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Populations with age structures

- Survivorship
- Fertility
- Mortality curves
- Expectation of life
- Net reproductive rate, generation time and the intrinsic rate of increase
- Age structure and the stable age distribution
- Projecting population growth in age-structured populations
- The Leslie or population projection matrix
- Reproductive value
- Sensitivity analysis

4.1 Introduction

In the previous two chapters we either examined populations without distinct age classes or we specified that these populations had stable age distributions. We also assumed that models for continuous breeders would apply to seasonal breeders such as white-tailed deer (*Odocoileus virginianus*). We danced around the problem of forecasting population growth for populations with complex age distributions and the fact that the age distribution itself can govern the behavior of the population, at least in the short term. Knowledge of the age-specific survivorship and fertility patterns of a population allows us to understand what age categories are most important to the future survival of the population. If you wanted to help conservation biologists ensure the long-term survival of a sea turtle population, for example, what recommendations would you make? Would it be most effective to protect the beaches where the females lay their eggs? Limit predation on the eggs? Gather up the hatchlings, sequester and feed them for a year before releasing them? Or take steps to reduce the mortality of adults through monitoring and regulating fishing fleets? To answer these questions we will need to learn a number of skills that will allow us to extract growth rates from basic life-history data and to project population growth using different assumptions.

When age-specific fertility and survivorship data are gathered, we put them together in the form of a **life table**. From the information in the life table we are then able to calculate a variety of interesting statistics that acquaint us with the characteristics of the population. In addition to age-specific fertility and survivorship, we need information on the current number of individuals in each age class, since population growth in the short term is also strongly influenced by the latter.

The following example might fix in your mind the potential importance of age distribution on population growth. Imagine a group of several thousand young people attending a concert by the latest pop icon on an island off the coast of California. Suddenly a catastrophic series of earthquakes eliminates the entire local population while simultaneously California splits off from the rest of North America. Assume further that a few of the concertgoers are able to colonize the original island off California, and future population growth is now based on this group. Most of the concertgoers would obviously have been teenage girls (assume a few teenage boys also were dragged along). Further, assuming an abundance of food, this California island would rapidly be repopulated. Growth would, however, be irregular, since all of the girls would be the same age and reach menopause more or less simultaneously in the future. Growth would slow until their daughters began to reproduce. Now imagine the same scenario, except that survivors of the disaster were individuals attending an AARP (American Association of Retired Persons) convention. Presumably all, or almost all, of the females at the convention are over 55. What would the future of the California island population be in this case? Evidently age distribution can contribute to extinction of a population!

Many of the techniques we will examine in this chapter were developed for the life insurance industry and applied to human populations. For example, actuaries need to calculate the risk of insuring the life of their clients. Life tables were developed so that the probability that a 50-year-old pharmacist would live another 10 years could be determined; policy rates were then set accordingly. Such techniques were easily translated to animal populations, and the comparative study of survivorship among different groups of animals was initiated (Deevy 1947).

More problematic has been the application of life tables to plant populations. Rates of growth, reproduction, size, and mortality are not distinctly related to age in plants, as is the case for animals, but are highly variable and highly dependent on the local environment. This "phenotypic plasticity" can be demonstrated by growing genetically identical clones in different environments. Growth, size, and fertility, when measured against age, will be dramatically different (Silvertown and Doust 1993). The recommended solution is to develop a life-history table in which **stages** are used instead of age classes (Werner 1975, Werner and Caswell 1977, Hubbell and Werner 1979). For example, in her study of teasel (*Dipsacus sylvestris*), Werner (1975) used the following stages instead of age classes: (1) first-year dormant seeds; (2) second-year dormant seeds; (3) small rosettes; (4) medium rosettes; (5) large rosettes; (6) flowering plants. In teasel, plants die after flowering. Instead of calculating the probability that an individual would survive from one age class to the next, she calculated the probability that an individual of one life stage would survive to the next stage. We will also take a look at stage-based methods for animal populations later in this chapter.

Another problem in applying life tables to plants is that plant populations often spread through vegetative propagation. Grasses, for example, spread horizontally via rhizomes. New shoots arise from rhizomes and often separate from the original plant. A complex terminology has been developed to explain this phenomenon. For example, a **genet** is an individual that has arisen from a seed. A **ramet** is a new plant that is a clone but which has arisen through vegetative propagation and is now a completely independent plant with its own roots and shoots. Thus a population of grasses may consist of several genets, each of which has several ramets. Clonal populations may proliferate indefinitely without flowering. This has led to some fascinating life cycles such as that of the giant bamboo (*Phyllostachys bambusoides*), in which clones of perennial ramets proliferate, forming large populations that flower only once every 120 years (Janzen 1976). All of the clonal ramets flower simultaneously and then the entire population dies, leaving behind only seeds with which to found the next population. Studies conducted since the great 1988 fire in Yellowstone National Park have forced biologists to revise the conventional wisdom that aspen (*Populus tremuloides*) does not reproduce by seed, but spreads by cloning. Instead Turner *et al.* (2003) suggest that new genets of aspen as well as some of the perennial herbs of the forest floor are produced after fires, but recruitment of new individuals (ramets) during fire-free intervals is primarily through asexual reproduction.

In the sections below, as we refer to age-specific traits of survivorship or fertility, keep in mind that many plant and animal populations would often require a rather different approach in which we examine survivorship and fertility by size class or by stage in the life cycle.

4.2 Survivorship

The construction of a life table begins by gathering information on survivorship by age class. This sounds simple, but is easier described than actually done. For example, one method is to study a **cohort** of individuals all born at the same time, and follow the survivorship of these individuals until the last member of the cohort dies. At the beginning of such a study, it would be necessary to locate and mark all newborn individuals. Subsequently, one would need to verify when each individual died. Individuals that simply disappeared could not be assumed to have died; they might have emigrated. Studies of cohorts are obviously best done on small populations and on populations that move about in a predictable way. The advantage of studying a cohort is that one knows the exact age of each individual. The disadvantage is that such a study lacks generality, in that cohorts born in different years may have different survivorship schedules. In addition to the difficulties one might encounter in actually marking and gathering information on all members of a cohort, there are also practical problems. A cohort study on most species of turtles, for example, would require the entire professional life span of the investigator (picture a student waiting 50 years to finish her PhD dissertation). A life table developed in this manner is known as a **fixed-cohort**, **dynamic**, or **horizontal life table**.

A second approach is to locate and examine all of the dead individuals in a population during some defined period of time. We would need a method for estimating the age of the animals or plants at death. This approach to the construction of a life table assumes that the rates of survival in the population are fairly constant. If this is not the case, age-specific mortality rates will be confused with year-to-year variation in mortality of the overall population. Data gathered in this manner produce a **static**, **vertical**, or **time-specific life table**.

A third approach is to collect life-history data for several cohorts over as long a period as possible. In most populations there is a large difference between juvenile and adult