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Density-dependent growth and intraspecific competition

- Density dependence in populations with discrete generations
- Density dependence in populations with overlapping generations
- Nonlinear density dependence of birth and death rates and the Allee effect
- Time lags and limit cycles
- Chaos and behavior of the discrete logistic model
- Adding stochasticity to density-dependent models
- Laboratory and field data
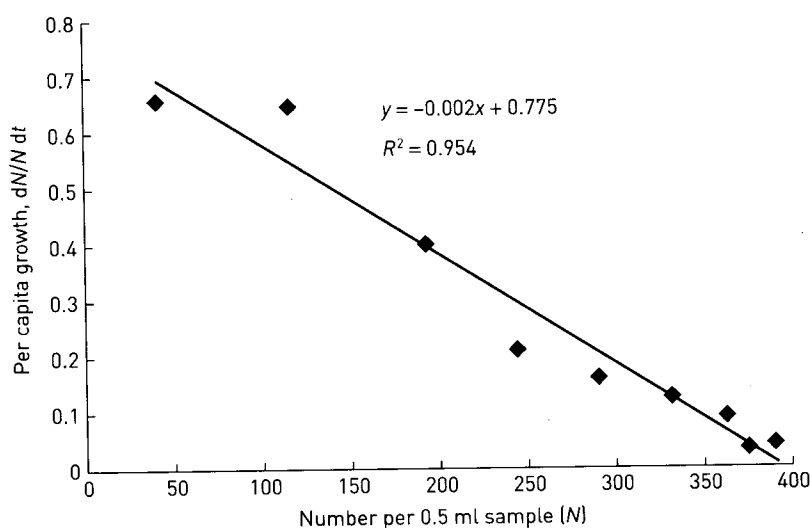- Behavioral aspects of intraspecific competition

2.1 Introduction

One of the great philosophical divides between ecologists and many economists is the application of the ecological principle of self-limitation to human populations. The late University of Maryland economist Julian Simon, long the bête noir of the environmental movement, was no believer in the ecological notion of a **carrying capacity** for humans. In his book *The Ultimate Resource*, Simon (1996) proposed that human ingenuity and technology would always triumph over any limiting resource. He had public disputes with ecologists such as Norman Myers and Paul Ehrlich. Simon famously won a series of ongoing bets with Ehrlich on whether certain raw materials would run out by specific dates. Now, as human population growth has ceased or gone negative in many European countries (Anonymous 1981–2004), publications decrying the coming "population crash" and its ramifications have materialized in the popular media. Basically, ecologists see self-limitation of all biological populations as inevitable, while most economists, especially those in the United States, see economic growth as both certain and beneficial.

The concept of a carrying capacity for biological populations is connected with the logistic equation, found in all ecology text books, and also introduced formally as Equation 2.8 later:

$$dN/dt = rN\left(\frac{K - N}{K}\right).$$

Figure 2.1 Population growth in a *Paramecium* population.

The logistic was originally formulated by the French mathematician Verhulst in pre-Darwinian times (1838), but was not applied routinely to biological populations until Pearl and Reed (1920) rediscovered it. Pearl (1927) then promoted the application of the logistic to a variety of biological populations. See Kingsland (1995) for an interesting review of this history.

Yet Turchin (2003) and many other population biologists now assert that, though the logistic is useful as a general framework, this equation is fundamentally flawed when applied to biological populations. The logistic model is not a general law of population growth, but is rather a special case. If an ecologist wants to win the argument with an economist about human (or any) population limitation he/she needs to understand the assumptions and flaws of logistic or logistic-like models. The goals of this chapter are: first, to describe density-dependent growth models for both discrete and continuously breeding populations; second, to examine the assumptions of these models; third, to investigate how violations of these assumptions shape the behavior of populations.

In the first chapter we assumed **density-independent growth**: that is, population growth unlimited by competition for resources. Most biological populations, however, do not long sustain such growth. Even in an isolated laboratory population, growing without competing species or predators, realized growth slows and ceases. Examine the *Paramecium* population history presented as Table 1.6 and plotted in Figure 2.1. Population growth slows after day 2 and almost ceases by day 7. Our experience in the laboratory is that a *Paramecium caudatum* population will stop growing at about 400 per 0.5 ml sample. Based on data such as this, one of the basic assumptions of most ecological models is that populations do not have unlimited resources, and that eventually the population encounters a limiting resource (or perhaps a parasite or predator) which restricts population growth. This is by no means a new idea. In 1840 Liebig, in his law of the minimum, asserted that under steady-state conditions the population size of a species is constrained by whatever resource is in shortest supply. According to the **logistic model**, population growth ceases when the population reaches the **carrying capacity** of the

Figure 2.2 Per capita growth in a *Paramecium* population.

The graph shows the equation $y = -0.002x + 0.775$ and $R^2 = 0.954$. The y-axis is labeled "Per capita growth, $dN/N\,dt$" and the x-axis is labeled "Number per 0.5 ml sample (N)".

environment for that population. This is a **density-dependent growth** model in which the carrying capacity is identified by the symbol K. For a given species, in a specific environment, carrying capacity is defined as the number of individuals that can be maintained indefinitely.

One way to visualize density-dependent growth is to graph the per capita growth rate versus population size. Figure 2.2 plots the growth rate per individual in the *Paramecium* population versus population size. From Table 1.6, per capita growth is found by dividing the growth between time intervals t and $t + 1$ by the population size at time $t + 1$. Notice that even though the population is growing through day 6, the trend per individual is steadily downward in a more or less linear fashion. Where this line intersects the x-axis, per capita growth has fallen to zero. The value of this point (N, 0) is an estimate of the carrying capacity, K. Note that the linear regression on these data indicates that K should equal around 390, which is in agreement with Fig. 2.1. The R^2 value means that the model has explained 95% of the variance in the data.

Since the logistic model is really based on competitive interactions, we should define **competition** before proceeding further. A formal definition of competition is: **a biological interaction between two or more individuals for a resource in short supply.** When the interaction is between individuals of the same species it is termed **intraspecific** competition; when between individuals of different species it is known as **interspecific** competition. A **resource** is any substance or factor in the environment that determines growth, survivorship, or reproduction of individuals in the population. Therefore, depletion of this resource decreases growth, survivorship, or reproduction. For competition to be meaningful, the resource must be in short supply now, or in the immediate future. Plants may compete for space, light, water, or nutrients, while animals often compete for food, nesting sites, hiding places, or mates. Certain aspects of the environment, such as temperature, are not resources per se, and cannot be competed for. On the other hand, if a lizard needs to raise its body temperature it will seek out a rock on which to bask in the sun. If there are limited numbers of basking sites, they become resources in short supply, and may be competed for.

Paradoxically, perhaps, the ultimate effect of competition is a decrease in fitness. Thus competition is said to be a **reciprocally negative interaction**. All individuals that engage in competition may lose energy and/or time that they could have invested in their own growth, survivorship, or reproduction. When sports teams or animals engage in competition, we identify a winner and a loser (throwing out the occasional tie). Male elk (*Cervus elaphus*) and bighorn sheep (*Ovis canadensis*) engage in some amazing combats. The winner mates with the female(s) and his fitness is increased, **relative to the losing male**. But, if that male had been able to mate with the females without combat, his long-term fitness would be greater still, since he would have conserved the energetic costs (and risks of injury) associated with combat. This theoretical point, however, ignores situations where competitive interactions between males are necessary for stimulation of reproductive activities.

Competition also differs in its manifestations. We recognize here two basic forms of competition: interference and depletion. The term **interference competition** seems to have originated with Park (1962). A similar concept is **encounter interference** (Schoener 1983). In interference competition access to the resource is blocked by behavioral or chemical means. Interference competition applies to territoriality, guarding behaviors, and, by this definition, allelopathy. In allelopathy, plants secrete chemicals that accumulate in the environment and prevent other plants from germinating or growing within this area. A similar phenomenon is the secretion of antibiotics by fungi that prevent growth of bacteria within a certain radius of the colony. In ants, when a high-quality bait such as a chunk of tuna is placed on the forest floor, one species often recruits soldiers to form a ring around the tuna. If they deny access to all workers and soldiers except those from their own colony, they are engaging in interference competition.

Depletion competition involves the simple removal of the resource without active interference. This is the same idea as **exploitation** competition (Park 1962) and **consumption** competition (Schoener 1983). All of these terms refer to situations in which plants or animals consume resources to the detriment of competitors, but without directly interfering with access to the resources. This is a sort of "first come, first served" type of competition. Sutherland (1996) compares depletion competition to "drinking the pub dry." We will avoid here the terms "scramble" and "contest" competition (Nicholson 1954), neither of which is biologically realistic.

Intraspecific competition manifests itself through density-dependent modifications in (i) birth and death rates, (ii) growth rates, and (iii) adult size, especially in organisms with determinant life cycles. That is, the eventual size of an adult beetle, for example, is largely determined by the feeding rates and sizes of the larval stages (within genetic constraints). Finally, intraspecific competition is reflected in complex behavior patterns such as male–female interactions. These latter topics will be explored near the end of this chapter.

In the following sections (2.2 and 2.3) we will do a simple derivation of equations that describe density-dependent growth for populations with discrete and with continuous growth. We will analyze how these equations work and what they might tell us about how populations behave in nature.

2.2 Density dependence in populations with discrete generations

As we saw in Figs 2.1 and 2.2, in a density-dependent population we expect growth to slow and eventually stop as a population increases, and reaches the carrying capacity. For populations with discrete generations, we can begin with Equation 1.4: $N_t = N_0 R^t$.
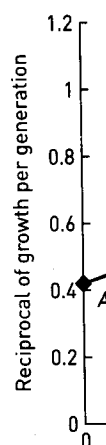
Figure 2.3 Reciprocal of growth per generation versus population density.

To incorporate intraspecific competition into a model, we simply modify the growth-rate factor, R. One approach is to graph the reciprocal of increase per generation, N_t/N_{t+1} versus N_t (Fig. 2.3). If a population is very small (virtually zero), the population is assumed to grow at the maximal rate, R. Rearranging Equation 1.3, we have $N_t/N_{t+1} = 1/R$. Point A is therefore $(0, 1/R)$. The carrying capacity, K, occurs when $N_t/N_{t+1} = 1.0$: that is, when there is no population change from one generation to the next. Point B, then, is $(K, 1)$. If we assume that population growth per generation follows a straight line between points A and B, we have the y-intercept at $1/R$ and the slope is therefore:

$$\frac{1 - (1/R)}{K - 0} = \frac{1 - (1/R)}{K}$$

The general linear equation $y = a + mx$ becomes:

$$N_t/N_{t+1} = 1/R + \left(\frac{1 - (1/R)}{K}\right)N_t$$

Rearranging and providing the common denominator RK,

$$N_t/N_{t+1} = \frac{(K) + \left(1 - \dfrac{1}{R}\right)(N_t R)}{RK} = \frac{(R - 1)(N_t) + K}{RK}$$

Therefore: $\quad N_t = N_{t+1}\dfrac{(R - 1)(N_t) + K}{RK}$

And, $\quad N_{t+1} = (N_t)\dfrac{RK}{(N_t)(R - 1) + K}$

If we divide the numerator and the denominator of the right side of the equation by K, we get:

$$N_{t+1} = (N_t)\frac{(RK/K)}{[(N_t)(R-1)/K] + (K/K)}$$

Finally:

$$N_{t+1} = \frac{N_t R}{1 + \frac{(N_t)(R-1)}{K}} \tag{2.1}$$

Equation 2.1 is known as the **Beverton–Holt** (1957) model, well known among fishery scientists, and is very similar in behavior to the traditional logistic equation (Gurney and Nisbet 1998).

By convention, and to simplify Equation 2.1, we let $a' = (R-1)/K$. Equation 2.1 becomes:

$$N_{t+1} = \frac{N_t R}{1 + a' N_t} \tag{2.2a}$$

A good way to see how this equation encompasses density dependence is to distinguish R_I, the density-independent growth parameter, from R_A, the density-dependent or "actual" growth parameter. In this case, Equation 2.2a becomes:

$$N_{t+1} = N_t R_A \tag{2.2b}$$

$$R_A = R_I(1 + a'N_t)^{-1} = \frac{R_I}{1 + a'N_t} = \frac{R_I}{1 + N_t\left(\frac{R_I - 1}{K}\right)} = \frac{R_I}{1 + \left(\frac{N_t R_I - N_t}{K}\right)} \tag{2.3a}$$

$$R_A = R_I\left[1 + \left(\frac{N_t R_I - N_t}{K}\right)\right]^{-1} \tag{2.3b}$$

Equation 2.3b tells us that the maximal or density-independent growth rate, R_I, is modified by the population size at time t relative to the carrying capacity, K. For example, if N is very small, the actual growth rate, R_A, is virtually equal to R_I.

If $N = K$, however, and if we replace N_t by K, the expression inside the bracket collapses to R_I. Therefore, $R_A = R_I \times R_I^{-1} = 1.0$. This means that $N_{t+1} = N_t(1.0) = N_t$. So if $N = K$ there is no growth in the population and $N_{t+1} = N_t$.

In Table 2.1 notice how Equation 2.3b modifies the R_A and the actual population size with time. The population size after 13 generations for the density-dependent population is about half that of the density-independent population, and the actual R steadily drops toward the no-growth value of 1.00.

We must remember, however, that equation 2.3b is based on the two points, $(0, 1/R)$ and $(K, 1)$, from Fig. 2.3. Furthermore, we assumed a straight line would connect these two points. This, in turn, is based on the assumption of **exact density dependence** or "exactly compensating" density dependence (Silvertown and Doust 1993). This assumption appears unrealistic. Hassell (1975) therefore proposed that we could relax this assumption of exact or linear density dependence by simply modifying equation 2.3b

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Table 2.1 Density-independent growth compared to density-dependent growth using Equation 2.3b. $N_0 = 100$, $R_1 = 1.2$, $K = 1000$ in all cases.

Time, t	Density-independent net reproductive rate, R_1	Density-dependent net reproductive rate, R_A	N_t in the case of density-independent growth	N_t in the case of density-dependent growth
0	1.20	1.20	100	100
1	1.20	1.17	120	118
2	1.20	1.17	144	138
3	1.20	1.16	173	161
4	1.20	1.16	207	187
5	1.20	1.15	249	217
6	1.20	1.14	299	249
7	1.20	1.14	358	285
8	1.20	1.13	430	323
9	1.20	1.12	516	364
10	1.20	1.11	619	408
11	1.20	1.10	743	452
12	1.20	1.09	892	498
13	1.20	1.08	1070	543
14	1.20	1.07	1284	588

and replacing -1 with the exponent: $-b^*$ (Eqn. 2.4). Exact compensation (linear density dependence) occurs when $b^* = 1$, producing a slope of -1, but **overcompensation** ($b^* > 1$, implying a slope < -1) is the result when plant yield, for example, drops more rapidly than expected with increases in density.

$$R_A = R_1 \left[1 + \left(\frac{N_t R_1 - N_t}{K} \right) \right]^{-b^*} \tag{2.4}$$

Undercompensation occurs when $b^* < 1$, and means that population size drops more slowly than expected (as compared to exact compensation) as density rises. From Fig. 2.4 you can see that while the actual value of R declines in the density-dependent model, it declines fastest when $b^* > 1$ (that is, **overcompensation**), and declines more slowly when $b^* < 1$ (**undercompensation**). The thick line in Fig. 2.4 is a linear regression showing how R is reduced along a linear path when $b^* = 1$.

Figure 2.5 illustrates the time path of population growth under the conditions specified in Fig. 2.4. Population growth is obviously most rapid with density-independent growth and is slowest with density-dependent growth and overcompensation ($b^* = 1.6$).

The preceding model can be applied directly to the **law of the constant final yield**, well known from botanical and agricultural research. The law essentially states that agricultural yield per area will increase with plant density up to the maximum or "final" yield. Thereafter, increasing the number of plants per area simply reduces the average size per plant (or animal) without increasing total yield (Fig. 2.6). In simple terms we can write:
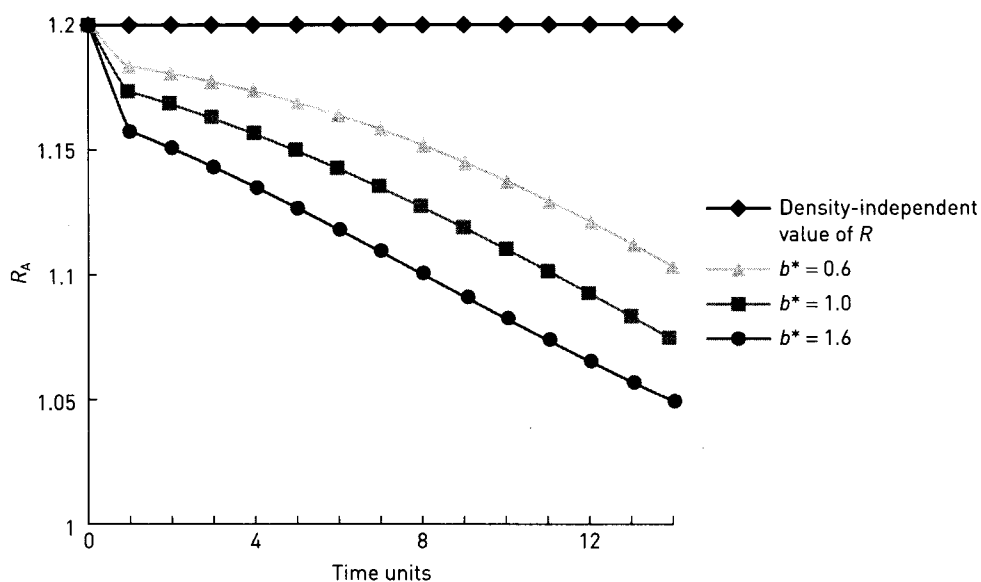
Figure 2.4 Effect of density on the actual rate of increase, R_A.
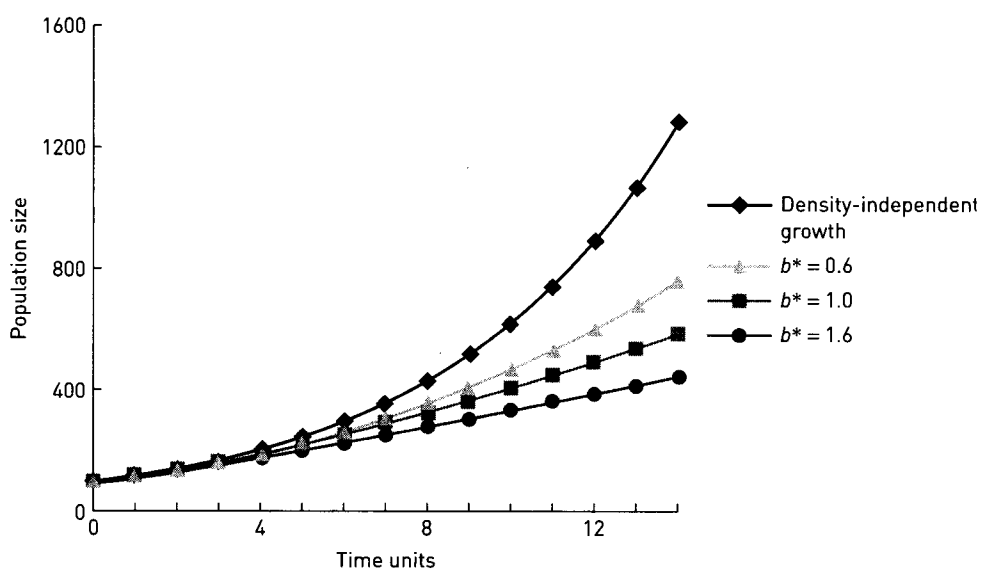
Figure 2.5 Density-independent and density-dependent growth with various values of b^*.

$$C = N\bar{w} \qquad (2.5)$$

where
C = the final constant yield in kilograms per area,
N = the density of plants, that is, the number per unit area, and
$\bar{w}$ = mean mass per plant in kilograms.

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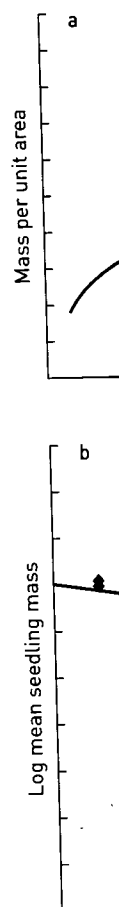
Figure 2.6 The law of the constant final yield for plants and sessile animals.
(a) Yield (mass) per unit area increases with density until it reaches a threshold,
after which there is no increase in total yield. (b) As density increases, mass per
individual decreases linearly on a log–log scale.

This equation, however, only provides information about the end point of a dynamic
process. Just as $R_A = R_I(1 + a'N_t)^{-1}$ in Equation 2.3a, the actual mean mass per plant,
$\bar{w}$, can be expressed as a function of its maximum potential mass when grown under
density-independent conditions.

$$\bar{w} = w_m(1 + a'N)^{-b*} \tag{2.6}$$

where
w_m = maximum potential mass per plant
a' = a carrying capacity parameter.

In this case, a' is often interpreted as the amount of area needed for each individual plant
to achieve its maximum growth potential, and $b*$ provides a mechanism for different

reaction rates to density. As before, when $b^* = 1$, there is exact density-dependent compensation and the law of the final constant yield is obeyed in a linear fashion. Combining Equations 2.5 and 2.6, we have an equation that describes the effects of density-dependent growth on yield under a variety of conditions. Plant populations may vary between plots, and different plant parts (grain yield or above ground biomass, for example) may respond differently to changes in density. Equation 2.7 produces different-shaped curves as the value of b^* is varied.

$$C = Nw_m(1 + a'N)^{-b^*} \tag{2.7}$$

The shapes of the curves would be similar to those of Figure 2.5, except that the y-axis would be output in mass rather than population density. Part of the dynamic process leading to the law of the constant yield involves an increase in mortality (self-thinning) over time as populations increase in density. As a new population is established in a suitable habitat, self-thinning follows several steps. (i) As individuals grow, they increase in size (mass). (ii) When a critical density is reached, known as the thinning limit, density-dependent mortality begins; this step occurs earlier in populations with higher initial density. (iii) Eventually the population reaches a stage where any increase in the mass of some individuals is offset by mortality of other members of the population. Total mass no longer increases and the final constant yield in mass per unit area has been reached (Figure 2.6). The point of final yield is reached more quickly in populations with higher initial densities.

Although the increase in mortality with population density is usually assumed to be linear in models such as the logistic (see below), we can introduce nonlinear responses, as shown in Equations 2.4, 2.6, and 2.7 above, and in Equations 2.11 and 2.13 below.

2.3 Density dependence in populations with overlapping generations

The logistic equation

The more familiar treatment of density dependence is to examine growth curves such as Figure 2.1, and apply a modification of the differential equation: $dN/dt = rN$. The resultant equation, known as the logistic, can be derived as follows. Examine Fig. 2.2 once more. The y-axis is per capita growth rate $(dN/dt)(1/N)$. Since the per capita growth rate $= r$ when N is very small, we can identify a point A as the y-intercept $(0, r)$. When $N = K$, according to theory, per capita population growth stops. Therefore point B, along the x-axis, would be the point $(K, 0)$. As in the previous example, if we assume that populations respond in a linear manner to population density, we use these two points to describe a straight line. The slope of this line is:

$$(0 - r)/(K - 0) = -r/K$$

The y-intercept is r and we have:

$$(dN/dt)(1/N) = (-r/K)N + r$$

Rearranging, we now have:

$$dN/dt(1/N) = r\left(1 - \frac{N}{K}\right) = r\left(\frac{K - N}{K}\right)$$

Multiplying both sides of the equation by N reveals the usual form of the logistic.

$$dN/dt = rN\left(\frac{K - N}{K}\right) \tag{2.8}$$

Although the logistic is in the form of a differential equation, it is fairly easy to understand how it affects population growth. Again, it is useful to examine what the equation does to the growth rate, r. As above, we will distinguish between r_a, the actual growth rate as modified by carrying capacity, and r_m, the density-independent growth rate. r_m has also been called r-max or the Malthusian parameter. r-max represents the maximal growth rate of a genotype as it interacts with the environment without competition.

$$r_a = r_m\left(\frac{K - N}{K}\right) \tag{2.9}$$

When the population is very small, $N \approx 0$, and $\left(\frac{K - N}{K}\right) \approx 1$. Therefore, $r_a \approx r_m$.

When $N = 0.5K$, then the expression $\left(\frac{K - N}{K}\right) = 0.5$, and $r_a = (0.5)r_m$.

When $N = K$, the expression $\left(\frac{K - N}{K}\right) = 0$ and $r_a = 0$.

Finally, when $N > K$, the expression $\left(\frac{K - N}{K}\right) < 0$. Therefore r_a is negative and the population drops back toward K.

The differential form of the logistic equation can be integrated and solved, resulting in the following:

$$N_t = \frac{K}{1 + e^{a-rt}} \tag{2.10a}$$

where a is a constant of integration.

Dividing both sides of the equation by K yields:

$$\frac{N_t}{K} = \frac{1}{1 + e^{a-rt}}$$

Taking the inverse:

$$\frac{K}{N_t} = 1 + e^{a-rt}$$
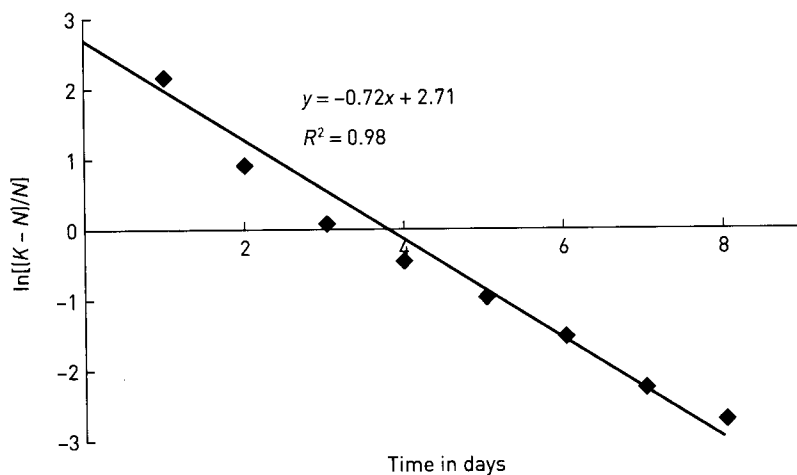
Figure 2.7 Estimate of actual r for a *Paramecium* population using the logistic equation.

Manipulating, we get:

$$\frac{K - N_t}{N_t} = e^{a-rt}$$

Finally, taking the natural log of both sides gives us:

$$\ln\left(\frac{K - N_t}{N_t}\right) = a - rt \qquad (2.10b)$$

This expression is useful because it becomes the equation for a straight line with $a =$ y-intercept and the slope equal to $-r$ (see Fig. 2.7). When $t = 0$ the y-intercept, a, becomes:

$$a = \ln\left(\frac{K - N_0}{N_0}\right)$$

This gives us another form of Equation 2.10a, in which a, the constant of integration, is replaced by the y-intercept:

$$N_t = \frac{K}{1 + \left[\left(\frac{K - N_0}{N_0}\right)(e^{-rt})\right]} \qquad (2.10c)$$

Furthermore, if we graph $\ln\left(\dfrac{K - N_t}{N_t}\right)$ versus t (Fig. 2.7), the absolute value of the slope of the line approximates r. This allows us to estimate the actual value of r over a specified time period. For example, if we use the example, once again, of the *Paramecium*

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Table 2.2 Estimating r_a, (r actual) from the solved form of the logistic equation. Data are for the *Paramecium* population in Table 1.6. K is approximated at 400. See Figure 2.7.

Time in days	Number per 0.5 ml sample, N	$\ln\left[\dfrac{K - N_t}{N_t}\right]$
0	14	3.32
1	41	2.17
2	116	0.90
3	193	0.07
4	244	−0.45
5	290	−0.97
6	331	−1.57
7	363	−2.28
8	375	−2.71

population in Table 1.3 and Figure 2.1, we can determine its actual growth rate, r_a, over the eight days of the experiment. We simply add a column for the expression $\ln\left(\dfrac{K - N_t}{N_t}\right)$ (Table 2.2). To do this, however, we must have an approximation for the carrying capacity, K. In Table 2.2, K is estimated as 400.

In Fig. 2.7 a linear regression identifies the slope as −0.73 (R^2 is the proportion of the variance explained by the linear model). The actual r is therefore 0.73, as compared to the r_{max} of 0.89 calculated in Chapter 1.

In understanding how the logistic affects population growth, it is instructive to examine population growth, dN/dt, as a function of population size. Since $dN/dt = rN\left(\dfrac{K - N}{K}\right)$, it also equals $rN\left(1 - \dfrac{N}{K}\right)$, which equals $rN - (rN^2)\left(\dfrac{1}{K}\right)$. If we set dN/dt equal to zero, there are three solutions to this equation: $r = 0$, $N = 0$, or $N = K$. If we assume that $r > 0$ we are left with two solutions ($N = 0$ and $N = K$). That is, $dN/dt = 0$ when $N = 0$ and when $N = K$. The result of plotting dN/dt versus N results in a parabola (Fig. 2.8). Maximum growth (dN/dt) occurs where $N = K/2$, which is 500 in this case, since we have set $K = 1000$. The problem with this solution is that, since maximum growth theoretically occurs at half carrying capacity, harvesting of wild living resources was managed with that number as a goal. This has led to the decimation of many populations since stochastic and density-independent mortality were not accounted for.

Assumptions of the logistic equation

How much trust can we put in either the traditional logistic equation or the Beverton–Holt equations? Is the typical logistic growth curve actually found in biological populations? Laboratory studies on growth of protozoan populations such as *Paramecium caudatum*, yeast, *Drosophila*, grain beetles and diatoms (Gause 1932, 1934, Vandermeer 1969, Pearl 1927, Crombie 1945, Park *et al.* 1964, Tilman 1977), do consistently show a logistic growth

Figure 2.8 Population growth as a function of N based on the logistic equation.

curve. A number of field populations have also followed logistic growth fairly closely. Examples include Tasmanian sheep (*Ovis aries*) (Davidson 1938), wildebeest (*Connochaetes taurinus*) (Deshmukh 1986), willows (*Salix cinerea*) (Alliende and Harper 1989) and barnacles (*Balanus balanoides* and *Chthamalus stellatus*) (Connell 1961a, 1961b). However, there are many more cases where populations grow cyclically or unpredictably and generally do not display logistic growth. An examination of the assumptions of the logistic equation explains why many populations display non-logistic growth patterns.

Assumptions of the logistic equation:

1 The carrying capacity is a constant;
2 population growth is not affected by the age distribution;
3 birth and death rates change linearly with population size (it is assumed that birth rates and survivorship rates both decrease with density, and that these changes follow a linear trajectory);
4 the interaction between the population and the carrying capacity of the environment is instantaneous: that is, the population is "sensitive" to the carrying capacity with no time lags;
5 abiotic, density-independent factors do not affect birth and death rates (no environmental stochasticity);
6 crowding affects all members of the population equally.

Considering all of the above, it is not surprising that populations in the field do not often stay at a given density for long periods of time. In the laboratory, when we grow a *Paramecium* population, its growth curve often fits the logistic since: (1) it is maintained in a constant environment, which should have a constant carrying capacity; (2) it reproduces via binary fission and has no age structure; (3)–(6) are seemingly irrelevant or satisfied. Once we step into the field and work with insects, vertebrates, or plants, several of these assumptions are violated.

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2.4 Nonlinear density
the Allee effect

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Figure 2.9 Linear
rate; *d*, death rate

Because these assumptions cannot be met, a natural population is unlikely to long remain "at equilibrium" with the environment. In the next two sections we will examine assumptions 3 and 4 in some detail, since their effects on population growth are less obvious and more interesting than might be expected.

2.4 Nonlinear density dependence of birth and death rates and the Allee effect

As mentioned above, density-dependent birth and death rates are assumed to vary linearly with density (Fig. 2.9). Although it is known from both laboratory (Smith and Cooper 1982) and field studies (Arcese and Smith 1988) that birth and death rates are often nonlinear (Fig. 2.10), such differences seem to have a minimal impact on natural populations. One major exception, however, is known as the Allee effect (Allee 1931). Allee proposed that many species have a **minimum viable population** (MVP) size. As described in Chapter 1, although Allee may have had a specific number in mind, below which death rates rise and/or birth rates collapse, a more modern view is that the probability of extinction has become unacceptably high when a population becomes small (Shaffer 1981, Miller and Lacy 2003), but there is no one specific number described as a MVP.

Why should there be higher death rates in very small populations? Proposals include: (i) group cooperation reduces losses from predators; (ii) group foraging for food is more efficient (foraging facilitation); and (iii) small populations are more subject to density-independent or stochastic extinctions as well as genetic effects such as inbreeding depression. Low birth rates in small populations could result from pollination failure in plants, male and female animals unable to locate each other, or the chance of a very unequal sex ratio (large number of males, few females).
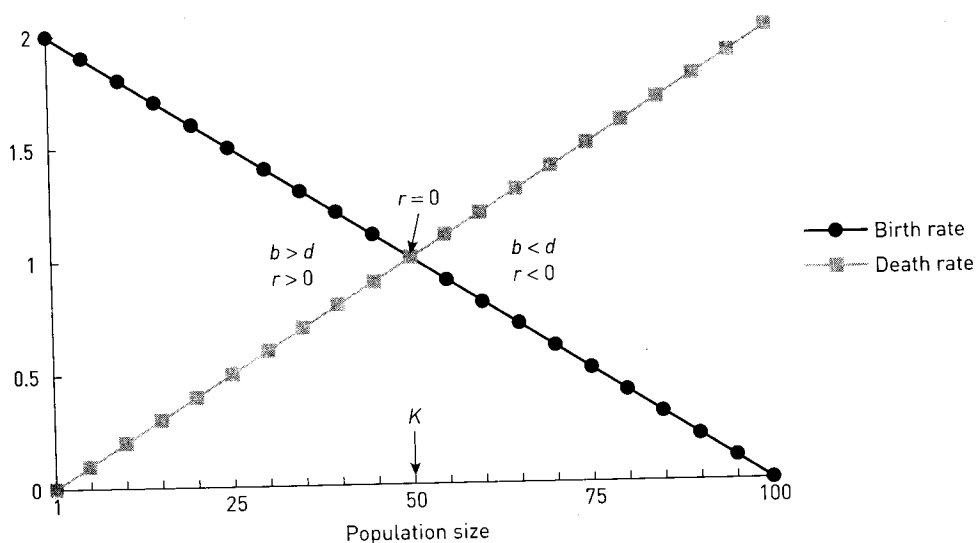
Figure 2.9 Linear response of birth and death rates to population density. *b*, birth rate; *d*, death rate; *r*, intrinsic rate of increase; *K*, carrying capacity.
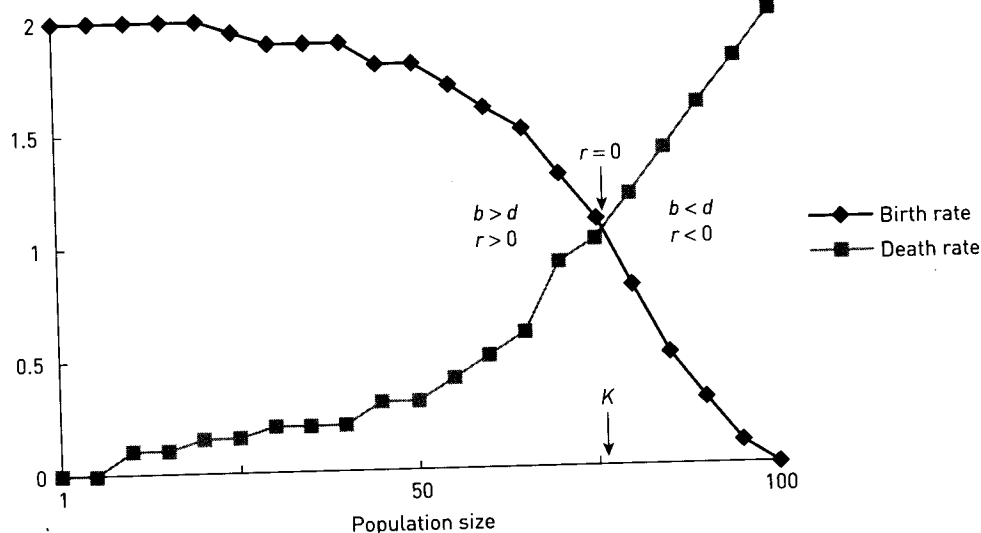
Figure 2.10 Nonlinear response of birth and death rates to population density.

For example, the common guillemot or murre (*Uria aalge*) nests in colonies. Breeding success in south Wales was found to be only 25% in the least dense populations as compared to an average of 75% in the densest populations (Birkhead 1977). The reason for this appears to be that predation on eggs and chicks by gulls is reduced in dense guillemot populations. A similar result was obtained in a study on lapwings (*Vanellus vanellus*) in which egg clutches lost to avian predators declined with an increase in the number of close neighbors (Berg *et al.* 1992). Nest parasitism also appears to increase in low populations. For example, small dickcissel (*Spiza americana*) populations are particularly hard hit by brown-headed cowbirds (*Molothrus ater*) (Fretwell 1986).

Other studies have found that cooperative hunters such as lions, hyenas, wolves and various fish species have much higher success rates when hunting in large groups and do poorly when population sizes fall (Caraco and Wolf 1975, Major 1978). This translates into a higher mortality rate in the smaller groups. From the perspective of the prey, a dense population is harder to surprise, and mortality from predation is lower in larger prey populations (Kenward 1978, Jarman and Wright 1993). Colonial nesting sunfishes have even been found to suffer lower rates of fungal infections on their eggs as compared to solitary sunfish (Cote and Gross 1993). Therefore higher density leads to higher, not lower, survivorship.

Although this is an oversimplification, we can illustrate the Allee effects graphically by identifying a minimum viable population size, **MVP** (Fig. 2.11). Below point MVP, the population declines to extinction. Above point MVP the population increases rapidly before slowing down as it approaches K. The value of r is positive above MVP and below K, but is otherwise negative (Figure 2.11).

The extinction of the heath hen (*Tympanuchus cupido*) is a likely example of the Allee effect. By 1870, hunting and habitat loss had restricted it to Martha's Vineyard off the coast of Massachusetts. In 1908 a 650 ha refuge was established and the population grew to about 2000 birds. In 1916, however, a fire swept across the island, destroying nests, eggs, and females on the nests. The following winter was severe and an unusually heavy concentration

Figure 2.11 Birth and death rate versus population density, showing the Allee effect. MVP, minimum viable population.

of goshawks (*Accipiter gentilis*) arrived. The population was reduced to less than 150, of which most were probably males. By 1928 the population had declined to a single male that died in 1932. In this case, abiotic effects contributed significantly to the extinction of the heath hen. Although we can never be sure, it appears likely that something of a similar nature happened to the passenger pigeon (*Ectopistes migratoris*) described in the introduction to Part I. They were mercilessly hunted and no one imagined the possibility of extinction. But once their flocks were drastically reduced, they appeared unable to recover (Souder 2004).

Nonlinear modifications to the logistic

In order to evaluate the potential for a nonlinear feedback on the logistic population response, we can modify Equation 2.10c by adding the term b^*, as we did in Equation 2.4 and Figs 2.4 and 2.5. Recall that a value for b^* of 1.0 describes "exact compensation" and depends upon the linear response by the population to a carrying capacity. A $b^* > 1$ illustrates overcompensation and a $b^* < 1$ describes undercompensation. We can modify Equation 2.10c by adding a b^*-value:

$$N_t = \frac{K}{1 + \left[\left(\dfrac{K - N_0}{N_0}\right)(e^{-rt/b^*})\right]} \tag{2.11}$$

Figure 2.12 illustrates the effect of a nonlinear feedback on logistic growth. The population with the b^*-value of 0.6 grows the most rapidly, whereas the population with the b^*-value of 1.6 grows the most slowly. As in Fig. 2.4, when $b^* > 1$, small increases in density result in a rapid drop in the actual value of the growth rate, r, as a result of
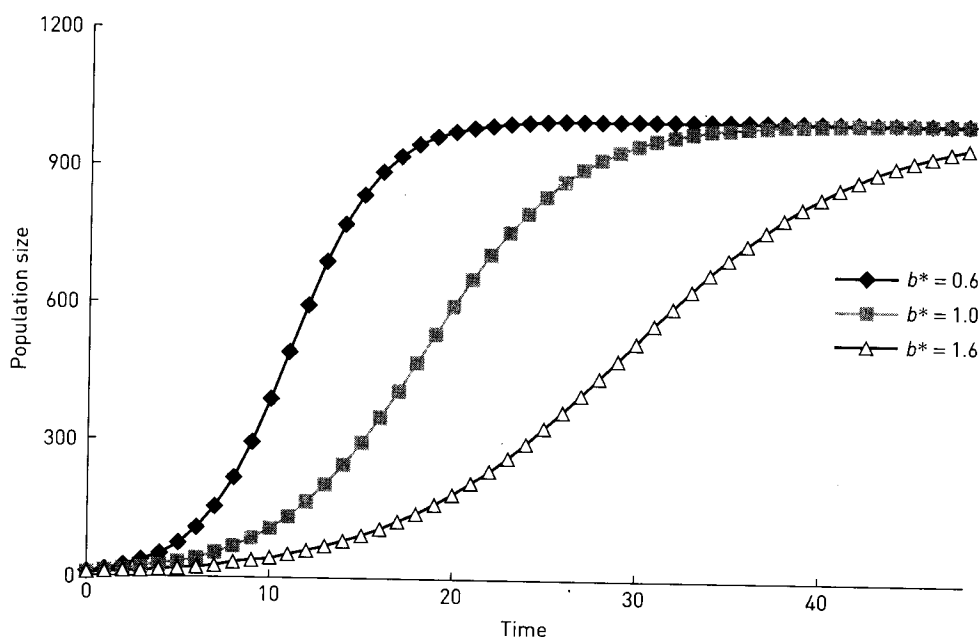
Figure 2.12 Effect of nonlinear feedback on logistic growth.

overcompensation. Similarly a b^*-value < 1 results in **undercompensation** and a higher actual r-value.

The theta logistic model

As illustrated by Figs 2.22–2.26 in section 2.8, the life history of a population frequently does not respond to increases in density in a linear fashion, as assumed by the logistic equation. A well-known variation of the logistic model, known as the theta logistic, more elegantly introduces nonlinear density dependence than we did in the previous section. First, we must introduce another model from fishery science, the Ricker (1952) model, which is a useful discrete form of the logistic.

To find the Ricker, we begin by making a distinction between the actual rate of increase, r_a and the exponential rate of increase, r_m or r_{max}, as we did above in Equation 2.9.

$$r_a = r_m \left(\frac{K - N}{K} \right) = r_m \left(1 - \frac{N}{K} \right)$$

Now let us substitute r_a for r in the equation for exponential growth (Eqn. 1.8), which gives us:

$$N_t = N_0 \, e^{r_a t}$$

Next we transform this to a simple difference equation for adjacent time intervals N_{t+1} and N_t. Since this is one time step and $t = 1$, we can remove t from the exponent in the above equation.
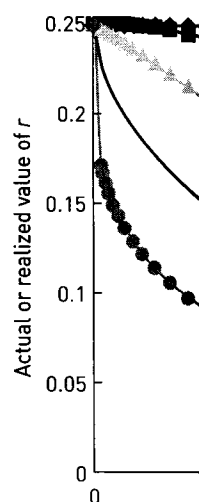
Figure 2.13 Behavior of the theta logistic. Effect of population size on the realized value of r. In all cases $r_{max} = 0.25$ and $K = 1000$.

Simultaneously we will substitute $r_m[1 - (N/K)]$ for r_a. The result is Equation 2.12, the Ricker equation:

$$N_{t+1} = N_t e^{r\left(\frac{K-N_t}{K}\right)} = N_t e^{r\left(1-\frac{N_t}{K}\right)} \tag{2.12}$$

This equation can be modified with the parameter θ (theta) as a superscript of the ratio N/K (Eqn. 2.13). The theta logistic was originally proposed by Gilpin and Ayala (1973). When $\theta = 1.0$, we have the traditional logistic growth response to density. When $\theta < 1.0$ density dependence is strong even when the population is far below the carrying capacity. By contrast, when $\theta > 1.0$ density dependence is weak until the population is close to the carrying capacity.

$$N_{t+1} = N_t e^{r\left(1-\left(\frac{N_t}{K}\right)^{\theta}\right)} \tag{2.13}$$

For example, in Fig. 2.13, we can examine the effect of θ on an actual or realized r-value. In each case the r_{max} is 0.25, the carrying capacity is 1000 and the initial population size equals 10. As predicted from the logistic, when $\theta = 1$ the decline in the actual r-value is linear as the population increases. When θ is less than 1.0 the actual r-value decreases rapidly with population size. By comparison, if θ is greater than 1.0 we can see that r remains close to r_m until the population gets much closer to the carrying capacity.

If we examine population growth versus time for the same theta values, the expectation is that growth will be suppressed at low population levels when theta is less than 1.0, but that the population will approach the carrying capacity quickly when theta is greater than 1.0. These predictions are borne out by Fig. 2.14.

As shown by Saether *et al.* (2002) the theta logistic is a powerful model for analyzing variation in density dependence among bird populations, and is the basis for other
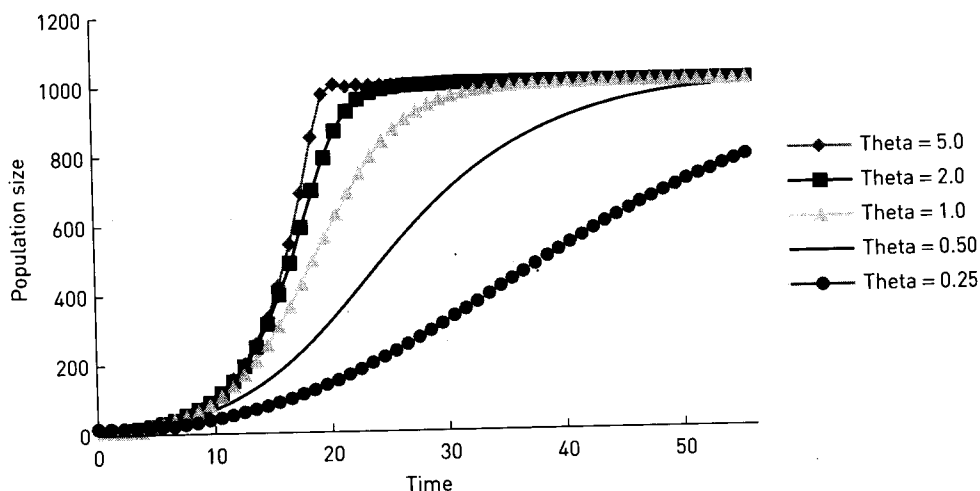
Figure 2.14 Behavior of the theta logistic. In all cases $r_{max} = 0.25$ and $K = 1000$.

population models (for example, predator–prey interactions) in which we do not want to assume a linear relationship between population density and survivorship, fertility, or r.

2.5 Time lags and limit cycles

Assumption 4 of the logistic equation, in which populations are assumed to respond immediately to carrying capacity, is highly unlikely for populations with great reproductive potential. In order to explore this possibility, we can introduce a "lag time" effect into the logistic equation. Using the discrete time form of the logistic (Eqn. 2.1), substituting λ for R, and remembering that $\lambda = e^r$, Equation 2.12 is an equivalent to Equations 2.1 and 2.10c. To introduce time lags, Equation 2.14 is modified as shown in Equation 2.15 (Pielou 1977).

$$N_{t+1} = \frac{\lambda N_t}{1 + \frac{N_t(\lambda - 1)}{K}} \tag{2.14}$$

$$N_{t+1} = \frac{\lambda N_t}{1 + \frac{N_{t-\tau}(\lambda - 1)}{K}} \tag{2.15}$$

A more familiar form of this same equation is simply:

$$dN/dt = rN_t \left(\frac{K - N_{t-\tau}}{K} \right) \tag{2.16}$$

in its continuous form, and
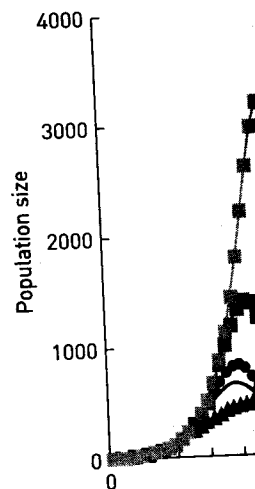
Figure 2.15 Logistic

in its discrete form.

Where N_t appears to the carrying capac Robert May and oth bined with the intri of modifications to the population. As carrying capacity, c that wander furthe equation.

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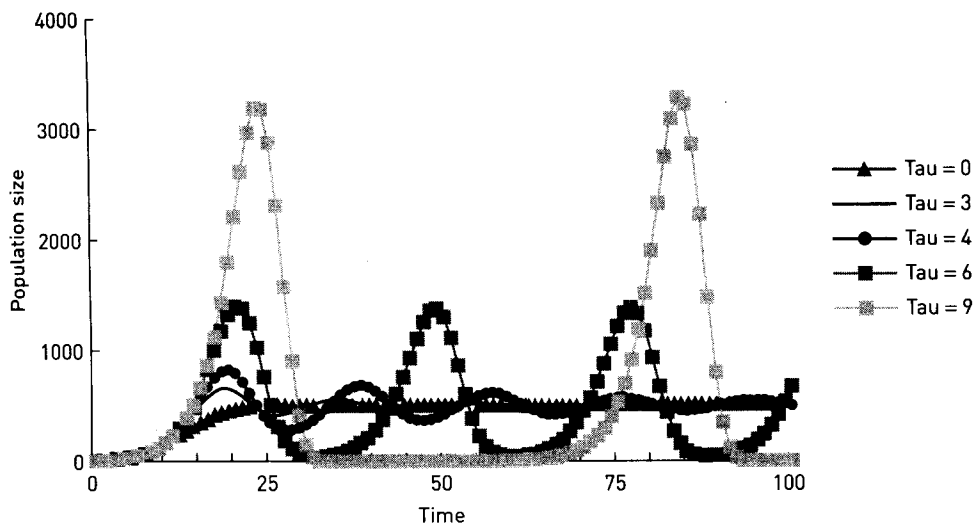
Figure 2.15 Logistic growth with time lags. In all cases $r_{max} = 0.30$ and $K = 500$.

$$N_{t+1} = N_t\, e^{r\left(\frac{K-N_{t-T}}{K}\right)} \tag{2.17}$$

in its discrete form. This is a simple modification of equation 2.12, the Ricker model.

Where N_t appears, it is modified by the Greek letter tau (T). The population responds to the carrying capacity based on what the population size was *tau* time-units in the past. Robert May and others (May and Oster 1976, May 1981a) have shown that lag time, combined with the intrinsic rate of increase (r), produces a predictable and interesting series of modifications to logistic growth. The product of r and T determines the behavior of the population. As summarized below, long time delays before the population reacts to carrying capacity, combined with a high growth potential, lead to population behaviors that wander further and further from the stable point at K predicted by the logistic equation.

- If $0.37 > rT > 0$, the population follows the logistic equation, and the population achieves a stable number (or **stable point**) at the carrying capacity with no oscillations.
- If $1.57 > rT > 0.37$, the population is temporarily oscillatory, but the oscillations dampen to a stable point at the carrying capacity.
- If $2.0 > rT > 1.57$, the population undergoes permanent oscillations around the carrying capacity. This is called a **limit cycle**.
- If $rT > 2.0$, the oscillations are so violent that the population goes extinct.

Figure 2.15 displays five simulations based on Equation 2.17. In series 1, *tau* = 0 and we have the usual logistic growth curve. In series 2 the product of $rT = 0.90$, and in series 3 the product is 1.20. We expect temporary oscillations converging on a stable point at the carrying capacity in both of these cases. In series 4 the product of $rT = 1.80$ and we have a stable limit cycle. Finally, in series 5, the product of $rT = 2.70$. We expect extinction, and

although the simulation shows two population cycles, in reality the population is extinct after 30 time units.

2.6 Chaos and behavior of the discrete logistic model

Time lags are implicit in the discrete logistic model. We can actually remove *tau* from Equation 2.17 and return to Equation 2.12:

$$N_{t+1} = N_t e^{r\left(\frac{K-N_t}{K}\right)} = N_t e^{r\left(1-\frac{N_t}{K}\right)}$$

As May (1975a, 1975b, 1981a), and May and Oster (1976) have shown, if the growth rate (r or λ) is very large, populations behave in unusual and unexpected ways.

Recall that if $b^* > 1$, the population shows overcompensation. That is, there is a larger than expected reduction in growth rate or biomass due to density dependence. As shown in Table 2.3, if the combined values of r and b^* produce a net rate of increase with a large reproductive potential, the population moves from a stable equilibrium at the carrying capacity to fluctuations which ultimately reach chaos when the net r is large enough. For example, when r is less than 2.0 (R or $\lambda < 7.39$), the population moves to a stable point (Fig. 2.16), although note that when $r = 1.5$ there is a small oscillation before the population settles in at the carrying capacity. At r-values between 2.0 and 2.53 (Fig. 2.17, Table 2.3) the population regularly cycles between two points. For r-values between 2.53 and 2.66, the population cycles among four points (Fig. 2.18). An eight-point cycle is produced by r-values between 2.66 and 2.69. Finally, at r-values > 2.69 (R or $\lambda > 14.761$) the behavior of the population is known as **chaos** (Fig. 2.19). That is, the population never enters into a predictable pattern. Over short periods, these chaotic fluctuations would be indistinguishable from seemingly random responses to the environment. A deterministic model, then, can produce results that appear to be stochastic and, if one were looking for biological causation for the behavior of such populations, one would be confused indeed.
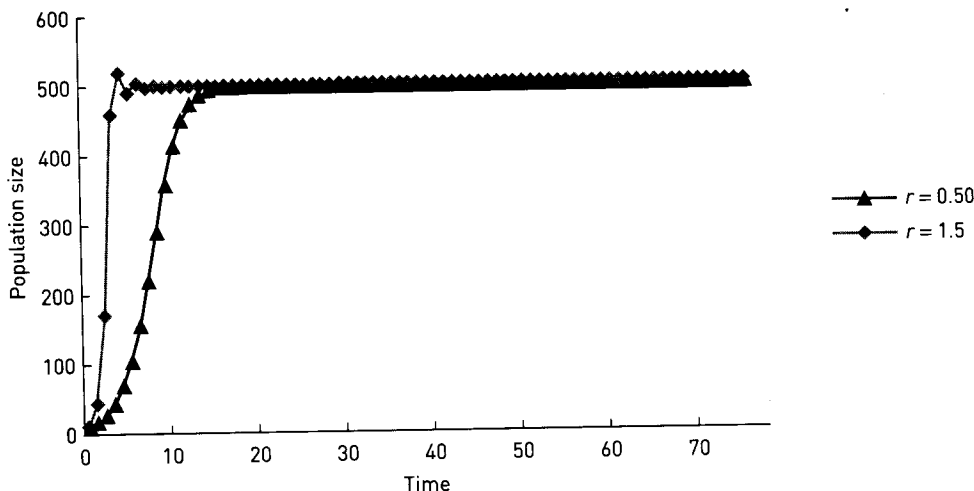
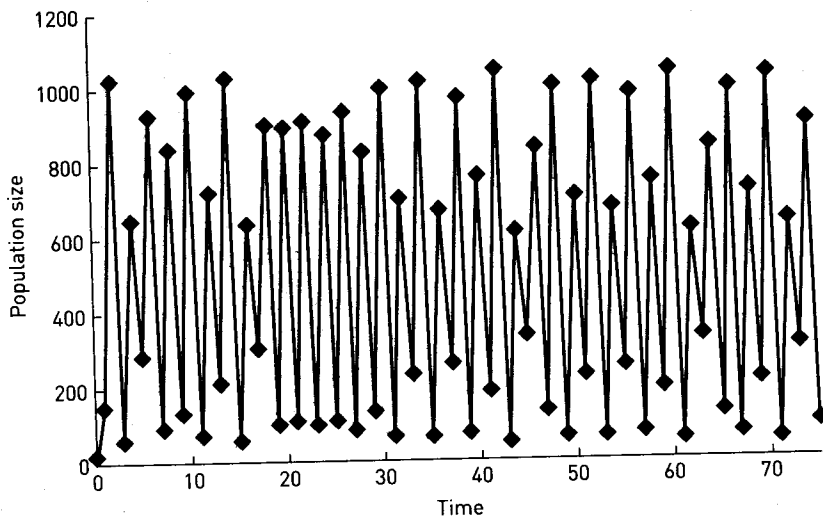**Figure 2.16** Behavior of the discrete logistic model: stable equilibrium point when $r < 2.0$.

Figure 2.17 Behavior of the discrete logistic model: two-point cycle when $r = 2.20$.
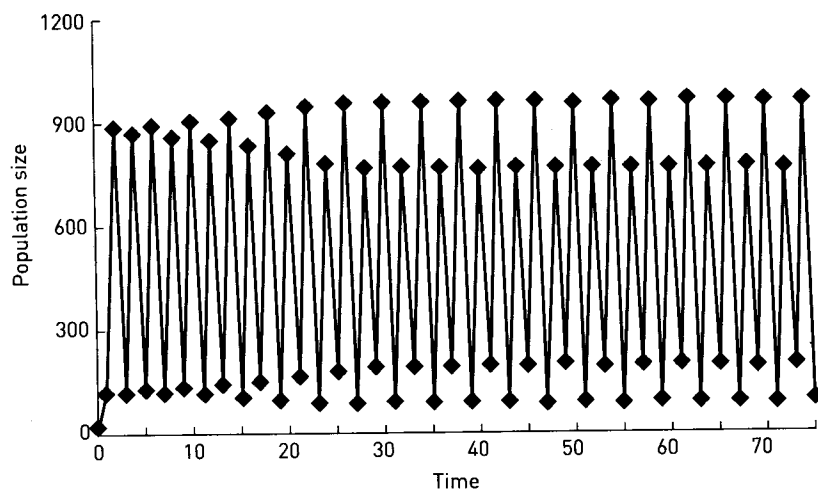
Figure 2.18 Behavior of the discrete logistic model: four-point cycle when $r = 2.60$.

Table 2.3 Behavior of the discrete logistic model based on the net growth parameter, r, with equivalent values of R or λ. Net growth is influenced by the nonlinear feedback parameter b^*, when $b^* \neq 1$. Adapted from May (1975b), May and Oster (1976), and Alstad (2001).

Net growth rate, r	Equivalent value of R or λ	Behavior of the discrete logistic model
$2.000 > r > 0$	$7.389 > \lambda > 1.000$	Stable equilibrium point
$2.526 > r > 2.000$	$12.503 > \lambda > 7.389$	Two-point cycle
$2.656 > r > 2.526$	$14.239 > \lambda > 12.239$	Four-point cycle
$2.685 > r > 2.656$	$14.658 > 14.239$	Eight-point cycle
$r > 2.692$	14.761	Chaos

Figure 2.19 Behavior of the discrete logistic model: chaos when $r = 2.75$.

2.7 Adding stochasticity to density-dependent models

Just as we did in Chapter 1, we can perform stochastic simulations with density-dependent models. Using the Beverton–Holt model (Eqn. 2.1), Fig. 2.20 shows a deterministic growth curve for an initial population size of 100, a carrying capacity of 1000, and a deterministic value for lambda of 1.1. In order to simulate the effects of demographic stochasticity, we can add a random function in Excel™ that allows lambda to vary with a mean of 1.1 but with a variance of 0.03. One such result is shown in Fig. 2.20. In this particular case, when the population is small it does not grow very quickly, but it eventually reaches the carrying capacity. Notice that it takes over 100 time units to reach carrying capacity even though the deterministic population reaches K at around 50 time units. Running 25 stochastic simulations in this manner produces a range of population sizes after 100 time units of 128–1000 with a mean of 904 individuals. The lessons are basically the same as in the previous chapter: adding variability leads, in most cases, to a smaller population than that expected from a deterministic model.

Using the Ricker model (Eqn. 2.12), we next simulate both demographic stochasticity (adding variability to r) and environmental stochasticity (by allowing K to vary with time) in Fig. 2.21. In all cases the initial population size is 50, the deterministic r is 0.1, and the carrying capacity is 1000. We have also allowed both r and K to vary simultaneously in one series of simulations. In Fig. 2.21 we see that the population in which both r and K are allowed to vary goes extinct. The population with the stochastic r eventually reaches carrying capacity and the population with the stochastic K goes through several crashes. The results of these simulations depend on how much variability we allow for demographic versus environmental stochasticity. Suffice it to say to the combined effects of demographic plus environmental stochasticity raise the probability of extinction and, as above, variability normally produces smaller populations.
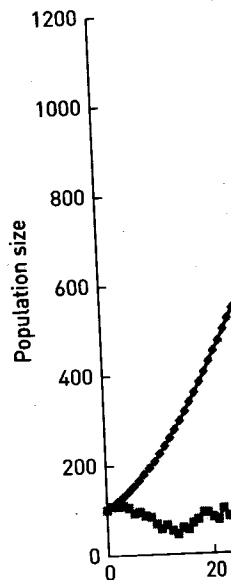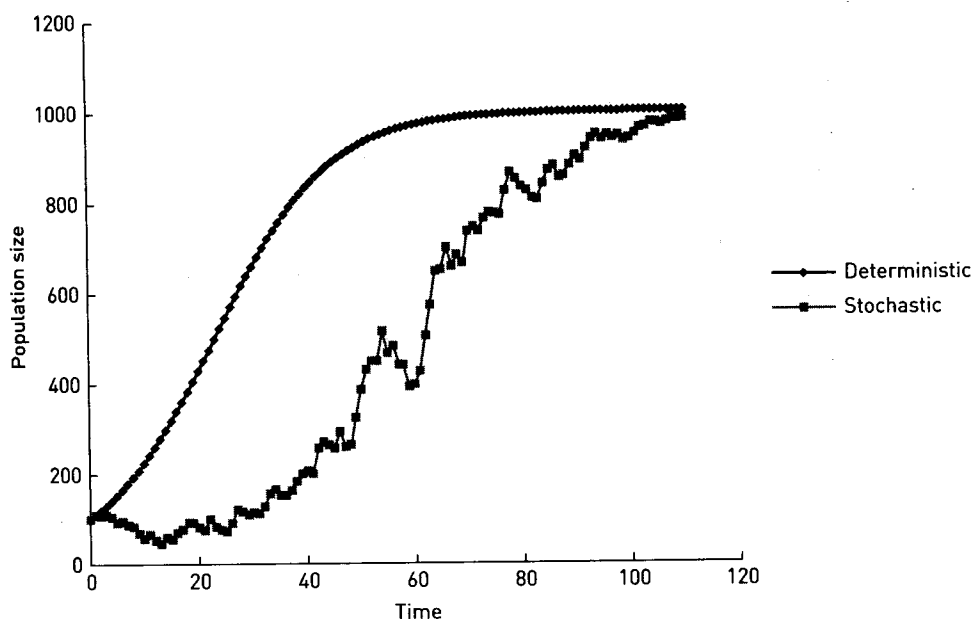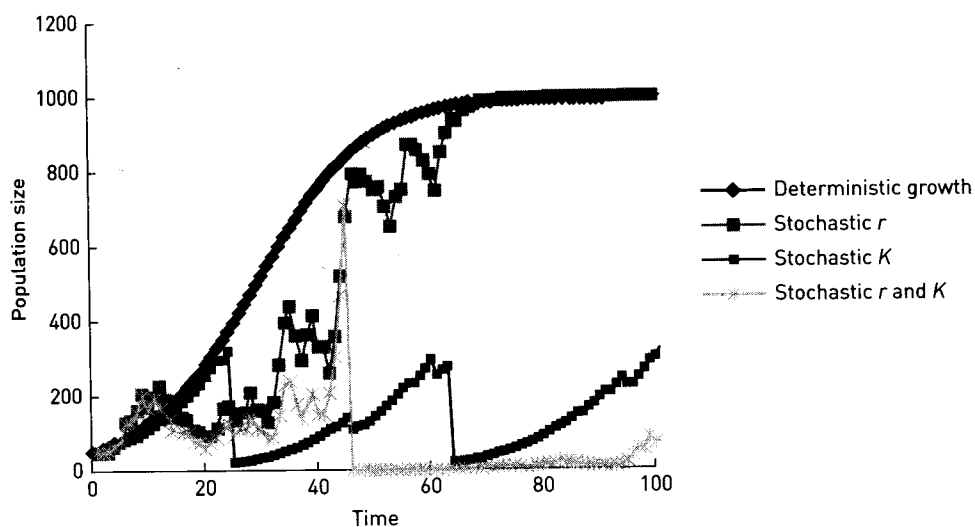
Figure 2.20 Deterministic versus stochastic growth in a population with an initial population size of 100, a carrying capacity of 1000, and a deterministic λ of 1.1. In the stochastic model, the deterministic average λ is 1.1 with a variance of 0.03.

Figure 2.21 Effect of demographic stochasticity (r) and environmental stochasticity (K) on behavior of the Ricker model. Initial population size = 50, deterministic $r = 0.1$, carrying capacity $K = 1000$.
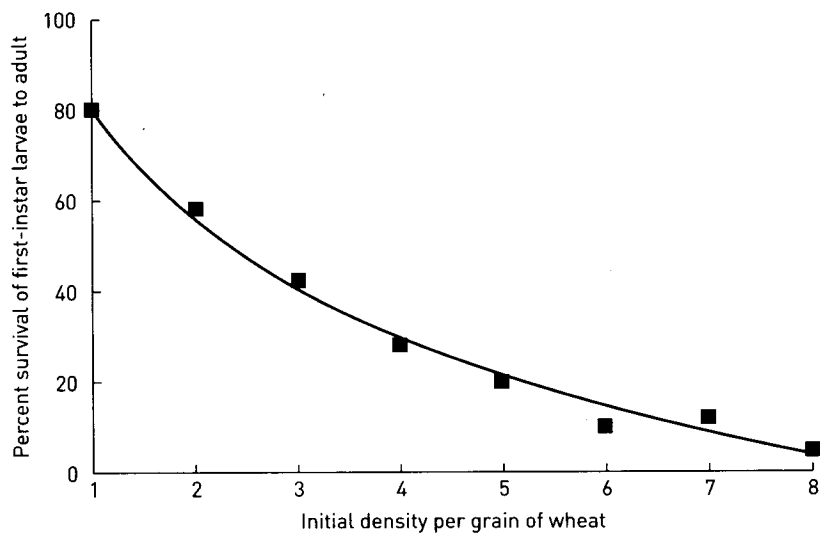
Figure 2.22 Survivorship of the grain beetle *Rhizopertha dominica* versus initial density of first-instar larvae.

2.8 Laboratory and field data

According to the assumptions discussed above, an increase in population density should lead to one or more of the following:

1 a linear increase in mortality;
2 a linear decrease in fertility;
3 a reduction in average growth rate; and
4 a reduction in the average size of adults.

Crombie (1942, 1944) showed that flour beetles (*Rhizopertha dominica*) raised in the laboratory were negatively affected by density. Both survivorship (Fig. 2.22) and fertility (Fig. 2.23) decreased with density, although in both cases the effects were nonlinear. Moreover, many large mammal populations have fertility and mortality patterns that show density dependence but are also nonlinear (Figs 2.24 and 2.25; Fowler 1981). Nonlinearity extends to bobwhite quail (*Colinus virginianus*) (Roseberry and Klimstra 1984) and clado-cerans (Smith and Cooper 1982). On the other hand, both elk (*Cervus elaphus*, called red deer in Europe) (Fig. 2.26, Houston 1982) and grizzly bears (*Ursus arctos*) (McCullough 1981) show a linear decrease in fertility with population density.

Two examples of reduction in growth rate with density will suffice here. The first is that of the growth of tadpoles of the frog *Rana tigrina*. Whereas it takes only two to three weeks for tadpoles to develop into mature frogs at densities of 5 to 10 (in a 2-liter aquarium), it takes almost ten weeks when there are 160 frogs in the same space (Dash and Hota 1980). In harp seals (*Phoca groenlandica*) sexual maturity is achieved when an individual reaches 87% of mean adult body weight. In low populations this occurs at between 4 and 5 years, whereas in dense populations sexual maturity is reached at between 6 and 7 years (Lett *et al.* 1981).
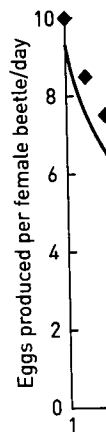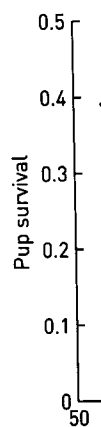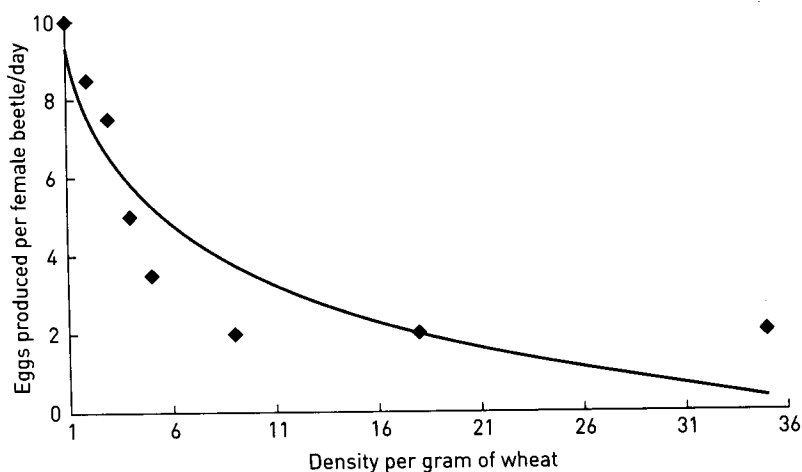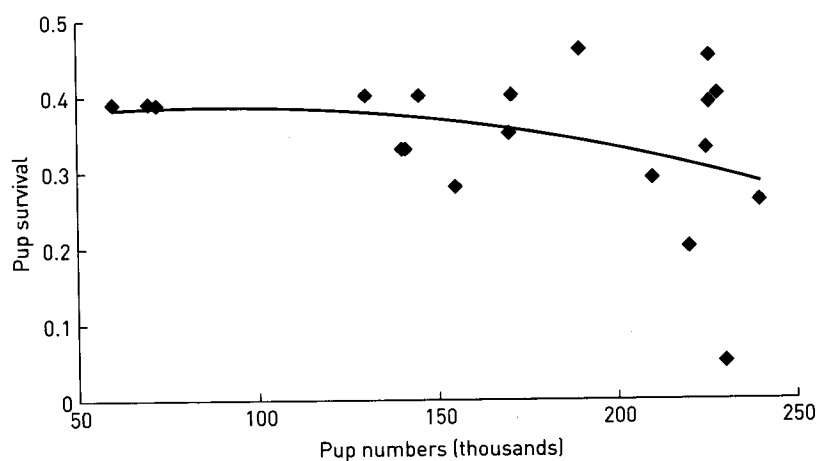
**Figure 2.23** Fertility versus density in *Rhizopertha dominica*.

Figure 2.24 Survivorship of northern fur seal (*Callorhinus ursinus*) pups as a function of pups born. After Fowler (1981).

The body size of adults is also affected by density in many populations. For example, in highly dense reindeer (*Rangifer tarandus*) populations, mean jaw size of adults is 23 cm, whereas at low density the mean size is between 24 and 25 cm (Skogland 1983). As we saw in Section 2.2, the response to an increase in density among plant populations is a reduction in mean weight per individual. The same principle applies to sessile animal populations. When Branch (1975) examined populations of limpets (*Patella cochlear*), the most common diameter was 60 mm when there were 125 individuals per square meter. When the density was increased to 1225 per square meter, the most common size class was 20 mm. The total biomass obeyed the law on the constant final yield (Fig. 2.6a). Biomass increased with density up to 400 individuals per square meter, but then leveled off at 125 g per square meter for all densities from 400 to 1225.
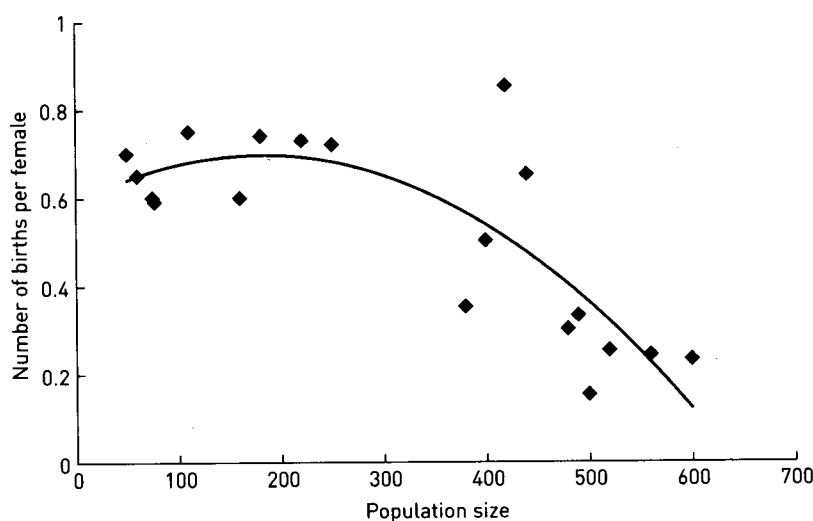
Figure 2.25 Birth rate of the American bison (*Bison bison*) as a function of population size. After Fowler (1981).
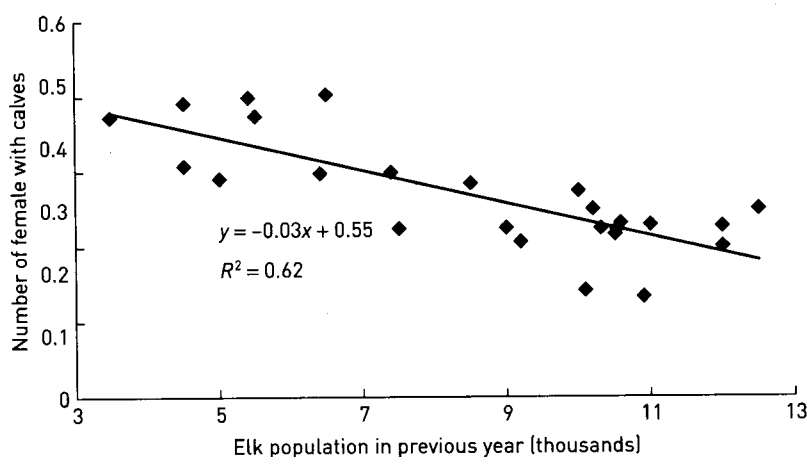
Figure 2.26 Recruitment of elk (*Cervus elaphus*) calves in Yellowstone National Park as a function of adult population size in the previous year. Based on Houston (1982).

2.9 Behavioral aspects of intraspecific competition

Castes in social insects

Passera *et al.* (1996) have shown that intraspecific competition may affect the ratio of castes among social insects. Colonies of the ant *Pheidole pallidula* increase their relative invest-ment in soldiers when exposed to other colonies of the same species. The worker force is divided into two basic castes: small-headed minors (workers) who do most of the labor,

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and large-headed majors (soldiers) specialized for defense. In a laboratory experiment, when colonies were exposed to odors from a conspecific colony, they increased the number of soldier pupae. After seven weeks, those colonies exposed to conspecific odors averaged 40.1 soldiers as compared with an average of 22.6 soldiers in the control colonies.

Male–male competition in horned beetles

The complexities of intraspecific competition are illustrated through elegant work on horned beetles (Emlen 2000). Beetle horns are rigid extensions of the exoskeleton and have evolved repeatedly within this order of insects. These horns are generally only expressed in males and are used in combat with other males for access to resources and/or females. These resources are in discrete, readily defensible patches, and the horns allow males to defend these sites and to mate with the females found there. The jousting contests between males can be dramatic and the winner is rewarded with mating privileges.

These horns, however, do not come without cost. They constitute a large investment in energy, and as much as 10% of body mass may be devoted to them. Horn growth prolongs development time and risk of larval mortality, and there is a trade-off between horn development and the ability to fly. Finally, the development of horns leads to lowered visual acuity and to smaller eyes. Nevertheless, it appears that since larger horns are useful in gaining access to females, the reproductive benefits gained from large horns offset the costs of production and maintenance.

The ability of males to grow horns is based on larval nutrition. Both final adult body size and the size of horns in males depend on the amount of food they consume as larvae. Males exposed to poor conditions as larvae are small and do not produce horns, whereas well-fed males become large adults able to produce horns. Horn production shows an insignificant level of heritable genetic variation (Moczek and Emlen 1999).

These complexities and trade-offs are illustrated through studies of dung beetles of the genus *Onthophagus*. The basic life history of these beetles is as follows. After finding a patch of dung, a female digs a tunnel in the soil beneath the dung. She then buries dung below ground to provide nutrition for the larvae. Females spend days inside a single tunnel, pulling down pieces of dung to various blind ends of tunnel branches, each with its "brood ball" of dung. A single egg is laid at the top of a brood ball, and a single larva develops in isolation within the brood ball.

Females mate repeatedly with males during the time of egg laying. Male reproductive behavior consists of securing their unique access to females in the tunnels. The large, horned males guard the tunnels and fight other males trying to approach the females. Larger males with larger horns win these fights. For two males of the same size, the one with the larger horns usually wins. Thus long horns provide males with significant advantages.

However, all is not lost for a small male. Although they are not adept at guarding entrances to tunnels or winning jousts, small males have other tactics. They attempt to slip undetected past the large males, or they dig side tunnels that intercept a guarded tunnel well below ground. Thus hornless males may manage to sneak undetected into guarded tunnels and mate with the female. If such a "sneaker" male is caught, he is chased out by the resident male, who then returns to the female and mates with her. This dilutes or displaces sperm from the sneaker male. Sneaker males actually do best when they have no horns at all, since horns get in the way of sneaking! Success for a small male depends on rapid and undetected entry into tunnels, and horns cause vibrations as they scrape against

tunnel walls, which would alert the resident male. Finally, as mentioned earlier, beetles with very large horns tend to have undeveloped eyes and/or a diminished flying ability due to smaller wing size and greater body weight. Since dung is a temporary resource, another component of fitness is the ability to disperse and locate new dung heaps. As the dung resource diminishes, some of the males, as larvae, will receive a less-than-optimum amount of food. They will be small and lack horns. Thus, although they would be poorly equipped to defend a female in a burrow, they are well adapted to disperse and find a new dung pile.

Both intraspecific competition and sexual selection are played out on the fields of manure.

Male–female competition in dunnocks

Another aspect of intraspecific competition is competition between the sexes as expressed through mating systems. Obviously ecological conditions can influence the mating behavior of individuals. As conditions change, a cooperative pair or an animal society may quickly dissolve into a set of competing individuals. The following study (Davies 1992, 1995) illustrates some of the complexities in what appears to be a simple pair-bonded mating system.

The dunnock (*Prunella modularis*), formerly known as the hedge sparrow, is not a true sparrow but an accentor. In Old English "dun" means brown and "ock" means little. Thus *P. modularis* is the archetypal little brown bird. It seems unremarkable as it shuffles about under the bushes collecting tiny insects for its young. The impression gained is of harmonious cooperation. The Reverend Morris (1856, in *A History of British Birds*) admired this species so much that he urged his parishioners to emulate its behavior. The Reverend, as quoted by Davies (1992), found this bird to be "unobtrusive, quiet and retiring, without being shy, humble and homely . . . sober and unpretending in its dress . . . while still neat and graceful . . ." Due to its extraordinary mating system, however, the Reverend Morris would hardly have been pleased had his congregation followed the example of these birds. Although a dunnock territory can contain one seemingly harmonious pair, a female in the territory next door may be mating with two males, or a male may be mating with two females.

The conventional view of pair formation in songbirds is that males first set up territories and advertise for mates by singing. Females then choose among male territories. However, in dunnocks females defend their own territories against other females, occupying exclusive areas with little overlap among neighbors. Females settle independently of the males, based on the quality of the territory. Males then compete to defend the females from other males.

The fact that males and females set up territories independently results in a wide variety of mating behaviors. In some cases, a single male defends one female territory (producing monogamy); at other times a male defends two adjacent females (producing polygyny). In other cases two males share the defense of one female (polyandry), or several adjacent females (polygynandry).

If two males share a territory with a single female, the dominant or alpha male (usually the older one) tries to evict the beta male. If he is unsuccessful, the two share defense of the joint territory. Some males wander for weeks before finding a permanent home. Sometimes a beta will overlap with two alphas. The larger the territory of the female, the

harder it is for a male to monopolize her. The larger the male territory, the more likely he is to have two females.

Once a female has built her nest, she solicits copulations from males. Mating begins 3–7 days before the first egg is laid, and lasts up to completion of the clutch of 3–5 eggs. One egg is laid per day during this period. Monogamous males chase off neighboring males who are interested in mating. When two males share a territory, the alpha male follows the female everywhere to prevent her from copulating with the beta male. A female often maneuvers to throw off the alpha male. She then solicits the beta for mating. Females have many tricks, and seem intent on preventing exclusive mating by the alpha.

The act of copulation was described by Selous (1933) as "bizarre." "The hen elevated her rump and stood still, when the male, hopping up, made little excited and very wanton-looking pecks in this region, that is to say the actual orifice. There was actually no mistaking the nature and significance of the actions, rather lecherous, as it seemed to me. This is a very remarkable thing . . . but I do not understand it" (Selous 1933, pp. 107–9). During the pecking described by Selous, the female cloaca makes pumping movements, resulting in the ejection of a small droplet of fluid. As soon as this occurs the male copulates with her.

Davies (1992) analyzed the droplets and discovered that they contain masses of sperm from the previous matings. Like other birds, female dunnocks store sperm. Females with two males may copulate up to six times per hour. As a result, there will be a pool of sperm in the female's cloaca and vagina for much of the mating period. The male's pecking stimulates the female to eject this pool of sperm to make way for his insemination and give his own sperm a better chance of being stored.

After the excitement of the mating period, life on a dunnock territory becomes peaceful during incubation. Females incubate the clutch of eggs alone for 11–12 days. Males help with chick feeding for 11–12 more days in the nest and for two weeks after fledging until the young become independent.

The results of DNA tests on the blood of the chicks and the parents showed that the female is the mother of all chicks in the nest. In monogamous and polygynous territories, the male was the father of all chicks. When two males guarded a territory with one female, however, if the female mated with both males, paternity was mixed. The alpha male fathered 55% of the brood and the beta male 45%.

From the female perspective, when both males mated with her they both helped feed the brood. If she mated exclusively with the alpha male, only he helped feed the brood. Males, however, cannot recognize their own young. If they have mated with the female, they will help raise the young, even in cases where they did not happen to father any of the chicks. If a beta male gained a large share of the copulations he more readily helped with feeding of the chicks. Similarly, if an alpha male was removed experimentally, allowing the beta a larger share of the matings, the beta male worked harder to feed the chicks than did the alpha. Thus, males varied their parental effort in relation to their chance of paternity, not simply according to dominance rank.

For a female, polygyny is the least desirable situation. She must share the help of one male with another female, and some of her chicks often starve to death. A polyandrous female was the most successful because she had the help of two males in raising her young. This explains why the females sneaked around and tried to get the beta males to mate with them. They hoped for future help in rearing of the young.

For a male, the situation is reversed. In polygyny, although each female is less productive, the combined output of two females often exceeds that of one female in monogamy.

Thus the mating system reflects an intraspecific competitive battle between the sexes in dunnocks. Behavioral and genetic studies of other bird species show that the dunnock mating system is not unusual. However, extra-pair copulations and fertilizations vary across species for reasons only poorly understood (Petrie and Kempenaers 1998, Blomquist et al. 2002). Extra-pair paternity is much less frequent in non-passerine than in passerine birds (Birkhead et al. 2001). For example Blomquist et al. (2002) found that in western sandpipers (*Calidris mauri*) only 5% of all chicks were the product of extra-pair matings. Nevertheless the application of molecular techniques to behavioral studies has allowed us to ask new questions about the mechanisms of intraspecific competition.

Competition versus cooperative behavior within a group

Research on lions by Heinsohn and Packer (1995) illustrates the behavioral complexities displayed by animals that are simultaneously territorial and cooperative group-foragers. African lions (*Panthera leo*) engage in a wide variety of group-level activities from hunting to communal cub rearing. At the same time, the group defends a territory from other groups of lions. When prey is difficult to capture they hunt cooperatively, but cooperation breaks down when prey is easy to catch. Female lions nurse each other's young, but, more importantly, they jointly protect their young from males that are intent upon infanticide. The threat of attack by conspecifics is a driving force in lion sociality. Large prides dominate smaller ones, and solitary lions are often killed or injured during attacks by lions of the same sex.

Using playbacks of recorded roars, Heinsohn and Packer found that lions are able to distinguish pride members from strangers. They also found that certain females show a consistent behavior of lagging behind their companions during group activities, including hunting.

Female lions live in social groups (prides), which contain 3–6 related adults, their dependent offspring, and a group of immigrant males. The males defend the pride against incursions by other males; females defend their young against infanticidal males, and the territory from other females. At least two females are needed for a territory, and they advertise ownership by roaring. Using broadcasted roars, the investigators showed that some females become "laggards" early in life, and this behavior persists into adulthood. Laggards were those individuals that hung back, and approached the audio speaker only after the leaders had already responded. The order in which the individuals approached the speaker was the same throughout the playbacks. Because territorial fights often lead to injury or death, laggards were ensuring their safety, at least from initial attacks. They typically followed the leaders by 30 to 120 seconds.

In the theoretical game or model known as "prisoner's dilemma," in any single task two individuals benefit when they work together (mutual cooperation) but both lose when neither contributes (mutual defection). However, in this game, the greatest payoff for one individual comes from providing no help (cheating) to a partner who cooperates, while the lowest payoff results from helping out (cooperating) while the partner cheats. In a repeated series of encounters, however, cheaters are eventually punished by withdrawal of further cooperation by other individuals. In large groups the game gets more complicated, but cheaters can eventually be detected and punished.

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In the case of the lion pride, female leaders approached the speaker slowly and stopped to look behind at the laggards. The leader females mistrust the laggards, but they do not directly punish them. Although lions might be tempted to reduce their risk of injury from territorial defense by withdrawing or not cooperating, they still need companions for territorial defense, to share the protection of the young from males, and for the capture of large prey. In addition, females are often closely related, usually sisters. Given their shared genes, laggards appear to be tolerated, and leaders continue to arrive alone at the speaker 30 seconds to two minutes before the laggards arrive.

Heinsohn and Packer classified the behavior of individual female lions as: (i) unconditional cooperators, who always led the response; (ii) unconditional laggards, who always lagged behind; (iii) conditional cooperators, who lagged least when needed most; (iv) conditional laggards, who lagged most when needed most.

The parallels with human societies are evident. How these behaviors developed and why they are tolerated in animal (as well as human!) societies will remain a fascinating topic for future investigations.

2.10 Conclusions

Models can be derived for density-dependent populations using both difference and differential equations for populations with discrete and overlapping generations. Although the equations differ in detail, all presume that the growth-rate parameter is dampened as the population approaches a carrying capacity. Modifications of the logistic include the introduction of the Allee effect and the inclusion of time lags. In populations with discrete generations there is an inherent time lag which produces an overshoot of the carrying capacity when the net growth rate is large enough. In continuously breeding populations, if we introduce a time-lag variable (*tau*), a large value of *r* combined with even a modest time lag can cause populations to exhibit a variety of behaviors commonly found in nature. These include limit cycles and dramatic growth phases followed by spectacular population crashes ("boom and bust" cycles). Therefore, when we study populations in nature we should never be surprised when many of them, particularly those populations with high growth potentials, do not remain constant from one year to the next. Finally, the logistic equation is merely a starting point for encompassing the idea of limitation to population growth. It is, as suggested by Turchin (2001), a special case assuming a linear relationship between population density and vital rates. Most importantly it does not allow for time lags, which we have seen have powerful effects on the behavior of populations.

Intraspecific competition has a major influence on the life history of a population. Fertility, mortality, growth and developmental rates, as well as behavior characteristics are all shaped by intraspecific competition, often in subtle and surprising ways.