the greater the reduction of the host population. The larger the ratio  $P_t/H_t$ , the smaller the number of hosts per parasite resulting in a reduction in the parasite population (Pielou, 1977).

It is easy to see that solutions to (3.3) are positive for  $t > 0$ . In addition, if  $\alpha_1 < 1$ , then  $\lim_{t \rightarrow \infty} H_t = 0$  and if  $\alpha_2 < 1$ , then  $\lim_{t \rightarrow \infty} P_t = 0$ . In Exercise 6, the dynamics when  $\alpha_i < 1$  for  $i = 1$  or  $i = 2$  are summarized. In the following analysis, the parameters  $\alpha_i$  are assumed to be greater than one,  $\alpha_i > 1$ ,  $i = 1, 2$ .

Model (3.3) has a unique positive equilibrium given by

$$\bar{P} = \frac{\alpha_1 - 1}{\gamma_1} \quad \text{and} \quad \bar{H} = \frac{\gamma_2}{\alpha_2 - 1} \bar{P} = \frac{\gamma_2(\alpha_1 - 1)}{\gamma_1(\alpha_2 - 1)}.$$

The Jacobian matrix evaluated at the positive equilibrium has a simple form,

$$J = \begin{pmatrix} 1 & -\frac{\gamma_2(\alpha_1 - 1)}{\alpha_1(\alpha_2 - 1)} \\ \frac{1}{\alpha_2 \gamma_2} & \frac{1}{\alpha_2} \end{pmatrix}.$$

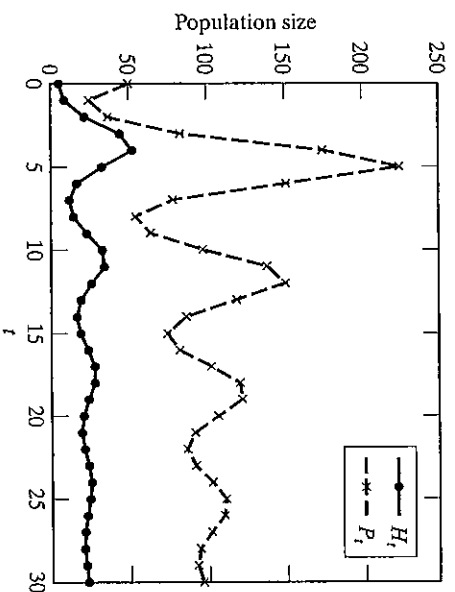
The conditions in Theorem 2.10 can be easily checked to see whether the equilibrium is locally asymptotically stable. It is straightforward to see that the trace is positive and the trace is also less than one plus the determinant. Hence, the only condition to check for local stability is that the determinant is less than one,

$$\frac{\alpha_1 \alpha_2 - \alpha_2 + 1}{\alpha_1 \alpha_2} < 1.$$

This latter condition reduces to  $\alpha_2 > 1$ . The stability conditions in Theorem 2.10 are always satisfied under the conditions  $\alpha_i > 1$ ,  $i = 1, 2$ .

If the host population is a pest, then according to the Leslie-Gower model, a fast-growing parasite population with a growth rate larger than that of the host that significantly reduces the host population,  $\alpha_2 > \alpha_1$  and  $\gamma_1 > \gamma_2$ , would help in reducing the pest population. A numerical example in Figure 3.5 illustrates the dynamics of model (3.3).

**Figure 3.5** Leslie-Gower model (3.5) of a host-parasite system, ( $\alpha_1 = 5$ ,  $\alpha_2 = 10$ ,  $\gamma = 0.04$ , and  $\gamma_2 = 2$ ). The stable equilibrium is 100 and  $H = 22.22$ .



### 3.6 Predator-Prey Models

Predator-prey models are similar to both host-parasite and host-parasitoid models. However, unlike the latter two systems, the predator does not live on the host. The prey serves as a food source for the predator. In this section, we discuss a discrete-time predator-prey model studied by Neubert and Kot (1992). This model is related to the well-known continuous-time, Lotka-Volterra predator-prey model, named after Alfred Lotka (1880–1949) and Vito Volterra (1860–1940), who contributed to the analysis of the continuous-time predator-prey model. The continuous-time predator-prey model is studied in Chapter 6, Section 6.3. The dynamics of this model are much more complex than its continuous analogue or the Leslie-Gower model, although it appears to be much simpler. The Neubert-Kot model exhibits some new dynamics that are not present in scalar difference equations.

In the model of Neubert and Kot (1992), the per capita growth rates are linear. The model has the following form:

$$\begin{aligned} N_{t+1} &= N_t + rN_t \left(1 - \frac{N_t}{K}\right) - eN_t P_t, \\ P_{t+1} &= bN_t P_t + (1 - d)P_t, \end{aligned} \quad (3.4)$$

where  $N_t$  is prey density at time  $t$  and  $P_t$  is predator density at time  $t$ . The parameters  $r$ ,  $e$ ,  $b$ ,  $d$ , and  $K$  are positive. The term  $rN_t(1 - N_t/K)$  represents logistic growth,  $r$  is the intrinsic growth rate, and  $K$  is the carrying capacity. The term  $eP_t$  is the per capita prey reduction due to consumption by the predator (assumes the law of mass action). The term  $bN_t$  is per capita predator increase due to prey consumption and  $d$  is the death rate of the predator. Note that the original system (3.4) has five parameters. A simpler version of the predator-prey model (3.4) is formulated by reducing the number of parameters and assuming that predators only live one generation,  $d = 1$ .

A change of variable reduces the model with  $d = 1$  containing four parameters to one with only two parameters. This technique was used in Chapter 2, when the approximate logistic equation was reduced to a simpler form containing only one parameter. The new variables are chosen to be

$$x_t = \frac{N_t}{K}, \quad y_t = \frac{eP_t}{bK}, \quad \text{and} \quad c = bK.$$



Note that the variables  $x_i$  and  $y_i$  are dimensionless (e.g.,  $K$  has the same units as  $N_i$  and  $eP_i$  has the same units as  $bK$ ). There are other choices for the change of variables to put the system in dimensionless form, but this is a good choice for our purposes. With this change of variables, the new system has only two parameters,  $r$  and  $c$ :

$$\begin{aligned}x_{i+1} &= (r + 1)x_i - rx_i^2 - cx_iy_i, \\y_{i+1} &= cx_iy_i.\end{aligned}\tag{3.5}$$

System (3.5) is much simpler to analyze than the original system because now there are only two parameters.

Before we begin the analysis of (3.5), it must be noted that the question of nonnegative solutions has not been addressed. If the initial conditions,  $x_0$  and  $y_0$ , are sufficiently large, it is easy to see that  $x_1$  could become negative. The variable  $x_{i+1}$  could be redefined to alleviate this problem, for example,

$$x_{i+1} = \max\{0, (r + 1)x_i - rx_i^2 - cx_iy_i\}.\tag{3.6}$$

If  $x_{i+1} = 0$ , then at the next time step, both predator and prey are zero,  $(x_{i+2}, y_{i+2}) = (0, 0)$ ; complete extinction occurs. In all of the numerical simulations performed here, solutions remained nonnegative, even without the restriction given in (3.6). Therefore, in the following analysis, it is assumed that  $x_i \geq 0$  and  $y_i \geq 0$  for all time. Note if the predator is absent,  $y_0 = 0$ , then  $x_i$  satisfies the approximate logistic equation. In this case, for  $x_i$  to be positive for all time requires  $0 < x_0 < (r + 1)/r$  and  $r < 3$  (no restrictions on  $c$ ). But the presence of the predator,  $y_i$ , reduces the size of  $x_{i+1}$ . Thus, for solutions of (3.5) to be positive, the restrictions on  $r$  can be relaxed somewhat, new restrictions on  $r$  will depend on  $c$ . First, the equilibria of system (3.5) are identified, then their local stability is analyzed. The equilibria satisfy

$$\begin{aligned}\bar{x} &= \bar{x}(r + 1 - r\bar{x} - c\bar{y}), \\ \bar{y} &= c\bar{x}\bar{y}.\end{aligned}$$

It can be seen that there exist equilibria at  $\bar{x} = 0 = \bar{y}$  and at  $\bar{x} = 1$  and  $\bar{y} = 0$ . Also, there exists a positive equilibrium if  $c > 1$ ,

$$\bar{x} = \frac{1}{c} \quad \text{and} \quad \bar{y} = \frac{r(c - 1)}{c^2}.$$

The Jacobian matrix for system (3.5) is

$$J(x, y) = \begin{pmatrix} r + 1 - 2rx - cy & -cx \\ cy & cx \end{pmatrix}.$$

The Jacobian matrix evaluated at the zero equilibrium is

$$J(0, 0) = \begin{pmatrix} r + 1 & 0 \\ 0 & 0 \end{pmatrix}.$$

This matrix has a positive eigenvalue  $r + 1 > 1$ . The equilibrium with both species extinct is unstable.

The Jacobian matrix evaluated at  $(1, 0)$  is

$$J(1, 0) = \begin{pmatrix} 1 - r & -c \\ 0 & c \end{pmatrix}.$$

This matrix has the eigenvalues  $\lambda_{1,2} = 1 - r, c$ . The equilibrium with only the prey present is locally asymptotically stable if  $0 < r < 2$  and  $0 < c < 1$ . The growth rates of the prey and predator must be within a certain range, but not too large.

Finally, the Jacobian matrix at the positive equilibrium  $(\bar{x}, \bar{y})$ , where  $c > 1$ , is

$$J(\bar{x}, \bar{y}) = \begin{pmatrix} 1 - r/c & -1 \\ r - r/c & 1 \end{pmatrix}.$$

The stability criterion from Theorem 2.10 is

$$|2 - r/c| < 2 + r - 2r/c < 2.$$

Each of these inequalities can be stated separately,

$$2 - r/c < 2 + r - 2r/c,$$

$$2 - r/c > -2 - r + 2r/c,$$

$$2 + r - 2r/c < 2.$$

If the first condition fails there is a real eigenvalue,  $\lambda_1 \geq 1$ . If the second condition fails there is a real eigenvalue,  $\lambda_1 \leq -1$ . If the third condition fails and the eigenvalue is complex, its magnitude  $|\lambda_1| \geq 1$ . The three stability conditions simplify as follows:

$$c > 1,$$

$$r < \frac{4c}{3 - c} \quad \text{if } c < 3,$$

$$c < 2.$$

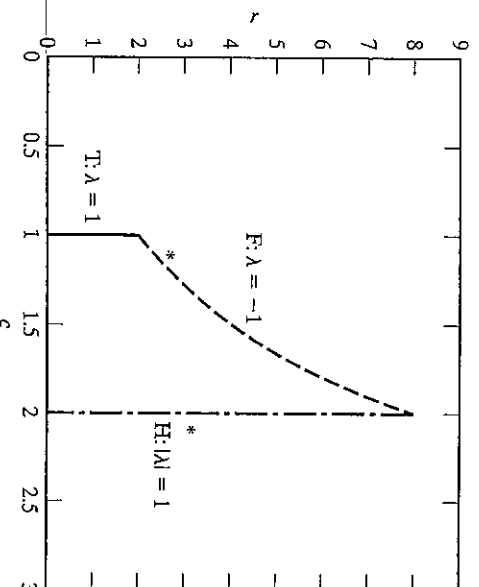
The three conditions together imply

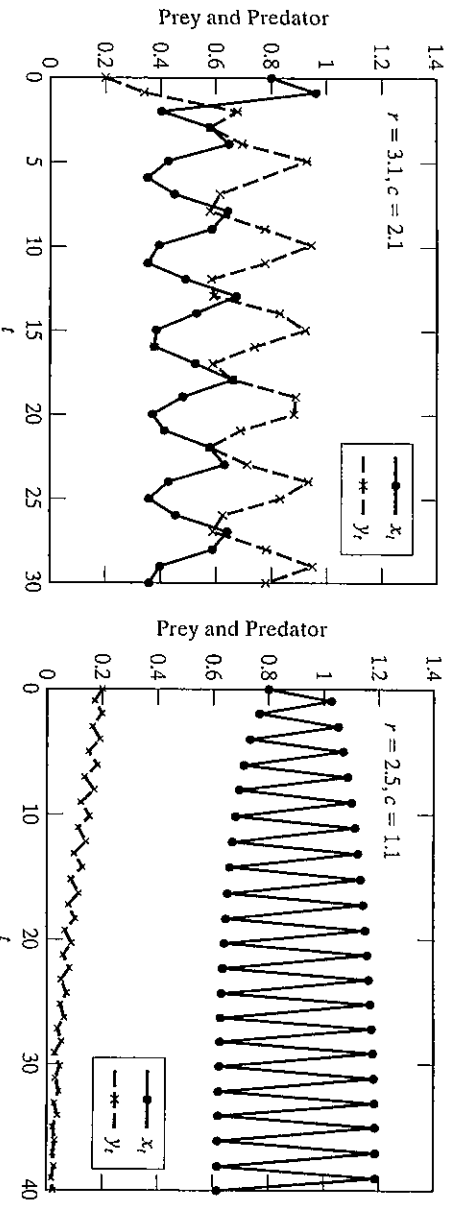
$$1 < c < 2 \quad \text{and} \quad r < \frac{4c}{3 - c}.$$

These conditions are graphed in the  $r$ - $c$  parameter space (Figure 3.6). The parameter  $c$  must be large to guarantee that the predator persists, but not too large. In addition, the parameter  $r$  must not be too large and its magnitude depends on the magnitude of  $c$ .

As a stability boundary is crossed in Figure 3.6, at least one eigenvalue has magnitude equal to one. The type of eigenvalue, positive or negative, real or complex determines the type of bifurcation. There exists a transcritical bifurcation when  $\lambda = 1$ , a flip bifurcation when  $\lambda = -1$ , and a Hopf bifurcation when the eigenvalues are complex and satisfy  $|\lambda| = 1$  (Neubert and Kot, 1992). The terminology “Hopf bifurcation” is more often used

**Figure 3.6** Stability region in  $r$ - $c$  parameter space. The axis  $T$ ,  $F$ , and  $H$  mean either transcritical, flip (period-doubling), or Hopf bifurcation as the stability boundary is crossed.





**Figure 3.9** Solutions to the normalized predator-prey system when  $r = 3.1$  and  $c = 2.1$  (periodic solution) and when  $r = 2.5$  and  $c = 1.1$  (period 2 solutions for the prey and the predator goes extinct).

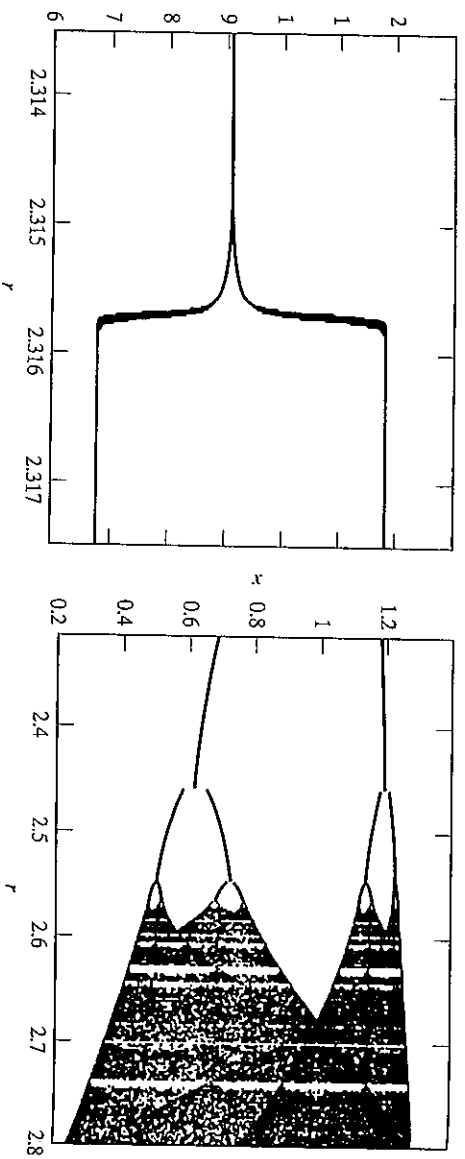
### 3.7 Population Genetics Models

Inheritance depends on the information contained in the chromosomes that are passed down from generation to generation. Humans have two sets of 23 chromosomes (diploid), making a total of 46 chromosomes; one set is obtained from each parent. Certain locations along the chromosomes contain the instructions for some characteristic, such as eye or hair color. The locations along the chromosomes are called the *loci* (a single location is called a *locus*). The instructions within the chromosomes are referred to as the *genes*. Each gene gives a unique instruction (for color of eyes, color of hair, etc.) and each human has two genes per locus because there are two sets of chromosomes. The physical characteristics (eye or hair color) unique to each individual are determined by that individual's genes. In simple organisms, such as bacteria, there are 2000 to 3000 genes, whereas in higher organisms such as plants and animals there are 50,000 to 100,000 genes (Clark and Russell, 1997). Each gene has different variant forms (the gene for eye color can be green, blue, brown, etc.). These different variant forms of the genes are referred to as *alleles*. Here, we shall consider the simplest possible case, the case where there are only two different alleles associated with a particular gene.

Suppose there are two alleles for a given gene. The two alleles are denoted  $a$  and  $A$ . A human with two sets of chromosomes could then have one of three different combinations on his or her chromosome:  $AA$ ,  $Aa$ , or  $aa$ . The combinations  $AA$  and  $aa$  are *homozygous*, whereas the combination  $Aa$  is *heterozygous*. The three combinations,  $AA$ ,  $Aa$ , and  $aa$ , are called the *genotypes* of the locus.

One of the two alleles may be *dominant*. For example, if  $A$  is the dominant allele, then  $a$  is referred to as the *recessive allele*. Then genotypes  $AA$  and  $Aa$  correspond to the same physical trait, but different from that of  $aa$ . This is also described as saying that genotypes  $AA$  and  $Aa$  have *phenotype A* and  $aa$  has *phenotype a* (Hoppensteadt, 1975).

We explore the question of whether the allele frequencies (associated with a particular gene) change in a given population over time as individuals within that population mate and reproduce. Our population genetics model is a simple one-locus-two-allele-model. We assume that during each time step, the population in generation  $t$  is replaced by the population in generation  $t + 1$ .



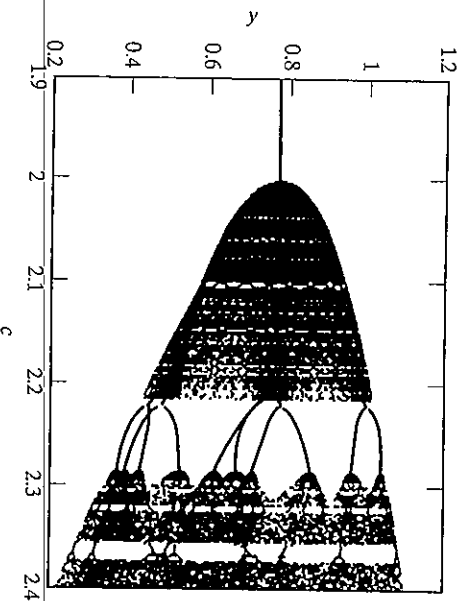
**Figure 3.7** Bifurcation diagram for the normalized predator-prey system when  $c = 1.1$  and  $r \in [2.317, 2.8]$  (flip or period-doubling bifurcations). The cycles of the prey  $x$  are indicated.

in connection with differential equations (see Chapter 5). In difference equations, such types of bifurcations are referred to as *Neimark-Sacker bifurcations* (Elaydi, 2000; Hale and Kocak, 1991). Figures 3.7 and 3.8 are bifurcation diagrams for a period-doubling bifurcation (flip) and a Neimark-Sacker bifurcation, respectively. When a flip bifurcation occurs, the predator becomes extinct and the prey exhibits period-doubling behavior (Figure 3.7).

A Neimark-Sacker bifurcation represents a new type of bifurcation that occurs in systems of difference equations, but not in scalar difference equations. When this bifurcation occurs, there is a pair of purely imaginary eigenvalues. In this case, there exists a periodic solution, but the period may not be integer valued (Figure 3.8).

Solutions to the normalized predator-prey system are graphed in Figure 3.9 when  $r = 3.1$  and  $c = 2.1$  and when  $r = 2.5$  and  $c = 1.1$  (when the flip and Hopf bifurcation boundaries are crossed in Figure 3.6). They illustrate a periodic solution for the prey and predator and a 2-cycle for the prey, respectively.

**Figure 3.9** Solutions to the normalized predator-prey system when  $c \in [1.9, 2.4]$  and  $r = 3.1$  (left) and  $r = 2.5$  (right).



## LAB VISIT I

## Boom, Bust, and Chaos in the Beetle Census

**D**AMAGE DUE TO flour beetles is a significant cost to the food processing industry. One of the major goals of entomologists is to gain insight into the population dynamics of beetles and other insects, as a way of learning about insect physiology. A commercial application of population studies is the development of strategies for population control.

A group of researchers recently designed a study of population fluctuation in the flour beetle *Tribolium*. The newly hatched larva spends two weeks feeding before entering a pupa stage of about the same length. The beetle exits the pupa stage as an adult. The researchers proposed a discrete map that models the three separate populations. Let the numbers of larvae, pupae, and adults at any given time  $t$  be denoted  $L_t$ ,  $P_t$ , and  $A_t$ , respectively. The output of the map is three numbers: the three populations  $L_{t+1}$ ,  $P_{t+1}$ , and  $A_{t+1}$  one time unit later. It is most convenient to take the time unit to be two weeks. A typical model for the three beetle populations is

$$\begin{aligned} L_{t+1} &= bA_t \\ P_{t+1} &= L_t(1 - \mu_l) \\ A_{t+1} &= P_t(1 - \mu_p) + A_t(1 - \mu_a), \end{aligned} \quad (1.5)$$

where  $b$  is the birth rate of the species (the number of new larvae per adult each time unit), and where  $\mu_l$ ,  $\mu_p$ , and  $\mu_a$  are the death rates of the larva, pupa, and adult, respectively.

We call a discrete map with three variables a three-dimensional map, since the state of the population at any given time is specified by three numbers  $L_t$ ,  $P_t$ , and  $A_t$ . In Chapter 1, we studied one-dimensional maps, and in Chapter 2 we move on to higher dimensional maps, of which the beetle population model is an example.

*Tribolium* adds an interesting twist to the above model: cannibalism caused by overpopulation stress. Under conditions of overcrowding, adults will eat pupae

Costantino, R.F., Cushing, J.M., Dennis, B., Desharnais, R.A., Experimentally induced transitions in the dynamic behavior of insect populations. *Nature* 375, 227–230 (1995).

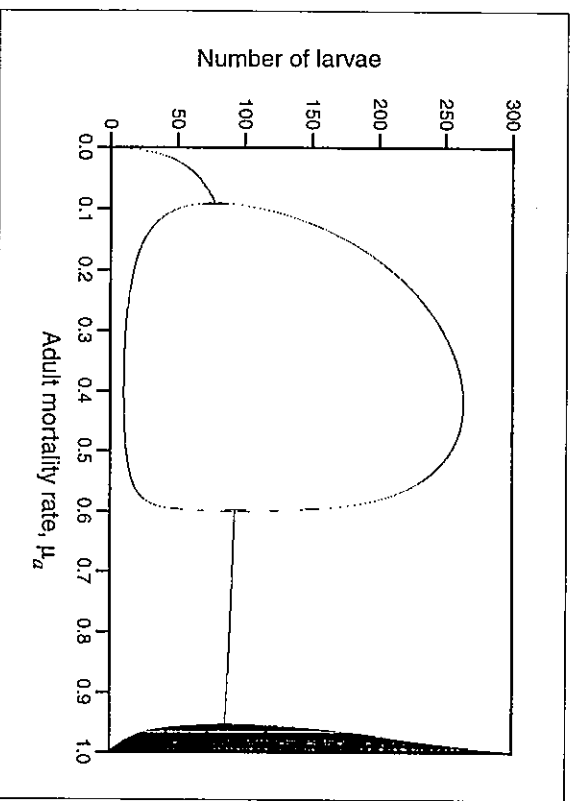
and unhatched eggs (future larvae); larvae will also eat eggs. Incorporating these refinements into the model yields

$$\begin{aligned} L_{t+1} &= bA_t \exp(-c_{ea}A_t - c_{el}L_t) \\ P_{t+1} &= L_t(1 - \mu_l) \\ A_{t+1} &= P_t(1 - \mu_p) \exp(-c_{pa}A_t) + A_t(1 - \mu_a). \end{aligned} \quad (1.6)$$

The parameters  $c_{el} = 0.012$ ,  $c_{ea} = 0.009$ ,  $c_{pa} = 0.004$ ,  $\mu_l = 0.267$ ,  $\mu_p = 0$ , and  $b = 7.48$  were determined from population experiments. The mortality rate of the adult was determined from experiment to be  $\mu_a = 0.0036$ .

The effect of calling the exterminator can be modeled by artificially changing the adult mortality rate. Figure 1.17 shows a bifurcation diagram from Equations (1.6). The horizontal axis represents the mortality rate  $\mu_a$ . The asymptotic value of  $L_t$ —found by running the model for a long time at a fixed  $\mu_a$  and recording the resulting larval population—is graphed vertically.

Figure 1.17 suggests that for relatively low mortality rates, the larval population reaches a steady state (a fixed point). For  $\mu_a > .1$  (representing a death rate of 10% of the adults over each 2 week period), the model shows oscillation between two widely-different states. This is a "boom-and-bust" cycle, well-known to population biologists. A low population (bust) leads to uncrowded living con-



**Figure 1.17** Bifurcation diagram for the model equations (1.6). The bifurcation parameter is  $\mu_a$ , the adult mortality rate.

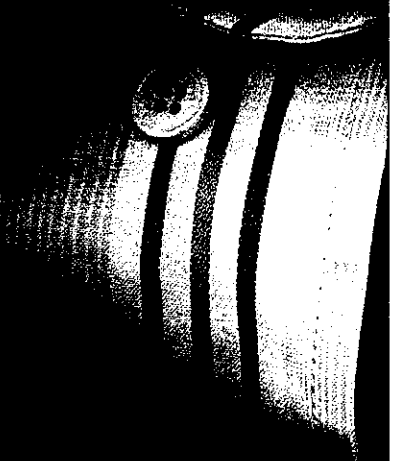
ditions and runaway growth (boom) at the next generation. At this point the limits to growth (cannibalism, in this system) take over, leading to a catastrophic decline and repeat of the cycle.

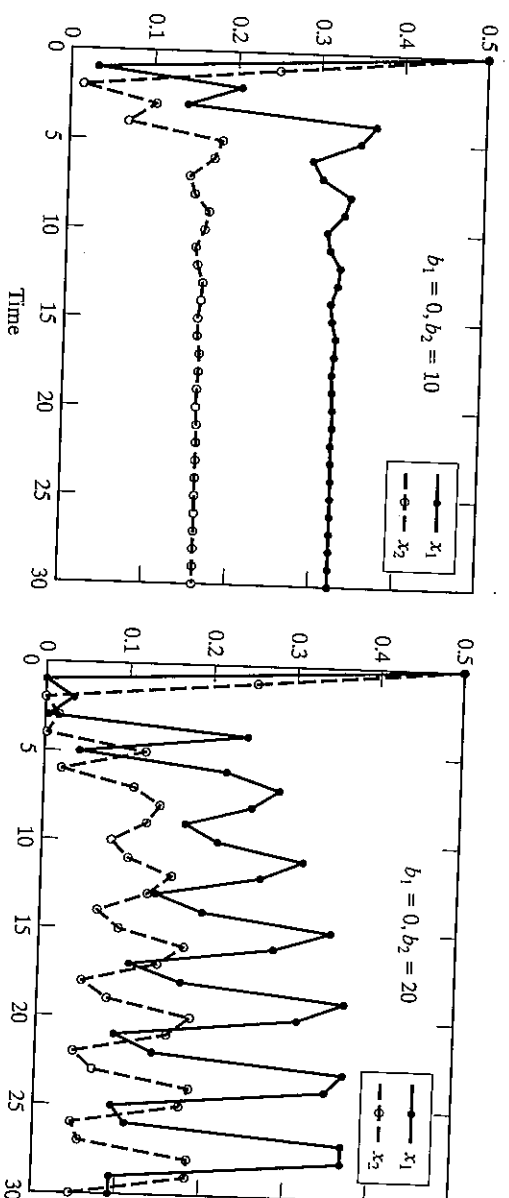
The period-doubling bifurcation near  $\mu_a = 0.1$  is followed by a period-halving bifurcation at  $\mu_a \approx 0.6$ . For very high adult mortality rates (near 100%), we see the complicated, nonperiodic behavior characteristic of the logistic map.

It is one thing to find "chaos" in a mathematical model. A much more significant finding would show that the model is true enough to a real-world system that its chaotic behavior can be reproduced in the laboratory. The experimenters put several hundred beetles and 20 grams of food in each of several half-pint milk bottles. They recorded the populations for 18 consecutive two-week periods. Five different adult mortality rates,  $\mu_a = 0.0036$  (the natural rate), 0.04, 0.27, 0.50, 0.73, and 0.96 were enforced in different bottles, by periodically removing the requisite number of adult beetles to artificially reach that rate. Each of the five experiments was replicated in four separate bottles.

Figure 1.18 shows the population counts taken from the experiment. Populations of adults from the four separate bottles are graphed together in the boxes on the left. The four curves in the box are the adult population counts for the four bottles as a function of time. The boxes on the right are similar but show the population counts for the larvae. During the first 12 weeks, the populations were undisturbed, so that the natural adult mortality rate applied; after that, the artificial mortality rates were imposed by removing or adding adult beetles as needed.

The population counts from the experiment agree remarkably well with the computer simulations from Figure 1.18. The top two sets of boxes represent  $\mu_a = 0.0036$  and 0.04, which appear experimentally to be sinks, or stable equilibria, as predicted by Figure 1.18. The period-two sink predicted also can be seen in the populations for  $\mu_a = 0.27$  and 0.50. For  $\mu_a = 0.96$ , the populations seem to be governed by aperiodic oscillations.





**Figure 3.12** The LMDDR model with two ages,  $g(x) = e^{-x}$  and  $R(t+1) = g(w(t))w(t)$ ,  $a = 1$ . (a)  $b_1 = 0, b_2 = 10$ , and  $s = 0.5$  (b)  $b_1 = 0, b_2 = 20$ , and  $s = 0.5$ .

### 3.8.2 Structured Model for Flour Beetle Populations

The structured model for the flour beetle has received much attention because it is one of the few mathematical models that has not only been investigated theoretically but has been tested against data collected from many laboratory experiments. The population of flour beetles from the species *Tribolium* is modeled. In the structured model, the population is subdivided into three developmental stages, larval, pupal, and adult stages, denoted as  $L$ ,  $P$  and  $A$ , respectively (e.g., Costantino et al., 1997, 1998; Cushing et al., 1998, 2003; Henson and Cushing, 1997; Henson et al., 1998). Deterministic and stochastic formulations of this model have been analyzed mathematically and statistically by Cushing, Dennis, and Henson and experiments have been set up and conducted in the laboratory by Costantino and Desharnais. A nicely written book describing their results is *Chaos in Ecology* (Cushing et al., 2003). You may consult a Web page for a current list of publications by this group of mathematicians, statistician, and biologists: <http://caldera.calstatela.edu/nonlin/1pamodel.html>. The results from the laboratory studies and the model agree very well.

The model is a system of difference equations satisfying

$$\begin{aligned} L_{t+1} &= bA_t \exp(-c_{ea}A_t - c_{el}L_t), \\ P_{t+1} &= L_t(1 - \mu_l), \\ A_{t+1} &= P_t \exp(-c_{pa}A_t) + A_t(1 - \mu_a), \end{aligned}$$

where all of the parameters  $b$ ,  $c_{ea}$ ,  $c_{el}$ ,  $c_{pa}$ ,  $\mu_l$ , and  $\mu_a$  are positive and, in addition,  $\mu_l$  and  $\mu_a$  are less than one. We shall refer to this model as the LPA model. The time unit,  $t$  to  $t+1$ , is two weeks, which is the average amount of time spent in the larval stage and is also the time unit for the duration of the pupal stage. The exponential terms are Ricker type density dependence and represent the effects of cannibalism. In particular, the coefficients  $c_{ea}$ ,  $c_{el}$ , and  $c_{pa}$  are rates of cannibalism of eggs by adults, eggs by larvae, and pupae by adults, respectively (see also Caswell, 2001; Cipra, 1999; Cushing, 1998). The fractions  $\exp(-c_{el}L_t)$  and  $\exp(-c_{ea}A_t)$  are the probabilities that an egg is not eaten in



the presence of  $L$ , larvae and  $A$ , adults in one time unit. The fraction  $\exp(-c_{pa}A_i)$  is the survival probability of a pupa in the presence of  $A_i$  adults in one time unit. The coefficient  $b$  represents the average number of larvae produced per adult, and  $\mu_a$  and  $\mu_l$  denote the mortality fractions of adults and larvae.

In the laboratory experiments, the beetles are kept in a bottle containing 20 grams of flour at a constant incubator temperature and humidity (Cushing, 1998). The flour is sifted every two weeks and the number of larvae, pupae, and adults counted, then returned to a fresh bottle of flour.

We examine a simple case for this model: the conditions for stability of the zero equilibrium or extinction equilibrium. The Jacobian matrix of the LPA model satisfies

$$J = \begin{pmatrix} -bc_{el}Ae^{-c_{ea}A}e^{-c_{el}L} & 0 & be^{-c_{ea}A}e^{-c_{el}L}(1-c_{ea}A) \\ 1-\mu_l & 0 & 0 \\ 0 & e^{-c_{pa}A} & 1-\mu_a-c_{pa}Pe^{-c_{pa}A} \end{pmatrix}.$$

At the extinction equilibrium, the Jacobian matrix has the following form:

$$J(0, 0, 0) = \begin{pmatrix} 0 & 0 & b \\ 1-\mu_l & 0 & 0 \\ 0 & 1 & 1-\mu_a \end{pmatrix}. \quad (3.13)$$

The characteristic polynomial is

$$p(\lambda) = \lambda^3 - (1 - \mu_a)\lambda^2 - b(1 - \mu_l).$$

The local asymptotic stability of the extinction equilibrium can be determined from the Jury conditions:

$$\begin{aligned} p(1) &= \mu_a - b(1 - \mu_l) > 0, \\ p(-1) &= -2 + \mu_a - b(1 - \mu_l) < 0, \\ 1 - b^2(1 - \mu_l)^2 &> b(1 - \mu_l)(1 - \mu_a). \end{aligned}$$

The first condition is satisfied if  $b(1 - \mu_l) < \mu_a$ . The second condition is always satisfied. Finally, the third condition follows from the first condition. That is,

$$b^2(1 - \mu_l)^2 + b(1 - \mu_l)(1 - \mu_a) < \mu_a^2 + \mu_a(1 - \mu_a) = \mu_a < 1.$$

Hence, the extinction equilibrium is locally asymptotically stable if

$$b(1 - \mu_l) < \mu_a. \quad (3.14)$$

In fact, it can be shown that the extinction equilibrium is globally asymptotically stable if condition (3.14) holds. Denote  $X_i = (L_i, P_i, A_i)^T$  and note that  $X_{i+1} \leq JX_i$ , where  $J \equiv J(0, 0, 0)$  is defined in (3.13). Since  $J$  is a nonnegative matrix, it easily follows that  $X_i \leq J^i X_0$ . The magnitude of the eigenvalues of  $J$  are less than one iff inequality (3.14) holds. Thus, if (3.14) holds, then  $\lim_{i \rightarrow \infty} X_i = (0, 0, 0)^T$ .

Condition (3.14) can be interpreted biologically. Extinction is possible if, in the absence of cannibalism, the number of new larvae that survive to the pupal stage during the two-week interval is less than the fraction of adults who die during that same period. When  $b(1 - \mu_l) = \mu_a$  there is a change in behavior; a transcritical bifurcation occurs (see Exercise 14).

It is interesting to note that a positive equilibrium  $(\bar{L}, \bar{P}, \bar{A})$  requires

$$1 = b \frac{(1 - \mu_l)}{\mu_a} \exp(-c_{ea} \bar{A} - c_{ea} \bar{L} - c_{pa} \bar{A}).$$

At a positive equilibrium, the exponential term is less than one. Hence, if  $b(1 - \mu_l) \leq \mu_a$ , then there cannot exist a positive equilibrium. Existence of a positive equilibrium requires that  $b(1 - \mu_l) > \mu_a$ . When this condition holds, the LPA model exhibits a wide array of behaviors as different parameters are varied—from periodic behavior to chaos. Please consult the references for more information about this interesting model and the experiments that have been conducted to test this model.

### 3.8.3 Structured Model for the Northern Spotted Owl

The northern spotted owl, *Strix occidentalis caurina*, is located in the Pacific Northwest of the United States and Canada. It is a monogamous, territorial bird requiring large tracts of mature, coniferous trees for its survival (Lande, 1988). Due to logging of old-growth forests in the Northwest, researchers have predicted extinction of the spotted owl if suitable habitat is not maintained (Lamberson et al., 1992; Lande, 1988). The species was given threatened status in 1990 (McKelvey et al., 1992). A number of models have been developed for the spotted owl, including a simple Leslie matrix model (Lamberson et al., 1992) and a spatially explicit, stage-structured, stochastic metapopulation model (Akçakaya and Raphael, 1998). We discuss a model first reported by Thomas et al. (1990) and later analyzed by Lamberson et al. (1992). This particular model is a density-dependent, structured model; it is also discussed by Caswell (2001), Cushing (1998), and Haefner (1996). The discussion follows that of Allen et al. (2005).

Suppose the landscape is fixed; only a fraction of the landscape is suitable for spotted owl occupation. The suitable area is made up of sites,  $T$  = total number of sites and  $U$  = number of available sites,  $U < T$ . Single females find a single male to become paired with or are eliminated from the population. Juvenile birds that survive disperse at the end of their first year; males seek an unoccupied site and females seek a site occupied by a solitary male. Let  $P_t$  be the number of paired owls in year  $t$ ,  $S_{m,t}$  be the number of single males, and  $S_{f,t}$  be the number of single females. The sex ratio between males and females is one, so that  $S_{m,t} = S_{f,t}$ . The number of occupied sites equals the number of paired owls plus the number of male owls,  $O_t = P_t + S_{m,t}$ . The number of available and unoccupied sites is  $A_t = U - O_t$ . To ensure that available sites remain nonnegative, we modify the definition of occupied sites,  $O_t = \min\{U, P_t + S_{m,t}\}$ .

We model the number of paired owls  $P_t$  and number of single male owls  $S_{m,t}$ . The model takes the following form:

$$P_{t+1} = P_t P_s + S_{m,t} S_f M_t = F(P_t, S_{m,t}), \quad (3.15)$$

$$S_{m,t+1} = \frac{1}{2} f s_f D_t P_t + S_{m,t} s_s (1 - M_t) + p_b P_t = G(P_t, S_{m,t}). \quad (3.16)$$

The model parameters are defined as follows:

- $D_t$  = probability of juveniles surviving dispersal,
- $M_t$  = probability of female finding a male,
- $s_s$  = fraction of single owls surviving one year,