Chapter 12

Resources and Population Dynamics

Alan R. Rogers
Department of Anthropology
102 Stewart Hall
University of Utah
Salt Lake City, UT 84112

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12.1 Introduction

Population ecology is concerned with the growth (and decline) of populations of plants and animals, including humans. This interest, of course, is also shared by demography, economics, and several other disciplines. Population ecology differs in its emphasis on ecology and evolution—the ecological interactions among individuals and among species, and the evolutionary forces that shape these interactions.

Earlier chapters in this volume discuss how natural selection shapes the characteristics of individuals: their use of resources, their distribution across the landscape, their life histories, and so forth. This chapter is concerned with the effects that these characteristics have on the dynamics and stability of populations. It will show that these effects are profound, and have important practical consequences.

This chapter begins by introducing the fundamental principles of population growth: the exponential increase of unregulated populations, various mechanisms that regulate population growth, and a method called "cobwebbing" that is useful for understanding the consequences of population regulation. As we shall see, these consequences may include not only the stability that the term "regulation" seems to imply, but also various forms of instability. Next, we shall take a closer look at the effects of dwindling resources, using the models of "scramble" and "contest" competition. Finally, we turn to the effect of resources on the reproduction of individuals, with particular attention to the case in which wealth can be inherited by offspring.

12.2 Dependence of Population Growth On Population Density

In 1990, there were roughly 5.292 billion people in the world, and this number was expected to increase to 6.251 billion by the year 2000 (Brown 1990). At this rate, the population would double every 42 years. Should this rate of growth continue for 420 years, the world population would double ten times and there would be over a thousand humans for each human alive today—over 5 trillion in all. It seems unlikely that this can happen. As a population increases in size, its rate of growth must eventually slow.

In the literature of population ecology, anything that limits the growth of a population is called a "mechanism of population regulation." These mech-

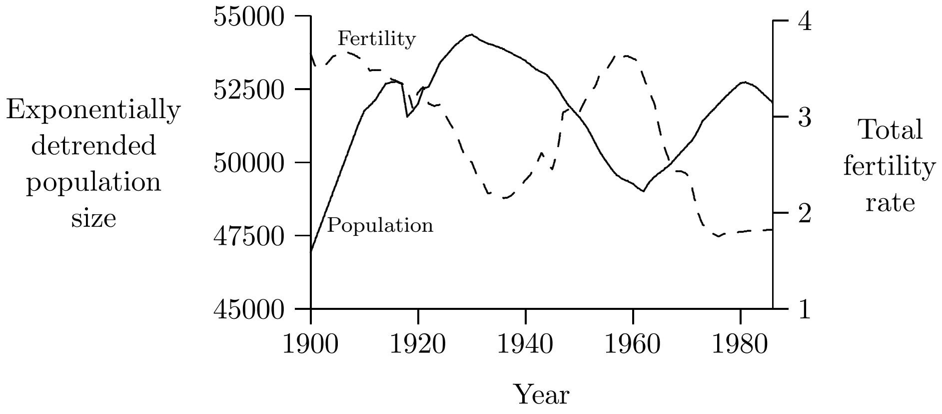

Figure 12.1: Fertility and population size
Data refer to the US during the 20th century. Population size has been "exponentially detrended." In other words, an exponential curve was fit to the original data, and the graph shows the deviations from this curve. After Lee (1987).

anisms fall into two important categories. *Density independent* mechanisms are those whose frequency and severity are unaffected by population density. This category would include, for example, natural disasters such as blizzards and earthquakes, but would not include hunger or infectious diseases that are transmitted more easily in dense than in sparse populations. Mechanisms that are affected by population density are called *density dependent.*

Nearly 200 years ago, Thomas Malthus (1798) argued that density-dependent mechanisms have a profound effect on human affairs. It seemed inconceivable to him that food production could increase rapidly enough to match the growth of an unconstrained population, and he concluded that population growth must ultimately be limited by starvation and disease. This view has been extremely influential, and tempts us to view the history of human population growth as a series of responses to technological innovations. For example, archeological evidence (Klein 1989) shows that new kinds of stone tools appeared and spread out from an African origin some 40,000 years ago, and genetic evidence (Rogers and Harpending 1992) suggests that a dramatic burst of population growth occurred at roughly the same time. Archeological data suggest that another burst of population growth followed the origin of agriculture some 6000 years ago. More recently, the industrial revolution in Europe allowed another spurt of population growth that still continues.

One influential point of view holds that the human population is usually regulated at a level, called the *carrying capacity*, that is determined by the availability of resources. The carrying capacity is determined not only by the environment, but also by our ability to extract resources from it. The major episodes of population growth may have resulted when technological innovations increased the carrying capacity.

This point of view has been criticized by authors who point out that the rate at which innovations are adopted or invented is itself density dependent. Population growth leads to gradually increasing scarcity, which encourages efforts to invent or adopt new technologies. This effect has been documented both in rural (Boserup 1965, Boserup 1981) and industrial economies (Simon 1977). Even in foraging societies, technological complexity increases with the number of people per unit of environmental productivity (Keeley 1988). Thus, it may be more useful to view innovation as an effect, rather than a cause, of population growth. If so, perhaps humankind has not been faced with the chronic shortages that Malthus envisioned; perhaps density-dependent population regulation has played no important role.

This last point of view is also influential, but is probably incorrect. That rates of innovation respond to density seems clear, but it does not follow that the rate of population growth is unaffected by density. Consider figure 12.1, which displays Lee's (1987) data on fertility and population size in the 20th century United States. Fertility is high when population size is relatively low (i.e. below the long-term trend), and vice versa. These data suggest that some mechanism of density-dependent population regulation is at work, even during a period of uninterrupted population growth. Analogous density-dependent effects on mortality are reported by Wood and Smouse (1982) in a study of a very different population: the Gainj, a horticultural people in Papua New Guinea. Density-dependent effects are weak, and may be masked by larger density independent effects. Over the long run, however, a weak effect with a persistent direction may overwhelm stronger effects with no persistent direction (Lee 1987). Thus, even weak density dependence may be important. Let us consider, therefore, how it affects the dynamics of population growth.

This is a subject to which unaided intuition is a poor guide. It is tempting to assume that density-dependent regulation will produce a time path like the logistic growth curve in figure 12.2. The population in that figure grows steadily until it reaches a limit determined by available resources, and then remains constant in size. Unfortunately, this is not necessarily so. Other,

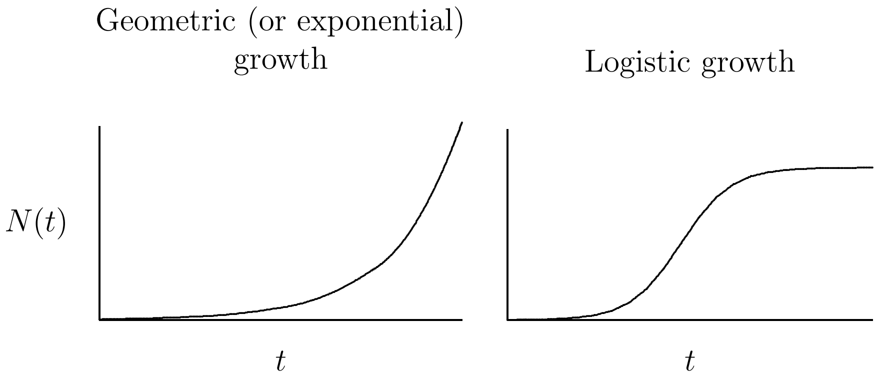

Figure 12.2: Geometric and logistic population growth.

Geometric growth results when age-specific rates of birth and death are constant. Logistic growth is one of many patterns that may arise when these rates are density dependent.

less pleasant, effects are also possible, and it behooves us all to be aware of them. The best way to develop intuition about population dynamics is to study simple mathematical models. Let us consider, then, the dynamics of simple models of population growth.

12.3 The Dynamics of Simple Populations

A population can change in size in only four ways: by birth, by death, by immigration, and by emigration. In this chapter, I deal only with the first two of these in order to keep things simple. This still leaves plenty of complexity, since rates of birth and death can vary in complex ways. Before plunging into these complexities, it will be useful to consider first the case in which these so called *vital rates* do not change.

12.3.1 Geometric (or exponential) growth

Even when vital rates do not change, the situation is far from simple. Since death rates are higher for the elderly, more deaths per capita will occur in a population with many elderly people than in a young population. By the same token, since fertility is highest for young adults, the number of births per capita will be high if there are lots of young adults. Thus, age-specific birth and death rates alone cannot tell us how fast a population will grow. We also need to know the *age structure* of the population, that is, the number of individuals in each age category. And as if this were not bad enough, there is also the matter of sex. A population with no females cannot grow, regardless of its age structure. Furthermore, vital rates often vary among social classes. When vital rates vary according to categories of any type—age, sex, social class, geographic region, or whatever—the population is said to be *structured.* In such a population we cannot predict how a population will grow until we know how many people are in each category.

Confronted by these complications, we can proceed either by building a complicated model to deal with them, or by sweeping them under the rug and pretending that they don't exist. This latter approach sounds irresponsible, but it is the best way to start. A realistic model will not help much if it is too complex for its workings to be understood. We proceed by looking first at models so simple that they are easy to understand. Then, one at a time, we add complications.

The simplest case is that of an organism without sex that lives a single season, reproduces and then dies. Suppose that each individual produces R offspring. If there is one individual to begin with, there will be R after 1 generation, R^2 after 2 generations, R^3 after 3 generations, and R^t after t generations. If there are N_t individuals in generation t, there will be

$$N_{t+1} = RN_t \tag{12.1}$$

in generation $t + 1$. This pattern of growth, in which the population size increases by a constant multiple each generation, is called *geometric* or *exponential* growth, and the time path of a population growing in this way is shown in figure 12.2.

In this simple case it is easy to see why growth is geometric. The remarkable thing about this result is that it usually holds even when you add the complications of age and sex structure back in, still assuming vital rates to be constant in time. Thus, the simple unrealistic model tells most of the story. This suggests that it will still be worthwhile to ignore age structure and sex as we explore the effect of relaxing our other assumption: that vital rates do not vary.

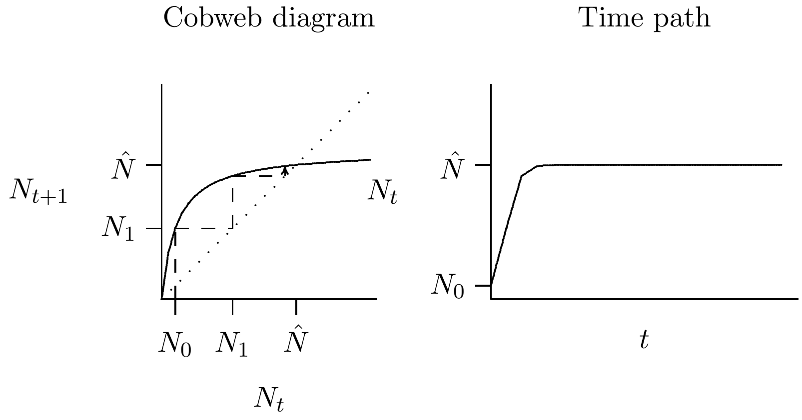

Figure 12.3: Monotonic convergence toward an equilibrium
This figure illustrates a trick called "cobwebbing" for studying population dynamics. The solid line on the left plots the size of a population in generation $t + 1$ against its size in generation t. The dotted line shows the points at which $N_{t+1} = N_t$. The time path of the population, beginning at point N_0, is derived by reflecting the dashed line back and forth as shown. This time path is graphed against t on the right.

12.3.2 Population regulation

It is not hard to see that the pattern of geometric growth shown in figure 12.2 cannot continue forever. Mechanisms of population regulation alter this pattern by adjusting rates of birth or death. Therefore, let us drop the assumption that the vital rates do not change, and assume instead that they vary as a function of N, the population size. To indicate this, I write the number of offspring per parent as $R(N)$, thus emphasizing its dependence on N. Now the equation for population change becomes

$$N_{t+1} = R(N_t)N_t. \tag{12.2}$$

In equation (12.2) the rate of growth depends on the size, or density of the population: it is *density dependent*. The supposition is that when N_t is large enough, R will be less than 1, so the population will decrease in size. When the population is small, R will be greater than 1 and the population will grow. At some intermediate *equilibrium* value $\hat{N}$, population size will tend to remain the same because $R = 1$.

Graphs such as the "cobweb diagram" in figure 12.3 are useful for thinking about density-dependent population growth. The solid line is a plot of N_{t+1} against N_t for some hypothetical population. The dotted line connects the points at which $N_{t+1} = N_t$. To the left of $\hat{N}$, the solid line lies above the dotted line, which means that $N_{t+1} > N_t$, that $R(N) > 1$, and that the population is growing. The reverse is true to the right of $\hat{N}$, which means that large populations will shrink. The curve in figure 12.3 does not (so far as I know) describe any real population; it is purely hypothetical. Analysis of hypothetical models cannot tell us what nature is really like, but can illustrate the range of behaviors that are possible. Let us consider, therefore, what figure 12.3 implies about the dynamics of growth in this hypothetical population.

12.3.3 Cobwebbing and dynamic stability

Given a graph like the left side of figure 12.3, it is natural to wonder what the time path of the population will be like. This is easy to figure out using a trick called "cobwebbing." Suppose that N_0, the population size in generation 0, is known. The size in the next generation generation, N_1, can be read off the vertical axis of the graph. In order to get N_2 we need to transfer the value of N_1 from the vertical axis to the horizontal axis. You could do this with a ruler and a pencil, but there is an easier way. Notice that the horizontal dashed line level with N_1 on the vertical axis strikes the diagonal line directly above N_1 on the horizontal axis. Thus, we can work out the time path of population size as shown by the dashed line in figure 12.3. Going straight up from N_0 to the solid line gives us N_1. Then "reflecting" a horizontal line from this point off the diagonal gives us N_2, and so forth.

Let us now use cobwebbing to investigate several kinds of dynamical behavior, which are illustrated in figures 12.3–12.5. The time paths generated are shown on the right in each figure. Try starting the population at different values on both sides of $\hat{N}$ in figures 12.3–12.5. Equilibria such as those in figures 12.3 and 12.4 (or the logistic curve in figure 12.2) are said to be *stable*, since populations away from the equilibrium tend to move closer to it. Equilibria such as that in figure 12.5 are called *unstable* since populations near them tend to move farther and farther away. Among stable equilibria there are two possibilities. The first of these, illustrated by figure 12.3, is called *monotone convergence*, and is the sort of thing that comes immediately to mind when we talk about population size being regulated. A small population will increase gradually toward its equilibrium value, while a large

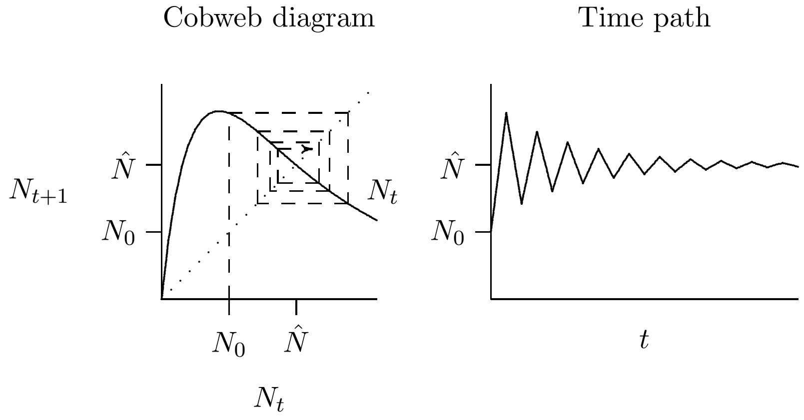

Figure 12.4: Damped oscillations

The solid line in the cobweb diagram crosses the dotted line with a steeper slope in this figure than in figure 12.3, producing damped oscillations.

population will decrease gradually. The other possibility is that a stable equilibrium may exhibit *damped oscillations*, as illustrated in figure 12.4. There the population always overshoots the equilibrium so that its time path oscillates back and forth about the equilibrium. Each overshoot, however, is smaller than the last so the oscillations get smaller and smaller. Finally, the unstable equilibrium in figure 12.5 exhibits what is called *diverging oscillations*. These oscillations get larger and larger rather than dwindling away. Actually, the oscillations in figure 12.5 do not continue to diverge indefinitely. They increase only until they reach a certain amplitude, which is then maintained. This is called a *stable limit cycle*.

These cases illustrated in figures 12.3–12.5 are by no means an exhaustive list of the kinds of dynamical behavior that can arise. Some models, for example, give rise to a phenomenon called “chaos” in which population size fluctuates but does not follow any cyclical pattern (May 1981). None of these models is complex enough to be an accurate description of any real population. The same sorts of instability, however, often arise in more complex and realistic models (Winterhalder et al. 1988). The lesson here is that population regulation need not lead to a stable, equilibrium population size. It can do so, but it can also lead to oscillations. Natural populations often fluctuate in size, and the principles that generate instability the simple models may contribute to this instability.

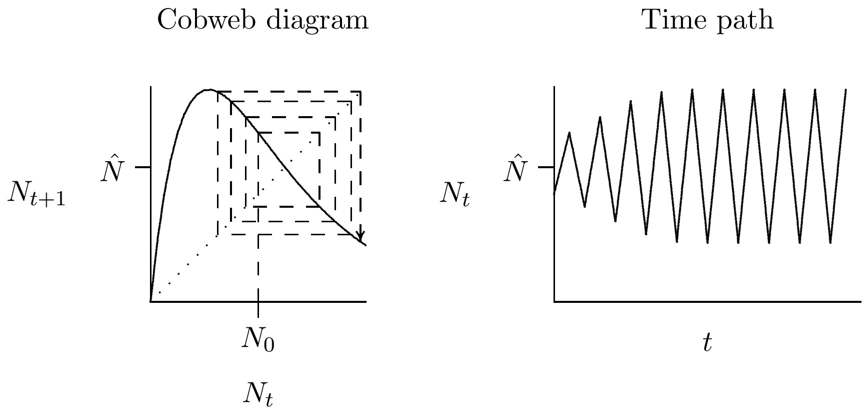

Figure 12.5: Diverging oscillations

The slope is even steeper here than in figure 12.4, and produces diverging oscillations in the neighborhood of the unstable equilibrium, $\hat{N}$. The oscillations increase in magnitude until a stable limit cycle is reached.

The next section will consider a variety of mechanisms that tend to "regulate" populations in that they tend to increase the size of small populations, and to decrease the size of large ones. The hypothetical graphs we have just considered show that even populations that are regulated may differ greatly in the stability of their equilibria. Unstable dynamics such as those in figure 12.5 might well drive a population to extinction. The equilibrium in figure 12.4 are somewhat more stable, but the violent swings in population size exhibited there would probably also increase the likelihood of extinction. The most stable equilibrium is that in figure 12.3, and it is only equlibria such as these that are likely to have the favorable results that are suggested by the phrase "population regulation." Thus, as we consider mechanisms of density-dependent population regulation, it will be important to ask how they affect the stability of equilibria.

12.4 Competition for Limited Resources

All organisms need food, and some need special dens or nesting sites in order to reproduce or to survive the winter. Populations that grow large enough to deplete the supply of such resources are said to be *resource limited.* In such populations, an individual's ability to survive or reproduce may depend on its success in competition with others for scarce resources. The larger a population grows, the more likely it is to deplete its resources. The human population has recently enjoyed several generations of uninterrupted growth, but there are indications that this trend is about end. While the world population has continued to grow, the growth in agricultural production has slowed because of "environmental degradation, a worldwide scarcity of cropland and irrigation water, and a diminishing response to the use of additional chemical fertilizer" (Brown and Young 1990). The result, shown in figure 12.6, is that per capita food production has begun to drop, and is projected to drop further. The world population may be approaching its carrying capacity. As food becomes increasingly scarce, competition for it will surely intensify.

Competition for limited resources is clearly a mechanism of density-dependent population regulation since it tends to decrease the size of large populations, but allows small populations to grow. Yet as we have already seen, this is no guarantee that the dynamics of population growth will be stable. Will the world human population converge gradually toward its carrying capacity like the hypothetical population in figure 12.3, or is it about to enter into a series of oscillations like those illustrated in figures 12.4 or 12.5? We cannot know, but some insight can be gained by considering how competition affects stability in simple models.

In order to predict how a change in the supply of resources would affect the growth of some population, we would need to know (1) how it would affect the way resources are distributed among individuals, and (2) how resources affect individual survival and reproductive success. The second of these factors can be described by the *fitness function*, $w(x)$, whose value is the expected number of offspring born to individuals with x units of resource. For the sake of brevity, I will hereafter refer to x as "wealth," with the understanding that this term will apply to a squirrel's supply of acorns as well as to money that one of us might have in the bank.

At the outset, let us make a simplistic assumption about the second of these factors in order to concentrate on the first: let us assume that $w(x)$ is a "step function," as shown in figure 12.7. The vertical axis, $w(x)$, is the average number of offspring per individual of wealth x, and the horizontal axis is wealth. The graph illustrates the assumption that individuals whose wealth is below a threshold value, x_0, have zero fitness, whereas the wealthier have fitness m. In real populations, fitness may often increase with wealth (more on this later), but it would be surprising to find a threshold as abrupt

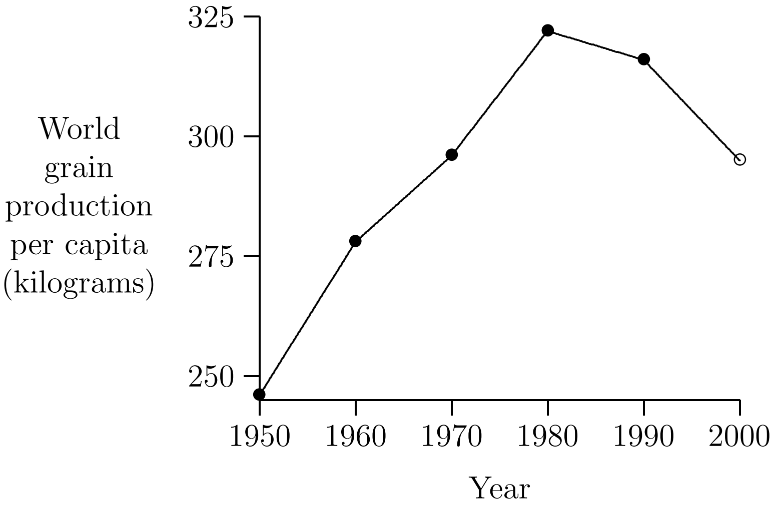

Figure 12.6: World per capita grain production
(After Brown and Young 1990:76)

as the one in figure 12.7. Thus, our assumption is only a caricature of reality. Nonetheless, it will illuminate effects that are only dimly perceived in more realistic models.

12.4.1 The distribution of resources among individuals

The distribution of resources among individuals is affected both by the nature and spatial distribution of the foods that are eaten, and by social and foraging behaviors. Some behavior patterns tend to concentrate resources in the hands

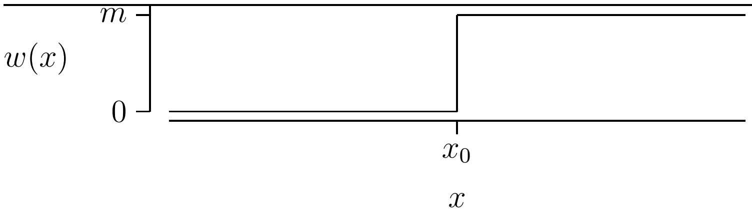

Figure 12.7: A step function.

The simplest assumption about the fitness function, $w(x)$, is that fitness is nil if wealth (x) is less than a threshold value, x_0, and is equal to a constant value, m, if x exceeds this threshold.

of a few successful individuals, while others tend to distribute resources more evenly. For example, where rich, dependable patches of resource can be found, a system of behavior called *territoriality* (discussed further in chapter 8 of this volume) is common. Powerful individuals gain exclusive access to rich patches, or "territories," by defending them against all comers. Those who acquire rich territories are well provided for; the others may starve, freeze, or be eaten by predators. Social dominance has a similar effect, if subordinate individuals are unable to feed until the dominant individuals are satisfied.

At the other end of the spectrum are populations in which resources are relatively evenly distributed among individuals. This may occur, for example, if resource patches are not rich enough or lasting enough to be worth defending, and foraging is done by individuals rather than groups. These differing patterns of behavior have profoundly different consequences for population dynamics. This can be seen most easily in two extreme cases: *scramble competition*, in which resources are divided evenly, and *contest competition* in which they are monopolized by a few individuals.

Scramble competition

Scramble competition will here refer to the hypothetical extreme case in which resources are divided perfectly evenly. (This usage of the term "scramble competition" follows that of Begon and Mortimer (1986), and differs from that of Nicholson (1954) and Łomnicki (1988).) The idea of an even distribution of resources sounds nice, but its effect on population dynamics can be decidedly unpleasant. To demonstrate this, we make use of the cobweb method described above.

The cobweb method requires a graph relating N_{t+1} to N_t, and this requirement impels us to ask how scramble competition affects the reproductive success of individuals. Suppose that each generation is allotted c units of resource. Since wealth is divided evenly, each individual in generation t will have wealth c/N_t. We can read the consequences of this off of figure 12.7. If individual wealth (c/N_t) exceeds x_0, then each individual will produce m offspring, so $N_{t+1} = mN_t$. This occurs when $N_t < c/x_0$. When the population is larger than this, no offspring are produced at all, and $N_{t+1} = 0$.

The critical population size, $K = c/x_0$, is the carrying capacity of the environment. In figure 12.8, the cobweb method is used to demonstrate the catastrophic consequences of pure scramble competition. The population

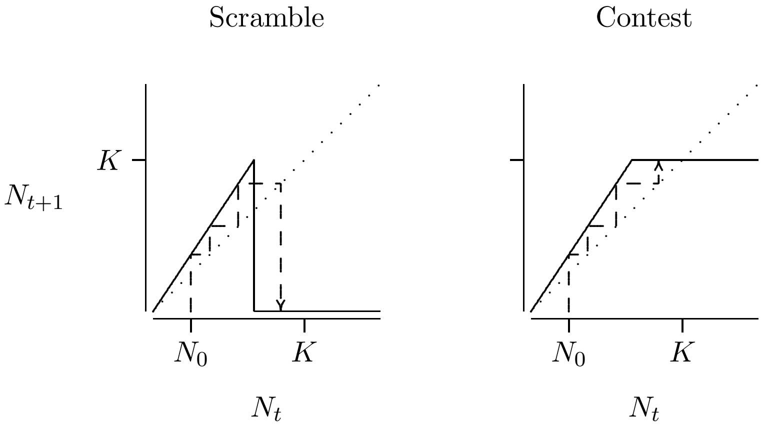

Figure 12.8: Scramble and contest

Under scramble competition, $N_{t+1} = mN_t$ if $mN_t \leq c/x_0$, and otherwise $N_{t+1} = 0$. Under contest competition, $N_{t+1} = mN_t$ if $N_t \leq K$, and otherwise $N_{t+1} = mK$. In both plots, $m = 1.5$.

grows until it exhausts the supply of resources (i.e. until $N_t > K$), and then "crashes," and goes extinct. If some small fraction of the population is able to survive the crash, the population will grow again until it reaches carrying capacity, and will then crash again.

The term "carrying capacity" is used in the literature in two different ways (Dewar 1984). One usage takes carrying capacity to be the maximum number of individuals that can survive if resources are divided evenly. The other takes it to be the equilibrium population size. In either case, we may expect the carrying capacity to vary, and these variations generate interesting kinds of instability (May 1974, Harpending and Bertram 1975). This chapter, however, deals only with the simple case in which carrying capacity (in either sense) is constant.

The model of scramble competition shows that the two definitions of carrying capacity are not equivalent. In our model, K is the carrying capacity since all the individuals in a population that size (but no larger) would be able to survive and reproduce. On the other hand, K is not an equilibrium because the mK children of such a population would all perish. Thus, the carrying capacity is not necessarily an equilibrium. A catastrophic fate may await any population that—like the human population of planet earth—is approaching carrying capacity. The extreme case of scramble competition gives us the worst case imaginable. What of the other extreme?

Contest competition

The other extreme is “contest competition.” In this case everyone gets an equal share if $N_t \leq K$, but not if $N_t > K$, for the available resources are then divided evenly among only K individuals, and the rest get nothing. The consequences of this form of social inequality can be derived using the cobweb method, as before.

For concreteness, let us consider a system of territoriality in which there are K territories, each rich enough to enable one individual to breed. This implies that each territory contains at least x_0 units of resource, and that each territory holder will produce m offspring. If there are no more than K adults, each will acquire a territory and produce m children. If fewer than K children are thus produced, each child will acquire a territory and survive. Thus, $N_{t+1} = mN_t$ provided that $mN_t \leq K$. If there are more adults than this, more children will be produced, but only K of them will find territories, and the rest will perish. Thus, $N_{t+1} = K$ if $mN_t > K$. The cobweb diagram representing this case is shown in figure 12.8, and demonstrates that contest competition produces stable population dynamics. The population will increase monotonically to its equilibrium value, K, and then stay there. In contrast to the case of scramble competition, the carrying capacity *is* an equilibrium under contest competition.

This is good news, because the human population approximates the case of contest competition a good deal more closely than that of scramble competition. Not only do individual humans own property of various sorts, and defend it against one another, they maintain police forces that aid them in these efforts. In addition, vast resources are also controlled and defended collectively, by corporations and by nations. Even when resources are shared, larger shares often go to individuals of high status (Betzig 1988). Consequently, resources are not divided evenly among nations, or among individuals within them. As resources become scarce, poor nations (and individuals) will suffer more than rich nations (and individuals). This inequality causes a great deal of suffering that, in my opinion, justifies the prevailing view that inequality is a social evil. All the same, its beneficial effects on population dynamics should not be overlooked.

The distribution of individuals across the landscape

Ordinarily, individuals that are far apart do not compete. The intensity of competition depends less on the number of other individuals in the species as a whole than on the number of near neighbors. If individuals are distributed evenly in space, the number of neighbors will be smaller than if individuals are clumped together. For example, Lewontin and Levins (1989) point out that although there are about 60 humans per square mile in the United States as a whole, the average US citizen shares his or her square mile with 3105 neighbors. This is because the US population is "clumped" into cities and towns whose population density is quite high.

These observations suggest that any behavior that, like those discussed by Cashdan (chapter 8), affects the way in which individuals are distributed in space, will also affect the stability of population dynamics. In simple mathematical models, clumping reduces stability (Hassell and May 1985). However, this effect is most pronounced in populations that are capable of extremely rapid growth. The effect of clumping on human population dynamics may be small because of the limitation on growth rate that is imposed by our comparatively low reproductive capacity.

12.4.2 Relaxing assumptions

The analysis above of scramble and contest competition produced rather unpleasant results, which should not be accepted uncritically. Perhaps they are due to some unrealistic feature of the models. To find out, we must add realism to the models.

We have relied on simplistic assumptions both about the shape of the fitness function and also about the way in which resources are divided among individuals. To add realism, let us drop the restrictive assumption that w is a step function, and assume only that it is a non-decreasing function of wealth—that wealthier people produce at least as many children, on average, as those who are less wealthy. This seems plausible, and is not a controversial assumption in animal ecology. It is not at all clear, however, that this pattern holds among humans. This controversy is discussed below, but let us ignore it for the moment.

I have also made extremely simple assumptions about the distribution of wealth among individuals. I now assume instead that wealth is distributed among individuals in some arbitrary fashion. I shall not specify whether

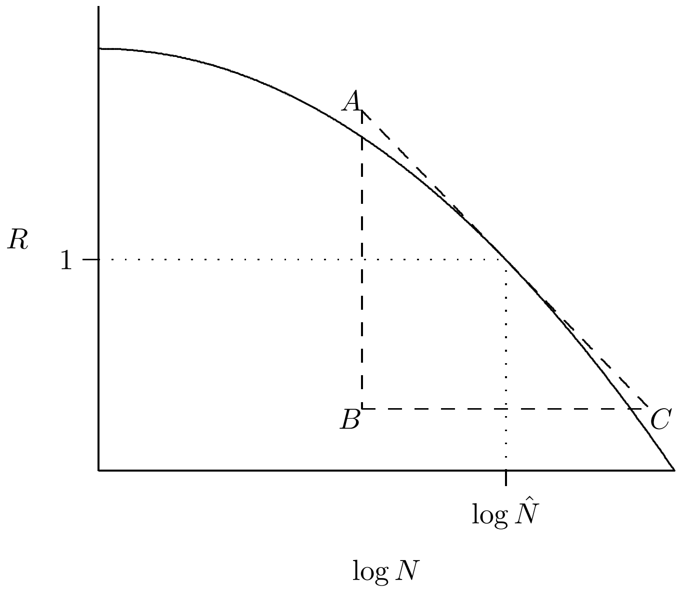

Figure 12.9: The meaning of $dR/d\log N|_{N=\hat{N}}$
The solid line graphs R as a function of $\log N$ for some hypothetical population. The equilibrium, $N = \hat{N}$, occurs at the point where $R = 1$, as shown by the dotted lines. Line AC is drawn tangent to R at this point, so that the slope of AC is equal to that of R at the equilibrium point. This slope is equal in magnitude to the ratio of lengths of line segments AB and BC, and is negative because R decreases as $\log N$ increases. Thus, $dR/d\log N|_{N=\hat{N}} = -\overline{AB}/\overline{BC}$.

wealth is distributed evenly or unevenly, or whether poor individuals are common or rare. I shall say only that there is some arbitrary function, $f_N(x)$, that measures the relative frequency of individuals of wealth x in a population of size N. To be precise, if dx is some very small value, then $f_N(x)dx$ is the number of individuals whose wealth lies between x and $x + dx$. (In the language of probability theory, I am saying that $f_N(x)$ is the *probability density* of individuals with wealth x.) In this notation, the function R can be written as

$$R(N) = \int_0^\infty w(x) f_N(x) dx, \tag{12.3}$$

which is merely a formal way of saying that R is the average reproductive success of the individuals in the population.

In this more general context, the method of cobwebbing breaks down, for

Table 12.1: Criteria for local stability of an equilibrium at $\hat{N}$.
The quantity $\frac{dR}{d\log N}|_{N=\hat{N}}$ is the derivative (or slope) of R as a function of $\log N$, evaluated at the equilibrium point, where $N = \hat{N}$ (see figure 12.9).

$\frac{dR}{d\log N}\|_{N=\hat{N}}$	Behavior near $\hat{N}$	
> 0	Monotone divergence	(Unstable)
–1 to 0	Monotone convergence	(Stable)
–2 to –1	Damped oscillations	(Less stable)
< -2	Diverging oscillations	(Unstable)

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in order to construct the necessary graph, we would first need to specify the functions w and f_N, thereby losing the generality we seek to introduce. To evaluate the stability of equation 12.2 *in general*, we must abandon graphical analysis in favor of mathematics. The price that is paid for this generality (apart from the need for mathematics) is an enormous loss of detail. The mathematical analysis will tell us only about the behavior of populations that are already very near the equilibrium. An equilibrium is said to be *locally stable* if a population very near to it tends to get closer, and locally unstable if such populations tend to move away. The mathematics will not tell us what happens to populations that are far from the equilibrium, nor will they allow us to reconstruct the time path of population growth.

Mathematical analysis of local stability rests on a well known relationship (Maynard Smith 1968: 22) between the local stability of an equilibrium at $\hat{N}$, and the derivative $dR/d\log N|_{N=\hat{N}}$. As explained in the legend of figure 12.9, this derivative tells how the rate of reproduction (R) changes when the population is perturbed a little ways away from its equilibrium. Table 12.1 says that an equilibrium is stable provided that a small increase in population size reduces the rate of reproduction, but not by too much.

To use these results, we must evaluate the derivative, $dR/d\log N$, which depends both on the fitness function, w, and on the way in which the frequency distribution of wealth changes as the population grows. Let us reexamine the two forms of competition discussed above in this more general context.

Generalized scramble competition

In the earlier model of scramble competition, a reduction in overall wealth would have produced an equal proportional reduction in the wealth of each individual. For example, if each individual in a population of size 100 had wealth 10, then there must have been $10 \times 100 = 1000$ units of wealth in all. If the population had doubled, each individual would have had $1000/200 = 5$ units. Thus, doubling the population size would halve the wealth of each individual. We now dispense with the assumption that wealth is evenly divided, but let us continue to assume that an increase in population size produces an equal proportional reduction in the wealth of each individual. This provides a generalized model of scramble competition, in which the ratios of the wealths of individuals are unaffected by changes in overall wealth. The generalized model includes the earlier one as a special case in which all individuals have the same wealth, so that the ratios of individual wealths are all 1:1. The generalized model is more realistic, and may be a fair description of *exploitation competition* (Park 1954), the case in which individuals compete by exploiting a resource to which all have access. Under exploitation competition, differences in wealth arise solely from differences in ability to exploit the resource. If Joe can harvest twice as much resource per hour as Jack can, then he will be twice as wealthy. We are assuming that the magnitude of Joe's advantage does not depend on the richness of the habitat.

The question is, under what circumstances is this new, generalized model stable? This will depend on the slope ($dR/d\log N$) that is referred to in table 12.1. In an earlier paper (Rogers 1986), I showed that, under the assumptions just stated, this slope is equal to –1 times the slope of the graph of mean fitness ($\bar{w}$) against the mean of log wealth. If this latter slope is small—if mean fitness increases only slowly with the mean of log wealth—then table 12.1 ensures that equilibria will be stable under generalized scramble competition. Before trying to decide whether this condition is likely to be satisfied, consider carefully what it means.

Three hypothetical graphs relating mean fitness ($\bar{w}$) against mean log wealth is shown in figure 12.10. Log wealth is assumed to follow a normal distribution (the familiar bell-shaped curve), and curves are shown for three different values of the standard deviation, σ. When $\sigma = 0$ all individuals have identical wealth, so mean fitness ($\bar{w}$) is the same as individual fitness (w). In that case, the curve shown is strongly sigmoid, or "S" shaped. Why? Because in most species, reproduction is probably impossible unless wealth

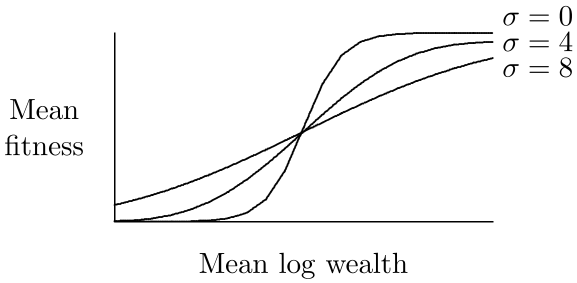

Figure 12.10: Mean fitness, $\bar{w}$, as a function of mean log wealth
Here σ^2 is the variance of log x. It is assumed that $f_K(x)$ is log-normally distributed and that $w \propto 1/(1 + 1/x)$.

exceeds some minimum value, so below that value the slope of w will be near zero. The slope will also be near zero where x is large, since there will be some physiological limit to the number of young that can be produced even if unlimited resources are available. Thus, the graph of w should be flat at the left edge of the graph (where x is small) and also at the right edge (where x is large). The slope should be steepest for intermediate values of x, and may even approximate a step function there. Thus, when there is no variation among individuals ($\sigma = 0$), the slope of the graph may be very steep in the central portion. Since this slope is -1 times $dR/d \log N$, table 12.1 shows that equilibria may easily be unstable. In general, the steeper the graph of $\bar{w}$ against log wealth, the more likely dynamics will be unstable.

Now study the curves for $\sigma = 4$ and $\sigma = 8$, which refer to populations with greater variation in wealth. Increasing variation tends to flatten out the curves, and thus makes equilibria more stable. Conclusion: an even partitioning of resources reduces the stability of population dynamics even in this generalized model of scramble competion. (For further discussion of this topic, see Łomnicki 1978, 1980, 1982, Łomnicki and Ombach 1984, Łomnicki and Sedziwy 1988, 1989, Rogers 1989).

So far, the news about the effects of scramble competition is mostly bad: The unpleasant results of the earlier model still hold. On the other hand, there is also good news. If the slope of the fitness function is everywhere less than two, then the slope of mean fitness ($\bar{w}$) must also be less than two, and equilibria will be stable regardless of the distribution of resources among individuals. Thus, the earlier unrealistic assumption that w is a step function served to exaggerate the adverse effect of social equality. Real populations may be able to survive these adverse effects, provided that their fitness functions are not too steep. It will be important, therefore, to consider how evolution affects the slope of the fitness function. But first let us generalize the earlier model of contest competition to see whether w plays an equally important role there.

Generalized contest competition

The task now before us is that of constructing a model of contest competition that allows an arbitrary distribution of wealth, and an arbitrary fitness function. To make it a sensible model of contest competition, we shall require that additional individuals do not affect the wealth of the individuals already there. Consider, therefore, a hypothetical territorial population that inhabits an environment in which the number of territories whose wealth lies between x and $x + dx$ is $h(x)dx$, where dx is some very small number. Assume that individuals always inhabit the best available territory, and let $x_0(N)$ denote the wealth of the poorest territory inhabited in a population of size N.

Box 1 shows that, in this model, $dR/d\log N|_{N=\hat{N}} = w(x_0) - 1$. Consequently, table 12.1 implies that population dynamics will be stable provided that $0 < w(x_0) < 1$. In other words, stability requires that the fitness of the poorest individual in the equilibrium population be between zero and unity. Now a fitness cannot be negative, so the first of these inequalities is always satisfied. The second will be satisfied provided only that w is an increasing function of wealth. With a bizarre fitness function in which fitness *decreases* with wealth over at least a part of its range, $w(x_0)$ might exceed unity, making equilibria unstable even under contest competition. But if, as intuition suggests (see below), fitness always increases with wealth, then contest competition will always lead to stable population dynamics, at least in deterministic models such as we have studied.

Real populations, however, are subjected to random perturbations of various kinds, and these tend to make dynamics less stable than table 12.1 would suggest. For example, if $w(x_0) = 0$, the analysis above indicates that the population will fall on the boundary between monotone convergence and damped oscillations. In reality, random effects would cause such a population to oscillate towards its equilibrium. On the other hand, if the fitness function is fairly flat so that $w(x_0)$ is close to unity, population dynamics will be more resistant to random perturbations, and therefore more stable. Thus, even in the case of contest competition, a steep fitness function tends to destabilize

Box 1: Stability under generalized contest competition

Let $H(x)$ denote the number of territories whose quality is less than x. Now x can take only integer values, but if the total number of territories is large, we can approximate $H(x)$ by a smooth curve, and write its derivative as $h(x) = dH(x)/dx$. The number of individuals in a small interval, $[x,\ x + dx]$, is $H(x + dx) - H(x)$, which approaches $h(x)dx$ as $x \to 0$. The total number of territories is therefore $\int_0^\infty h(x)dx$.

To model contest competition, let us assume that each territory can contain at most one individual, and that the best territories are always occupied first. Let $x_0(N)$ denote the quality of the worst territory occupied in a population of size N. Then

$$N = \int_{x_0(N)}^{\infty} h(x)dx \tag{12.4}$$

and the population size in generation $t + 1$ is related to that in generation t by $N_{t+1} = \int_{x_0(N_t)}^\infty h(x)w(x)dx = N_t R(N_t)$, where $w(x)$ is the fitness (reproductive success) of an individual in a territory of quality x, and $R(N) = N^{-1}\int_{x_0(N)}^\infty h(x)w(x)dx$. The stability of population dynamics depends on the derivative, $dR/dN = (-N^{-2})\int_{x_0(N)}^\infty h(x)w(x)dx + N^{-1}[w(x_0(n))h(x_0(N))x_0'(N)]$ where $x_0'(N) = dx_0(N)/dN$. To find $x_0'(N)$, differentiate both sides of equation 12.4 to get. $dN/dN = 1 = -h(x_0(N))x_0'(N)$ whence

$$\begin{aligned} x_0'(N) &= -1/h(x_0(N)), \\ \frac{dR}{dN} &= N^{-1}[w(x_0(N)) - R(N)], \end{aligned}$$

and

$$\frac{d\log R}{dN} = N\frac{dR}{dN} = w(x_0(N)) - R(N)$$

Since we are evaluating this derivative at the equlibrium, where $R(N) = 1$, we have

$$\frac{d\log R(\hat{N})}{dN} = w(x_0(\hat{N})) - 1.$$

This result, together with table 12.1, shows that the stabilities of equilibria under generalized contest competition are determined by $w(x_0(\hat{N}))$, the fitness of the individual in the poorest inhabited territory in the equilibrium population.

population dynamics.

12.5 Evolution of the Fitness Function

Evolution affects population dynamics in various ways. Since the behavior of individuals affects both the distribution of resources among individuals and the distribution of individuals across the landscape, the evolution of behavior affects population dynamics. In addition, evolution also affects population dynamics via its effect on life history strategies, for these strategies determine the fitness function, w. In simple evolutionary models, selection favors those who produce the largest number of surviving offspring. If, in addition, one assumes that the ability to rear offspring is constrained by wealth, then it follows that the rich should reproduce faster than the poor. Thus, it seems reasonable to expect that natural selection will favor a fitness function that increases with wealth.

The evolution of the fitness function is probably also affected by mechanisms of population regulation. MacArthur and Wilson (1967, 1972) distinguished between "r-selected" populations, which are usually kept well below their equilibrim size by density-independent mechanisms, and "K-selected" populations, which are usually near equilibrium. The terms refer to the suggestion that r-selection will increase r (the instantaneous growth rate), whereas K-selection will increase K (the equilibrium size, usually called the carrying capacity) (Armstrong and Gilpin 1977). This classification has been of enormous heuristic value in ecology, although it is of only limited value in describing nature (Begon and Mortimer 1986). More realistic classifications are available (Caswell 1982, Sibly and Calow 1985, Begon 1985), but require more detail than is present in the models developed here.

These selection regimes should have quite different effects on the fitness function, as illustrated in figure 12.11. Under r-selection, resources are usually abundant, so selection would tend to push the right side of the fitness function up, increasing its slope. On the other hand, resources are usually scarce under K-selection, so selection will tend to push up the left side of the fitness function, decreasing its slope. Consequently, r-selection should reduce the stability of population dynamics.

Humans are generally regarded as a K-selected species, so these arguments would lead us to expect fitness to increase gently with human wealth. There is a good deal of evidence, however, that this is not so. Figure 12.12

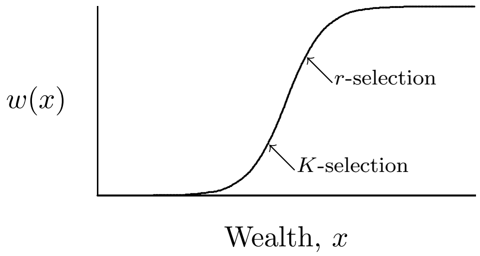

Figure 12.11: How r- and K-selection would affect the fitness function. In a K-selected species, resources are usually scarce, and selection will push up the left side of the graph. In an r-selected species, resources are usually abundant, and selection will push the right side up.

shows that the fertility of Brazilian males *decreases* with wealth, a blatant contradiction of our expectations. Similar data from a variety of sources are summarized by Vining (1986), who argues that they indicate that evolutionary arguments are of little relevance in the study of human behavior. If these data truly represent the human fitness function, then the arguments presented above suggest that

1. Under scramble competition, $d\bar{w}/d\bar{z} < 0$ and therefore $dR/d \log N > 0$, which means (as table 12.1 shows) that population dynamics will be unstable.

2. Under contest competition, it is possible that $w(x_0) > 1$, since the fitness function apparently has a negative slope. This would make population dynamics unstable even under contest competition!

Thus, a fitness function such as that in figure 12.12 would have bizarre consequences for population dynamics. It might produce instability even in a population such as our own, which resembles to the ideal of contest competition more than that of scramble competition.

There are, however, reasons to be skeptical of such conclusions. Even if the poor do enjoy an advantage during good times, it is hard to imagine that this advantage could survive under conditions of extreme scarcity. In addition, other evidence suggests a positive relationship between wealth and reproduction (Simon 1977, Mealey 1985, Irons 1979, Turke and Betzig 1985, Essock-Vitale 1984, Borgerhoff Mulder 1989). Furthermore, the number of one's offspring may not be a good indicator of reproductive success in the

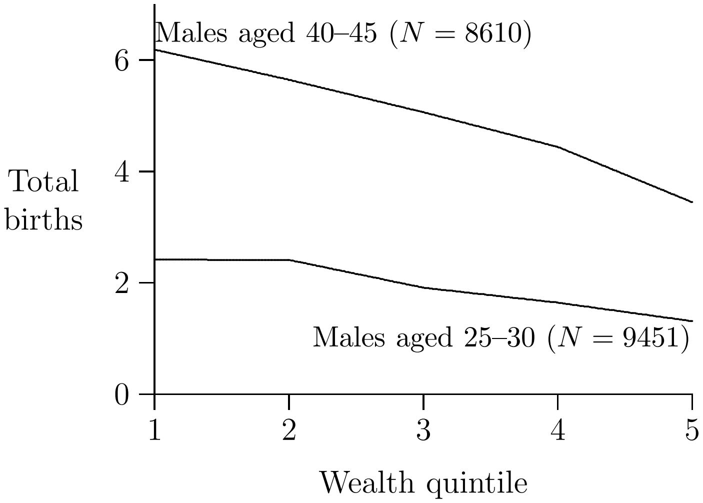

Figure 12.12: Mean fertility of Brazilian males by wealth quintile (Lam 1986).

long run. This is particularly true of species, such as our own, in which wealth can be passed on from generation to generation. To show why, the next section will discuss a model (Rogers 1990, Harpending and Rogers 1990) of natural selection with heritable wealth.

12.5.1 Optimal reproduction when wealth is heritable

Humans are unusual in that they can inherit wealth, as well as genes, from their parents, and can pass these bequests on to their own children if they choose. Thus, a bequest left by a parent may affect the reproductive success of his descendants for several generations. Wealthy parents must choose between producing many offspring who will each inherit relatively little, or a few who will each inherit much more. Which choices would be favored by natural selection?

To answer this question, we need a an evolutionary model that allows reproductive opportunities to vary with wealth, that allows wealth to be inherited, and that uses an unusual measure of fitness. In this context, the appropriate measure of fitness is not the number of one's offspring, but the number of one's descendants in some generation in the distant future. In a recent paper (Rogers 1990), I developed such a model, and showed that reproductive strategies that maximize the number of one's offspring do not necessarily maximize the number of one's descendants in the long run. Similar effects arise even when wealth is not heritable. For example, David Lack (1948) showed that birds must limit the number of offspring hatched in order to maximize the number that survive to breed. R.A. Fisher's (1958) model of sex ratio evolution looked beyond the number of offspring produced, and showed that selection maximizes the number of one's grandchildren. The novelty introduced by heritable wealth is that one must also look beyond the number of grandchildren. It no longer suffices to count either the surviving children or the grandchildren produced. One must count the number of descendants produced in some generation in the distant future.

My model allowed each parent to allocate some portion of her wealth (the "fertility allocation") toward the production of offspring, and divided the rest as bequests among the offspring that she produced. A reproductive strategy was taken to be a rule specifying the fertility allocation as a function of wealth, and optimal reproductive strategies were those which maximized the long-term rate of increase in the numbers of one's descendants. Increasing fertility allocations yielded increasing fertility, as specified by the fitness function, which was assumed to follow a law of diminishing returns. One of the fitness functions that was used is illustrated by the open circles in the upper panel of figure 12.13. In addition to inheriting wealth, offspring also earn some on their own, as specified in the figure legend.

The optimal reproductive strategy is the one that maximizes the ultimate rate of increase in the number of one's descendants, and is found by a method that is discussed in the next section. For now, it is important only to notice that, as the upper panel in figure 12.13 shows, optimal fertility is *not* an increasing function of wealth under these assumptions. It increases, then decreases, then increases again. The lower panel in this figure graphs what is called "long-term fitness" as a function of wealth. Long-term fitness is discussed further below, and measures one's genetic contribution to generations in the distant future. Note that long-term fitness increases with wealth even though fertility does not.

The assumptions of this model are too unrealistic for it to be of much use in data analysis. Its value lies in what it shows us about the possibilities that may arise under evolution in structured populations. When individuals may belong to one of several classes, and when these classes offer differing reproductive opportunities, we cannot measure fitness in terms of offspring produced. As we have just seen, there need be no simple relationship between the number of one's offspring, and one's expected genetic contribution to

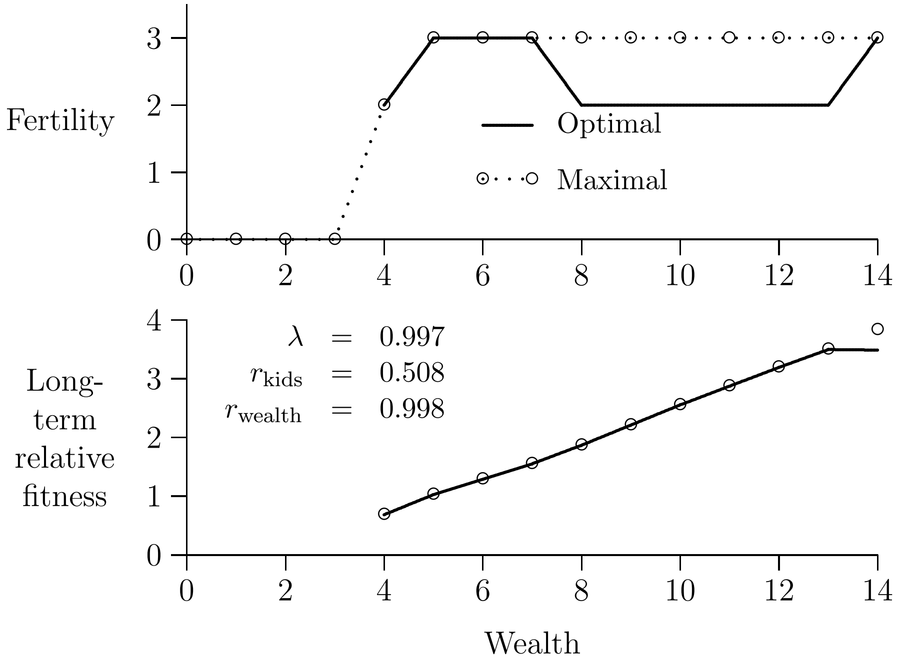

Figure 12.13: Optimal reproduction in an environment of intermediate quality

Upper panel: The dotted line panel shows the relationship between fertility and the allocation of wealth to fertility. The solid line shows optimal fertility as a function of total wealth, assuming that, in addition to her inheritance, each offspring may "earn" some wealth on her own. Earnings are a Poisson random variable with mean 3. Lower panel: The solid line graphs, as a function of total wealth, the long-term fitness of individuals adopting the optimal reproductive strategy. The open circles show long-term fitness in a model with the same parameters except that maximal wealth is 40 instead of 15. λ is the long-term growth rate, r_{kids} is the correlation between long-term fitness and fertility, and r_{wealth} the correlation between long-term fitness and wealth.

future generations. Thus, in structured populations, we should seek ways to measure long-term fitness. The next section shows how this can be done using, as an example, the fertility and mobility among four social classes in the population of England and Wales.

12.6 Long-term Fitness and Social Class

Berent (1952: 247) described the fertility and mobility among four British social classes. For convenience, I number these from 1 to 4, with 1 representing the lowest class and 4 the highest (Berent, incidentally, used the opposite system). The pattern of fertility and mobility among the classes in Berent's data can be described by a matrix,

$$\mathbf{G} = \begin{array}{c} \\ 1 \\ 2 \\ 3 \\ 4 \end{array} \begin{array}{c} \begin{array}{cccc} 1 & 2 & 3 & 4 \end{array} \\ \begin{pmatrix} 1.81 & 0.77 & 0.33 & 0.15 \\ 1.34 & 1.36 & 0.72 & 0.30 \\ 0.37 & 0.49 & 0.94 & 0.57 \\ 0.04 & 0.12 & 0.18 & 0.86 \end{pmatrix} \end{array}$$

whose ijth entry (the entry in row i and column j) is the mean number of offspring of social class i produced per parent of class j, after one generation. Clearly, we could construct such a matrix for categories of wealth, religion, or anything else. The approach described here is a simplified version of the methods described by Bartholomew (1982), Lam (1986), Chu (1987), Rogers (1990), and Harpending and Rogers (1990).

12.6.1 Projecting fitness forward in time

We are interested in the genetic contribution made by members of each class to the distant future, but let us begin by summing the rows of $\mathbf{G}$ to calculate the number of offspring born to members of each class. This gives 3.56 for class 1, 2.73 for class 2, 2.17 for class 3, and 1.88 for class 4. Now we can calculate the numbers of grandchildren for each class as follows.

$$\begin{aligned} 10.98 &= 1.81 \times 3.56 + 1.34 \times 2.73 + 0.37 \times 2.17 + 0.04 \times 1.88 \\ 7.72 &= 0.77 \times 3.56 + 1.36 \times 2.73 + 0.49 \times 2.17 + 0.12 \times 1.88 \\ 5.51 &= 0.33 \times 3.56 + 0.72 \times 2.73 + 0.94 \times 2.17 + 0.18 \times 1.88 \\ 4.20 &= 0.15 \times 3.56 + 0.30 \times 2.73 + 0.57 \times 2.17 + 0.86 \times 1.88 \end{aligned}$$

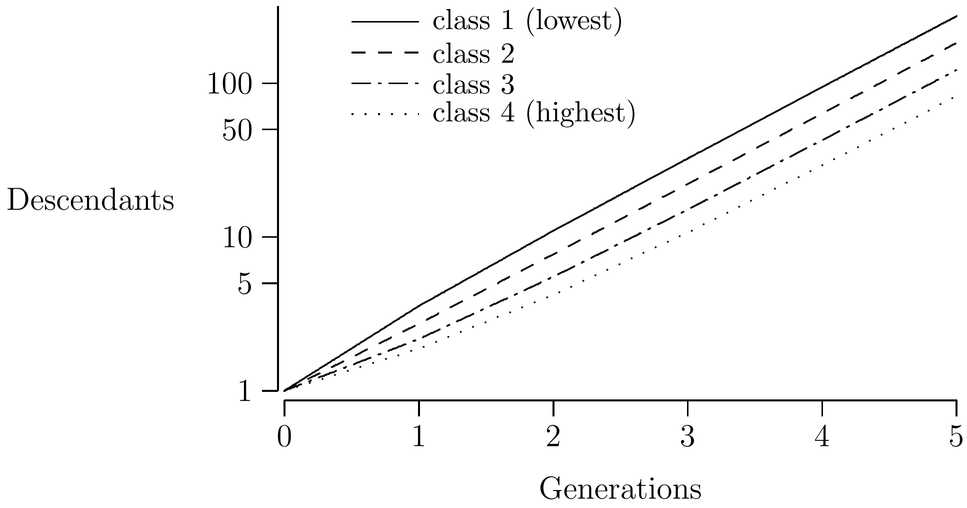

Figure 12.14: Projection of fitnesses using British social mobility matrix
Numerical projection of fitnesses using Berent's data (matrix **G**) on fertility and social mobility.

Note that each row above uses the values from one column of **G** along with the fertility values that we just calculated. The first row says that each parent in class 1 produces 1.81 class 1 offspring that each produce 3.56 grandchildren, 1.34 class 2 offspring that each produce 2.73 grandchildren, 0.37 class 3 offspring that each produce 2.17 grandchildren, and 0.04 class 4 offspring that each produce 1.88 grandchildren. Adding these up gives 10.98, the total grandchildren per parent in class 1.

To summarize these calculations, it is helpful to have an algebraic formula. Let us write $w_i(1)$ for the expected number of offspring of individuals of class i, $w_i(2)$ for the expected number of their grandchildren, $w_i(3)$ for their expected great grandchildren, and so forth. In general $w_i(t)$ will be called the "t-generation fitness" of individuals in class i. The arithmetic of the preceding paragraph is summarized by the formula

$$w_i(t+1) = \sum_j g_{ji} w_j(t) \tag{12.5}$$

By applying this recipe again and again, we can find the number of descendants in any future generation produced by individuals in each social class. The results of this procedure are shown in figure 12.14. Notice that the curves

Table 12.2: Stable wealth distribution and long-term fitness

"Fertility" is the number of offspring born per family within a ten year period, and "long-term fitness" of each class measures the eventual reproductive success per family in that class relative to that of an average family (see text for details). As the population grows, the relative frequencies of the four social classes converge to the "stable distribution."

Social Class	Fertility	Long-term Fitness	Stable Distribution
1	3.56	1.37	0.36
2	2.73	0.92	0.41
3	2.17	0.61	0.18
4	1.88	0.41	0.05

for the four social classes form straight, parallel lines after the first few generations. Since the y axis is on log scale, these lines can be straight only if the t-generation fitnesses are increasing exponentially. The fact that the four lines are parallel means that all four classes have the same rate of exponential increase. It also means that the ratios, $w_i(t)/w_j(t)$, between pairs of social classes have stopped changing. Thus, after two or three generations the t-generation fitnesses have converged to the "long-term fitness" values. These can be written in standard form by dividing $w_i(t)$ by the mean t-generation fitness. The result (table 12.2) shows that long-term fitness declines steadily with wealth, and that the poorest class has over three times the long-term fitness of the wealthiest class. This means that, eventually, individuals of the lowest class will achieve more than three times the genetic representation of individuals in the highest class. Incidentally, long-term fitness is equivalent to a quantity that is called the *reproductive value* in demography (Fisher 1958: ; see section 11.2.1). I have used a different term here since "reproductive value" conventionally refers to categories of age rather than social class.

We are now in a position to re-evaluate my criticism of Vining's (1986) argument that since fertility declines with social class, humans must not be striving to maximize reproductive success. In response to Vining's article (Rogers 1990), I objected that his conclusion was not justified because the number of one's offspring may be a poor indicator of long-term fitness. Poor parents might have lower long-term fitness in spite of their higher fertilty. However, the long-term fitnesses in table 12.2 suggest that Vining was right after all, at least for this British population. The poor have greater reproductive success even in the long run. If these data are to be believed, and if the pattern of reproduction that they describe continues, then the British population will eventually be dominated by the genes of those now in the lower classes, as Fisher (1958) first suggested in 1930.

There are, however, reasons to be skeptical of this conclusion. Berent's data on reproductive success tell us only the number of births during the 10 years before the sample was taken. We do not know what fraction of the infants born survived to maturity, and neither do we know what fraction of these survivors were able to form families of their own. It is possible that lower class individuals are less likely to survive, or to marry, than their upper class counterparts. Furthermore, I have taken no account of nonpaternity—the possibility that some of the offspring in Berent's data have been attributed to men not their biological fathers. Estimated rates of nonpaternity vary from population to population, ranging from 2.3% to 30% (Potthoff and Whittinghill 1965, Peritz and Rust 1972, Philipp 1973, Neel and Weiss 1975, Ashton 1980, Lathrop et al. 1983). If the biological father tends to come from a different social class than the putative father, then my calculation of the long-term fitnesses from Berent's data may be badly in error.

On the other hand, it is also possible that the human adaptation is out of date, as Vining suggested. Perhaps we behave in ways that increased the reproductive success of our ancestors, but no longer do so today. If so, evolutionary theory will still be useful in discovering why the human mind has evolved into its present form, but we should not expect humans to maximize reproductive success in modern environments (Symons 1989, Blurton Jones 1990).

12.7 Conclusions

The human population has grown at an unprecedented rate for longer than anyone now alive can remember, but this epoch of rapid growth appears to be drawing to a close. Mechanisms of density-dependent population regulation will have increasingly severe effects in the decades to come. Yet this need not imply that our population is converging toward some equilibrium size. Density-dependent population regulation can also generate various kinds of unstable dynamics, in which population numbers rise and fall cyclically. The response of our population to increasing scarcity will depend on a variety of factors. Behaviors such as territoriality and behavioral dominance tend to stabilize population dynamics while the clumping of populations into towns and cities may have the reverse effect.

All of these effects are mediated by the "fitness function" which relates reproductive success to wealth. Plausible assumptions about the fitness function imply that population dynamics will be somewhat more stable than simple models predict. However, there is evidence of a bizarre relationship between wealth and human reproduction. In many human societies, the poor consistently have more children than the rich. This need not imply that they have more descendants in the long run, for wealthy offspring may enjoy improved reproductive opportunities. Thus, the small, wealthy progeny of a rich woman may generate more great great grandchildren than the large, poor progeny of her impoverished sister. However, data from the post World War II population of England and Wales suggest that exactly the opposite is true. Individuals of the poorest class produce roughly twice the offspring of the richest class, and their advantage in long-term fitness is even greater. Members of the poorest class will ultimately produce more than three times as many descendants as do members of the richest class.

This finding does not settle the issue, for it is based on data that are inadequate in several ways. What it will do, I hope, is to show clearly what is at issue, and how that issue might be settled with better data.

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