Part II. PROCESSES OF HUMAN EVOLUTION

Chapter 8. BASIC DEMOGRAPHIC CONCEPTS

> The human species would increase in the numbers 1, 2, 4, 8, 16, 32, 64, 128, 256; and subsistence as 1, 2, 3, 4, 5, 6, 7, 8, 9.
>
> Thomas Malthus, 1798

O. Introduction to Part II of the Course

A. Culture Core and Human Variation Revisited

In the last section we saw that a large fraction of the variation in human behavior is correlated with environmental variation and is plausibly adaptive. Steward's culture core concept, with its ecological component, does lead to a compact taxonomy that organizes the mass of data on humans in a useful way. In addition an evolutionary schema of societies seems to emerge quite nicely.

What Steward's culture core concept lacks is a precise account of the mechanisms by which adaptive variations within technological types arise, and how evolutionary transformations between technological types occur. Ecological anthropologists like Steward developed a very successful *descriptive* scheme, but a less impressive *explanatory* system. The evolutionary concept of adaptation has been invoked, and the evolutionary process alluded to, *but what evolutionary mechanisms might account for these environmental correspondences and historical changes*? Seward imagined a progressive evolutionary impluse carrying societies from lower to higher technology, but the process driving the progressive improvement of technology was not clearly related to ecological mechanisms. The separation of evolution and ecology into two separate realms, strikes a biologist as very odd. For Darwinians, evolutionary processes are merely ecological processes plus lots of time.

What is required is a mechanistic understanding of the processes of evolution. Until recently there has been no synthetic theory describing how cultures adapted and evolved, comparable to Darwinian theory. The theory of human ecology and evolution had none of the pleasing explanatory elegance of the biologist's hypothesis that evolution proceeds mainly due to natural selection, even though the basic nature of the problem of cultural evolution is very similar to the problem of organic evolution, as Darwin (over)stressed.

Darwin's theory, and its successors today, are still incomplete and perhaps wrong, certainly in detail. But Darwinian evolutionary theory does give a comprehensive and plausible account of organic adaptation and evolution. It would be quite surprising if any theory utterly replaced, as opposed to modified, the modern synthetic theory of evolution. A viable candidate to make a radical replacement of Darwinian theory would have to be really impressive, because the accomplishments of Darwinian theory are so spectacular. On the other hand, it is widely acknowledged that the social sciences have no theoretical foundation of the same caliber; the relative inadequacy of Stewardian ideas is plain to all. We are now prepared to remedy this lack, as well as it can be remedied at the present state of our knowledge. Our approach will be to modify the very same Darwinian theory used by biologists to explain the human case.

B. Next Six Chapters Will Apply Darwinism to Culture

In the next six chapters we will be considering the basic processes that affect the evolution of human phenotypes[1]. This chapter we will consider the basic elements of demography, and next chapter of organic evolution (all of the basic neo-Darwinian theory in two chapters; be warned about the level of simplification here!). Chapter 10 will deal with application of neo-Darwinian theory to human behavior. In succeeding Chapters 11 and 12, we will turn to the analogous processes of cultural evolution and the processes that link them to genetic evolution. We will see what progress can be made in postulating a synthetic evolutionary theory that takes account of the coevolution of genes and culture. This theory suggests at least some provisional answers to the four basic problems of human ecology outlined in Chapter 2:

1. Why do humans have so much culture?
2. Why do humans live in such big, complex groups?
3. Why do humans engage in so much symbolic behavior?
4. What is the relationship between scientific and historical explanations for the variation we observe between human societies?

In order to keep things simple, we will focus on elementary general models of evolutionary processes. One of the most drastic simplifications will be to keep considerations of the environment at a minimum level. The ecological part of evolutionary processes will be reduced to very abstract selective regimes, influences on individual decisions, and the like. In Part IV of the course we will add some ecological realism back in. (This tactic of studying simple models first and adding complexity back in afterwards has been very useful in evolutionary biology and the social sciences, as was mentioned in the introduction.)

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[1] Remember the definition of ‘phenotype’: the visible properties of an organism that are produced by the interaction of the genotype and the environment. Thus, phenotype includes *both* physical factors such as amount of body fat and cultural factors such as adolescent dating behavior.

I. Introduction to Basic Demography (Basic Population Ecology)

Reverend Thomas Malthus was the first person to reason hard about the nature and behavior of populations. In *An Essay on the Principle of Population,* first published in 1798 and amended, altered, and enlarged up to 1830, he produced a landmark in many respects. His ideas founded the study of demography, the science of population growth and decline[2]. Both human demography and the study of plant and animal population ecology are built squarely on Malthus' foundation.

Malthus' ideas and method of investigation were, according to Darwin, the direct inspiration for his idea of evolution by natural selection. In the next chapter we'll discuss in detail how Darwin's ideas rest on a Malthusian foundation. The key idea of Malthus was to trace out clearly the implications of individual reproductive behavior for the longer run behavior of whole collections of individuals, the population. His method was the deductive mathematical argument in very simple form: "Give me a few plausible assumptions about human biology and environment, let me do some simple arithmetic, and I'll show you the most amazing conclusion, the inevitability of competition for limited resources." Such simple arguments are almost always oversimplified, and to that extent wrong, but they often give us a very clear insight into a particular process. They also tend to sharpen and clarify debate. Simple, clear arguments are the most important tools we use to think about causal processes that affect complex, diverse systems. Malthus was a pioneer in applying this style of thought to human ecology.

A population is a set of interbreeding individuals that interact with an environment, reproduce, and then die. According to the famous evolutionary biologist Ernst Mayr (1984), the concept of population (*"population thinking"*) is the greatest contribution of Malthus and Darwin to science. Malthus considered how such populations behave in the relatively short run; he pioneered ecology. Darwin took Malthus' ecological population, focused on variation between individuals, and considered how ecological interactions might produce longer run evolutionary change. Earlier thinkers had conceived of larger units as the key to biology, the species for example. This focus on the species instead of individuals-in-a-population Mayr stigmatizes as *"typological thinking"*, taking the types to be more real than the individuals and populations that make them up. In population thinking, it is individual level processes that give rise to species. In typological thinking, individuals are merely the imperfect vessels of the essence of a species that do nothing really important. Typological thinking was fine for basic taxonomy perhaps, Carl von Linné was a typological thinker. But it turns out that the key to understanding the *causal* processes involved in

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[2] Note that this is a more or less serviceable definition of ecology!

ecology and evolution is paying close attention to individual behavior then doing the math to go from individuals in the short run to populations in the medium and long run. Description alone doesn't explain *why* things change.

Population thinking is really very commonsensical and easy. Once you "get it", it is lots of fun. In the next seven chapters, we are going to trace out the basic implications of population thinking as applied to humans. Remember the basic idea is this simple:

The Key to Population Thinking:
Pay attention to what individuals do in the short run. Then add up over all the individuals in the population, and imagine the same basic processes go on for many generations. Do the arithmetic and see what ought to happen."

In this chapter we will forget Darwin's problem of variable individuals and examine Malthus' questions about the elementary processes of population growth and regulation. These questions form the foundation for all that follows.

II. Elementary Models

A. "Laws" of population growth

Malthus noted that biology by itself tends toward exponential (explosive) growth. Malthus' first assumption was that, forgetting about the environment for a second, each couple will tend to have a certain number of children. The "passion between the sexes is necessary and will remain nearly in its present state," Malthus (1798 [1970:70]) says. Put healthy young men and women together, and, well it makes an old fashioned clergyman blush, they'll tend to make babies. Malthus had data from several American censuses by 1830, indicating that human populations could double every 25 years or so when "passion" had relatively free play. In a relatively open environmentalist as land-rich America, the first assumption is very roughly correct. Now, the next step is a little arithmetic. (If you have a math anxiety, this is the time to tell it to be quiet. We'll keep things real simple, and it will be easy—if only you'll be calm and a bit patient. Take a deep breath, let it out slowly….)

a. Assume that growth is proportional to the number of individuals already present.

b. In a unit of time, each individual has so many offspring, say ***b***, and a certain probability of dying, say ***d***. *"**r**"*, the net expected contribution to population increase made by each individual, can therefore be calculated as ***r*** = ***b - d***. For example, your contribution to the growth of a population to which you belong *in any year* is the number of children you produce minus the probability that you will die during that year.

c. This leads to the formulation of a classic equation (where N = the number of individuals in a population, t= time, and r = the average net expected contribution per individual to population increase)[3]:

$$\frac{dN}{dt} = rN \qquad (1)$$

> ***In words: the*** growth rate of a population per unit of time (also known as the instantaneous rate of increase) is equal to *net* birth rate per individual times the number of individuals.

$$N_t = N_0 e^{rt} \qquad (2)$$

> ***In words: the*** population after time *t* is equal to the starting population times the base of the natural logarithm raised to the power of the instantaneous rate of increase times the elapsed time. This is Malthus' geometric progression of population. Figure 8-1 provides a graph and a table to illustrate how this works.

Note how the growth rate seems slow at first, but amazingly explosive after generation 20, even though individuals continue to do nothing but have 4 living offspring per couple. Given any time at all, exponential growth is a very rapid process, unless the excess number of children per couple above replacement is very, very small.

Clearly this model has strict limits. It cannot explain real populations very well; populations can grow exponentially only for limited periods at best. Exponential growth can be a fairly accurate model only for short periods of time, for example the first 500 years after the first people crossed the Bering Strait into the Americas. Most important, it does capture one essential element of population growth, populations are intrinsically capable of exponential behavior *in the absence of environmental limits* (***r*** interpreted as a biological constant, the intrinsic rate of natural increase). In fact, this was Malthus' point. The model also gives us a descriptive parameter which can be used as a variable to describe the growth rate of a population (***r*** can be interpreted as a descriptive variable, reflecting actual births and deaths in a population). The model tells us something if we use some common sense in interpreting its message.

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3. Don't let the notation confuse you here; in difference equations of this sort, *d* means "change." Thus you would read this equation as "The change in N per unit of time T is equal to *r* times *N*".

Figure 8-1. Exponential population growth is very fast. Start with a founder population of 5 couples that double every generation—much as humans might have done when they first reached North America 12,000 bp—and watch us grow. No wonder the Reverend Malthus was concerned!

THE NUMBERS:

Generation	Population Size (*N*)	Years Since Starting Population
0	10	0
1	20	25
2	40	50
3	80	75
4	160	100
5	320	125
6	640	150
7	1,280	175
8	2,560	200
9	5,120	225
10	10,240	250
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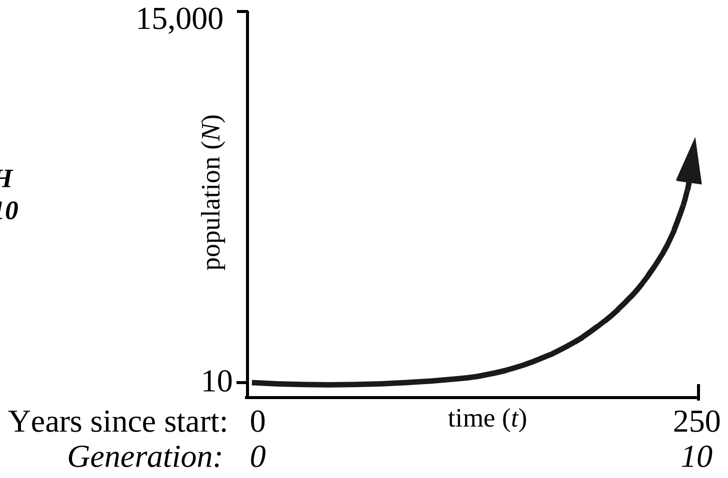
20	10,485,760	500
30	10,737,418,240	750
40	10,995,116,277,760	1,000

***Note**: This is close to the projected world population for the year 2,000.* → (generation 20)

PICTURE THE GROWTH RATE FOR THE FIRST 10 GENERATIONS:



The model also shows its weakness in very graphic terms. There must almost always be something limiting population growth. Without competition (or something else), l0 paleo-Americans could have produced more people than there are in the world today in about 750 years. Malthus' assumption about the power of "passion" seems safe enough, so we must look for another element to add to develop even the most basic theory of population—one that doesn't let populations get too large very fast.

Malthus' additional element was food limitation leading to the logistic model of population growth. Land area is fixed. Technological developments could certainly make improvements in production, but they could never be as rapid as the potential for population growth[4]. Therefore, population powered by passion will grow until it is limited by a shortage of food. The shortage can act through "positive checks" such as famine, disease and warfare due to crowding and competition for limited food; or in "preventative checks" such as late marriage and "vice." To Malthus (1830 [1970: 250]), vices included "unnatural passions and improper arts to prevent the consequences of regular connections." In other words, birth control and the x-rated practices for having sexual pleasure fun without risking babies; (Malthus was decidedly *not* pro-choice). Today we use the logistic model as the simplest exemplar of Malthus' idea:

a. Assume that there is some upper limit to how many organisms a particular habitat can support (a *carrying capacity*), and that reproduction is gradually reduced (e.g., by competition for resources) as this limit is approached.

b. Rate of growth = the intrinsic (Malthusian) capacity of individuals to **r**eproduce—(limiting effect on reproduction due to competition) x (size of the population).

c. To derive the logistic model: suppose there is a constant increment of competitive effect, ***C***, for each additional member of the population. Then Malthus' "law" becomes:

$$\frac{dN}{dt} = (r - CN)N \tag{3}$$

If we then let $r/K = C$ (where ***K*** is the "carrying capacity"), we recover the more familiar version of the logistic:

$$\frac{dN}{dt} = r\frac{K - N}{K}N \tag{4}$$

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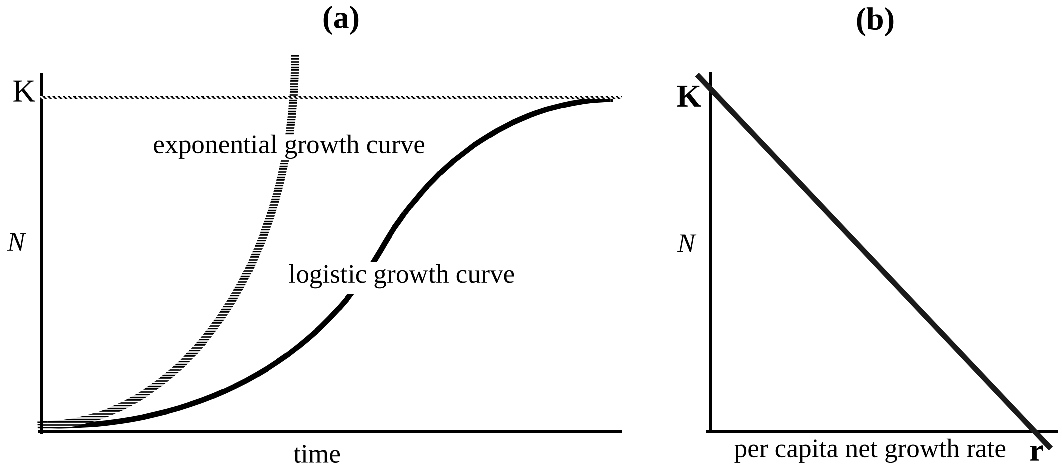
[4] Recall from the last chapter that Malthus lived at the very beginning of the Industrial Revolution; in Chapter 17 we'll review how good this assumption was in the context of his times.

A graphical description of the logistic is given in figure 8-2[5]:

Figure 8-2. Comparison of exponential and logistic growth curves. In (a) the logistic increases rapidly when the population (N) is far from the carrying capacity (K) then begins to slow as it approaches K. In (b) the per capita net growth rate = r when population is low; as the population approaches K, r → 0.



It is fairly easy to see how this model will apply to human groups. For example, take a population of hunters and gatherers. Food foragers probably limit populations because of need for mobility. Infants have to be carried, and young children can not walk very far very fast. If treks are infrequent and short because game is abundant, women might have as many as 8 children (allowing for 50% mortality, this will permit a doubling every generation). In this case, movements cannot be much further than a 2 year old can walk, and a mother can carry one infant, but not an infant and a toddler, say approximately 3 km/day. Moms could have the 8 birthsor a little more counting some children dying very young, assuming births are spread out over l6 years. As competition depletes game, and longer movements are required, births will still have to be spaced so that moms don't have to carry 2 kids, so that the second-to-last child is capable of the longer march. Births may have ultimately to be spaced to 4 years, giving 4 children in a 16-year reproductive span, and with 50% mortality, a stable population. Four year olds can walk perhaps l0 km/day. Note here how population thinking encourages us to make some assumptions about how individuals

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[5] **We strongly recommend that you spend enough time on all of the graphs and charts in this manual to really understand them; they are much more than just pretty pictures.** If you are unused to analyzing graphs and charts, one of the best ways to glean information from them is to ask yourself questions about what they tell you. For example: "What general relationship do you see between mortality and fecundity?" (High survivorship, as for humans, is associated with low fecundity….) "What does the vertical line for the fecundity of many invertebrates in figure 8-3 indicate?"

deal with their environment, and use these as the raw material for a little arithmetic (see Chapter 9).

Demographic theory can get pretty hairy, but the basic concepts are well illustrated by the very elementary models and calculations here. Often the very simplest calculations give you 50-75% of the insight into causal processes that could be obtained from the full-blown theory at a small fraction of the work. Even if you are a pretty inept mathematician it is worth trying to master the simplest models[6].

B. Age specific phenomena

Simple models ignore the fact that not all individuals in a population are equally capable of reproduction—populations are age structured. Figure 8-3 shows graphically how demographers think of age structured populations. At each age, an individual has a certain probability of surviving, and a certain probability of having an offspring. These "vital statistics" are often referred to as the fertility-mortality schedule of a population

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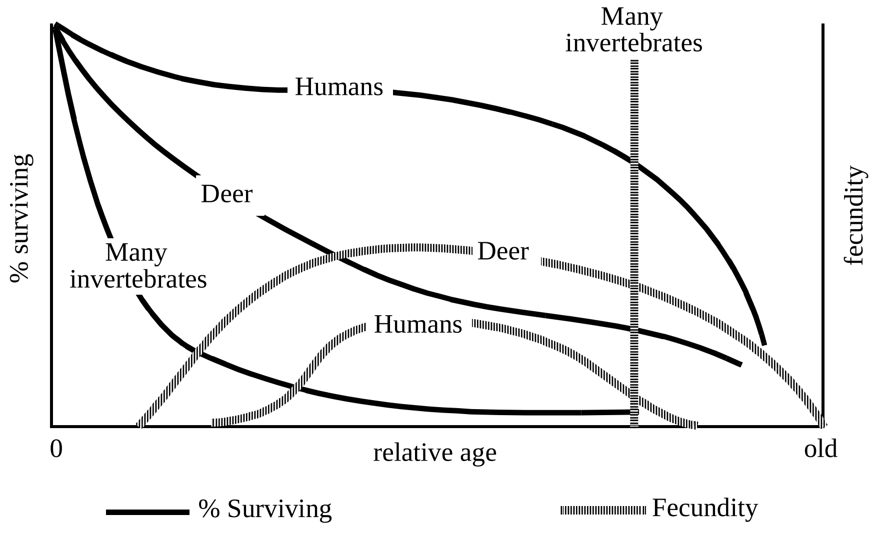
Figure 8-3. Comparison of fertility and mortality curves for various types of organisms. Note that 'age' is calculated relative to the organisms' respective life spans. Mortality is calculated as the proportion of an age cohort surviving. Fecundity is also in relative units.



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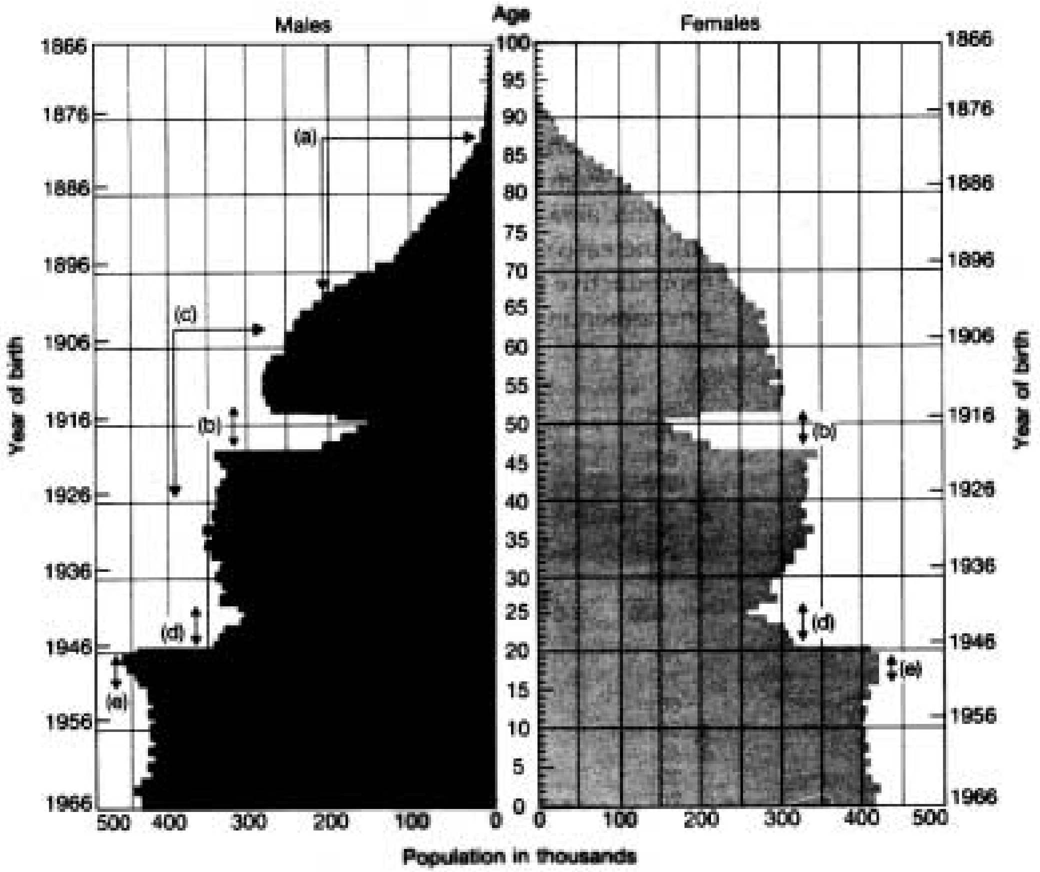
[6] If you are less fluent mathematically, you can still learn to understand the implications of these concepts by using a computer spreadsheet. Enter the equations, set things up to calculate changes over a number of generations, then watch how the graphs change when you modify the value of r, K, etc.

Figures 8-4 and 8-5 contain information about the age structure of different human populations. The data are presented in the form of what is known as a *population pyramid*. Each age-class is represented by a horizontal bar and the length of the bar indicates the size of the age class. Note that the youngest age classes or cohorts are on the bottom and the oldest are on top. Figure 8-4 shows a population pyramid for France on January 1, 1967. Note the literal 'bites' that World Wars I & II have taken out of the population. Figure 8-5 compares the sizes of age cohorts in populations that are stable, expanding, or declining. It is possible to compute "r" for age-structured populations, but the algebra's a bit complicated (see Begon, Townsend, and Harper (1986:153-157) for an accessible discussion.)

The age distribution of a population can have dramatic ecological effects. The dramatic swings in American fertility create small and large cohorts that move through society together. Most of you have "baby boom" parents and are members of the "baby nadir" cohort that followed. The economist R.A. Easterlin argues that these fluctuations have important demographic and economic consequences. Your parents' cohort had too many young adults for the economy to easily absorb. Their employment experience was bad relative to their parents, so they reduced their fertility relative to their parents. Conversely parents of Baby Boomers were mostly born during the hard years of the depression but there were relatively few of them and they enjoyed boom times in the 1950s and 60s, so they had large families.

Easterlin argues that hard times result when too many young people crowd the job market and that people adjust their fertility according to how their income expectations compare to those of their parents. Others attribute crime waves and revolutionary activities to baby boom cohorts. (When there are too many young folks, and too few old folks to control them, crime and revolution ensue to oversimplify the complex hypothesis of Goldstone, 1991.) According to this argument, the Boomer generation ran wild on the campuses in the 60s because there were always too few adults to really supervise them well, while your generation is pretty tame because there have always been plenty of boomers to keep an eye on so few of you! Figure 8-6 shows Easterlin's comparison of the earnings received at different ages by young male baby-boomers with those received by the previous generation at similar ages

Figure 8-4. A population pyramid for France on January 1, 1967. (Source: Begon et al. 1986:161.)



(a) Military losses in World War I
(b) Deficit of births during World War I
(c) Military losses during World War II
(d) Deficit of births during World War II
(e) Rise of births due to demobilization after World War II

Figure 8-5. Comparison of population pyramids for stable, expanding, and declining human populations.

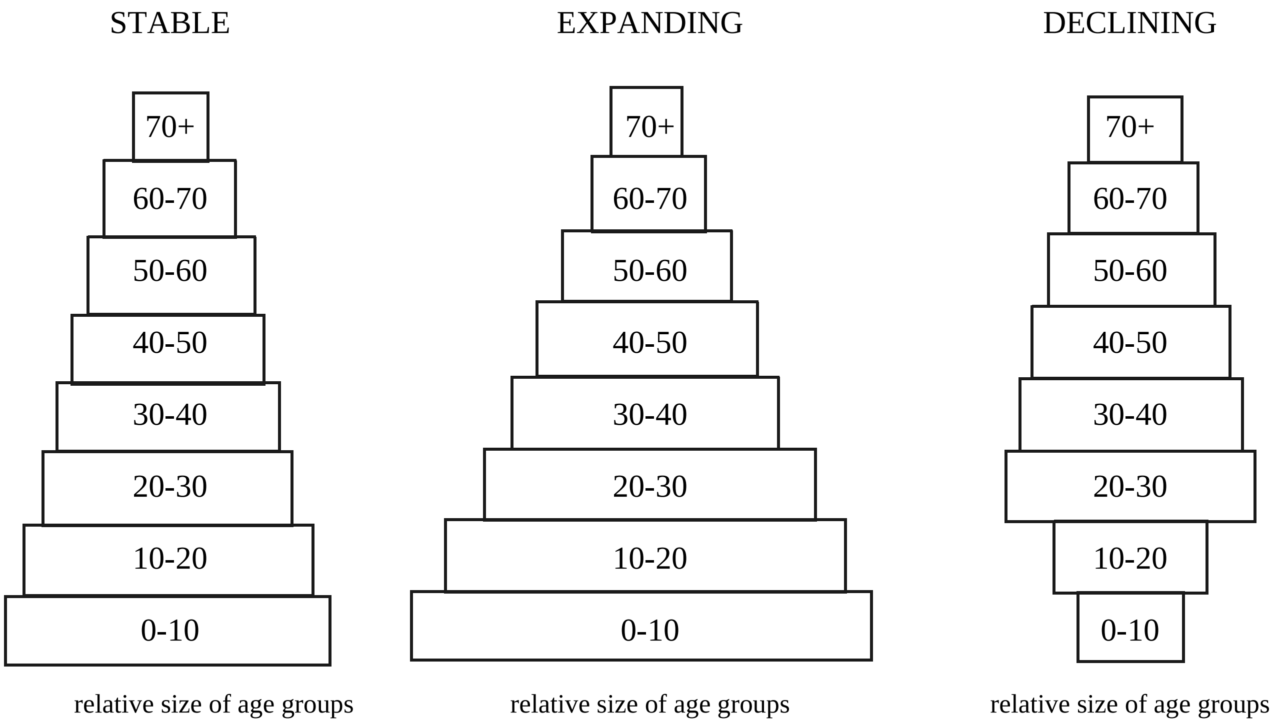
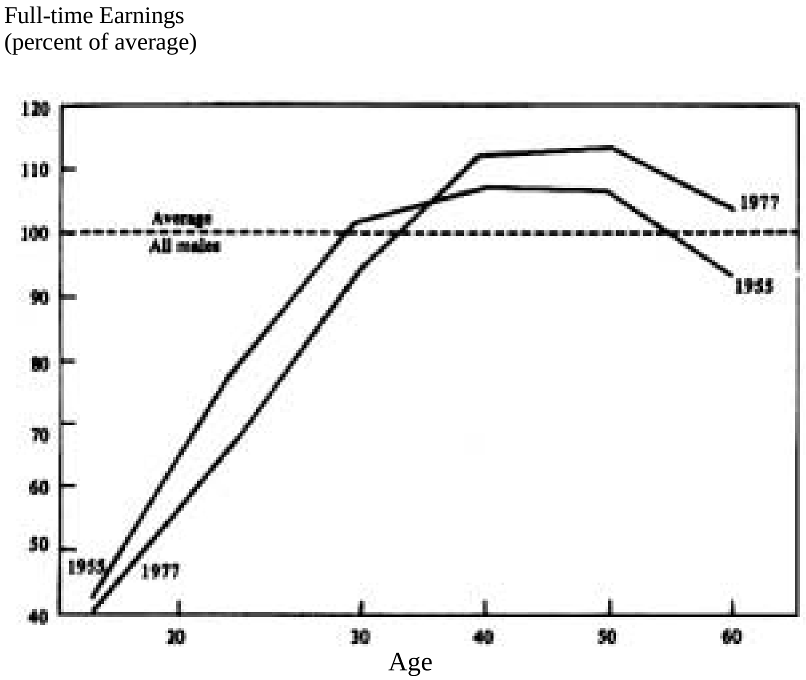


Figure 8-6. Comparison of the earnings received at different ages by young male baby-boomers with those received by the previous generation at similar ages. (Source: Easterlin 1987:22.)



For each date, earnings at the age shown at the bottom of the chart are expressed as a percentage of the average for all ages (the horizontal broken line). At both dates, the left-hand portion of the curve lies below the average, showing that younger workers earn less than older. In 1977, however, the shortfall for younger workers is greater than it was in 1955, showing that the relative position of younger workers is worse at a time when their relative numbers are greater.
Source: Appendix Table 2.2.

III. Mechanisms of Population Regulation

A. Density-independent factors:

Some factors like random weather catastrophes, tend to kill a certain factor of a population regardless of whether the population is abundant or rare. Such factors are *independent* of population density, and independent of competition; i.e., they do not cause some individuals to be more exposed to mortality than others. Biotic catastrophes such as hurricanes, volcanic eruptions, fires, etc. are the usual examples of density-independent factors. If we were to plot the growth of a population over time that was regulated solely by density-independent factors, its crashes would be independent of its size, or its nearness to the carrying capacity (K). Figure 8-7 illustrates this concept.

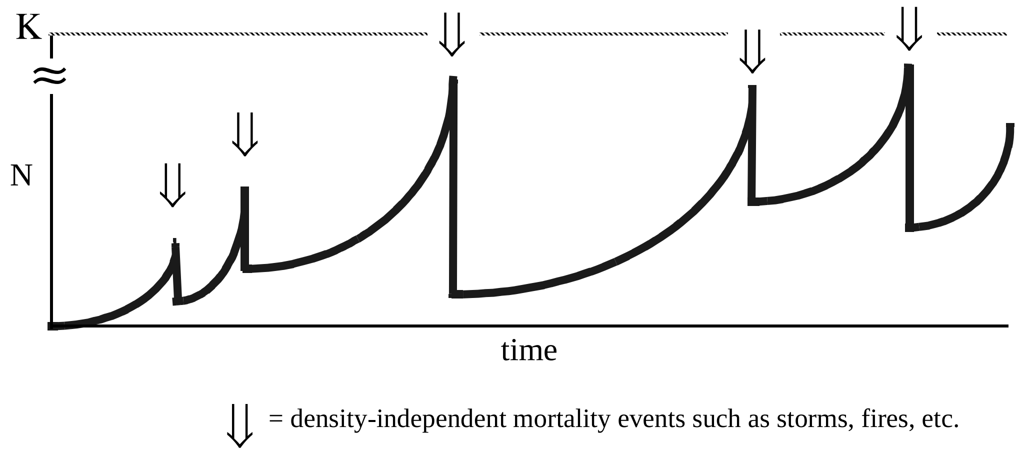


Figure 8-7. The effect of density-*independent* factors on population growth.
(K= carrying capacity. N=population size.)

B. Density-dependent factors:

If the mortality rate of a population is proportional to the number of individuals present, population growth is said to be (partially, at least) density-dependent. Under this regime of population regulation, biotic factors such as competition for scarce resources are often important. Figure 8-8 illustrates the manner in which a population which is controlled *solely* by density-dependent factors would change over time. Note that the carrying capacity in this illustration fluctuates over time although it need not be[7].

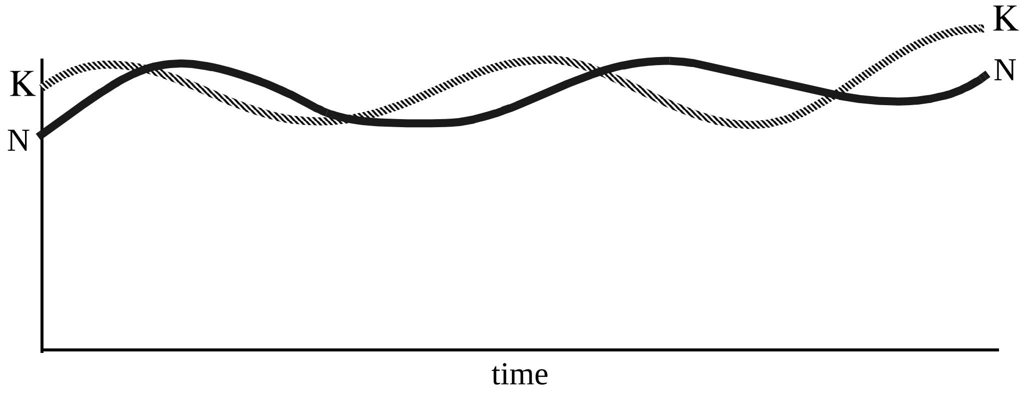


Figure 8-8. The effect of density-*dependent* factors on population growth.
(K= carrying capacity. N=population size.)

C. For Humans, Both Types of Factors are Often Important

Much human mortality is often caused by a mixture of both density-independent and density-dependent factors. Some examples:

1. Catastrophes—poverty, which may be a consequence of high population densities relative to prevailing technology, usually exposes the poor most severely to the consequences of flood, famine, and war. What are some recent examples?

2. Disease is usually a function of population density, but many epidemic diseases are effectively spread over a wide range of densities and have effects that are episodic, catastrophic, and weakly density-dependent.

Pure density-independent population regulation results in a "random walk" to zero or infinity. In other words, the population may increase or decline regardless of its size. What type of environment would be required for pure density-independence to occur[8]?

Fertility as well as mortality can be thought of in terms of density dependent and density independent factors. Think back to Malthus' "passion of the sexes". To what extent is this independent of population size?

There has been a good deal of debate about whether historical human populations responded mostly to density-dependent or density-independent regulation. Polgar (1972) made a case for density dependence via fertility limitation. In his view, population growth occurred mostly in response to technological changes that raised K. Others have argued that episodes of disease and famine cause most historical populations spent most of their time growing exponentially from the last catastrophe they experienced. (See figure 8-7.) There is some evidence that many peasant populations in Eurasia and some parts of the New World did spend long periods of time near the subsistence carrying capacity limited by high density-dependent mortality rates (the position Polgar explicitly argued against). Nevertheless there may have been considerable variation in demographic behavior among human populations, a subject we will consider in more detail in Chapter 16.

IV. Conclusion

The most important lesson of demography is that, historically speaking, even quite

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[7] Fluctuating carrying capacities are more realistic since stable environments are not found in the natural world. UC Santa Barbara biologist Daniel Botkin (1990) makes the point that our perception of some environments as stable is an artifact of scale—they actually fluctuate a great deal if one adopts an appropriate time scale!

[8] The environment would have to provide more resources than can be consumed by the growing population; i.e., K would have to be much greater than N (K >> N), since competition becomes appreciable far short of K. Such situations are improbable.

slow exponential growth can bring about large populations in a relatively short period of time. The biology of reproduction ensures that all populations have the potential for at least slow exponential growth. The natural “time scale” for population growth is 10 generations or so, depending on demographic details, say 250 years when we are speaking of humans. This is the time scale necessary for populations to recover from major catastrophes. It only takes a small multiple of this time scale for a tiny founding population to reach unimaginable sizes. Because the demographic time scale is so short, demographers since Malthus have put a lot of effort into trying to understand the processes that regulate animal and human populations. Work has concentrated on both density-dependent effects like those generated by competition, and on density-independent processes. We will use the basic ideas presented in this chapter as building blocks for later chapters.

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