

Chapter 2

Variation



2.1 Introduction

We view population ecology as an applied science that helps find solutions to practical problems in wildlife and game management, natural resource management and conservation, and other areas. All of the cases explored in Chapter 1 dealt with real world problems. Yet they ignored a fundamental component of the ecology of populations, namely variability in populations and in the environment in which they live. Such variation is pervasive. The

growth rate of the Muskox population on Nunivak Island varied substantially around the average of 1.148 that was used to predict future population sizes. The rate of decline in the Blue Whale population averaged 0.82 between 1947 and 1963, but in no year was it exactly 0.82. In this chapter, we introduce the concepts and the framework that are necessary to deal with natural variation in population ecology.

Ecologists think in terms of what is known as the central tendency of their data. The first questions to come to mind in any population study usually are of the kind: "What is the average growth rate?" A somewhat more thoughtful ecologist might also ask "What is the year-to-year variation in the growth rate?" or even "What are the confidence limits on the predicted population size?" These are all important concepts. It is equally important to consider the distribution of outliers. In practical situations, for example, it is often important to know the worst case we might expect, and how likely it is. The chances of extreme events are particularly relevant to people interested in keeping population sizes within predetermined limits. To look at data or to make predictions in this way first requires a special vocabulary.

2.1.1 Vocabulary for Population Dynamics and Variability

Stochasticity is unpredictable variation. If the long-term growth rate is less than 1.0, the population will become extinct, no matter how stable the environment. These populations are said to be the victims of "systematic pressure"; their decline results from deterministic causes. Populations that would persist indefinitely in a constant environment nevertheless face some risk of extinction through variation in fecundity and survival rates. These populations, when they decline, are the victims of stochasticity.

In Chapter 1, we began constructing models to represent the dynamics and ecology of populations. Population models that assume all parameters to be constant are called deterministic models; those that include variation in parameters are called stochastic models. Stochastic models allow us to evaluate the models in terms of probabilities, accounting for the inherent unpredictability of biological systems. The probabilities generated by stochastic models allow us to pose different kinds of questions. We might want to know the worst possible outcome for the population: If things go as badly as possible, what will the population size be? We might like to know which parameter is most important. When the problems that we face are subject to uncertainty (and they almost always are), then the questions we ask should be phrased in a specific way. For example, if our focus is the size of the population, then we should ask:

What is the probability of {decline / increase}
to [population size, N_c] {at least once before / at} [time, t]?

The components inside braces [...] are choices and the components inside square brackets [...] are quantities. Circumstances will ordain whether we are most interested in (or concerned about) population increase or population decline, or both. We must specify the critical population size or threshold (N_c) that represents an acceptable (or unacceptable) outcome, or a range of such values. We must specify a time horizon (t), a period over which we wish to make predictions. Lastly, we must say whether it is sufficient that these conditions are met at least once during the period or that they are met at the end of the period.

The words risk and chance may be used in place of the word probability, but they emphasize slightly different aspects of a problem. Risk is the potential, or probability, of an adverse event. When applied to natural populations of plants and animals, risk assessment usually is concerned with the calculation of the chance that threatened populations will fall below some specified size, or that pests will exceed some upper population size. Declines in population size may be seen as desirable when dealing with a pest, in which case we talk of reduction. They may be undesirable when dealing with rare species, in which case we may refer to the risk of decline or risk of extinction. Similarly, increases may be either desirable (recovery of rare or threatened species) or undesirable (explosion of pest species). If we wish to estimate the chance of decline or increase of a population to some specified size (a threshold) at least once in the specified period, we talk of the "interval" probability. If our interest is in the chance of being above or below a threshold at the end of the time horizon, we talk of the "terminal" probability.

The critical population size, or threshold, specified in the definition of risk often reflects an abundance that is considered to be too low (for rare or threatened species) or too high (for pest species). It may be determined on an economic basis for harvested species, for example, when a fishery manager wants to maintain a certain population of Brook Trout in a stream.

Over a given time period, there is a chance that any population will become extinct. This chance we term the background risk. If the consequences of different types of human impact are measured in terms of probabilities, it is possible to compare them against the background risks that a population faces in the absence of any impact. Added risk is the increase in risk of decline that results from some impact on a natural population. Similarly, if the consequences of different types of conservation measures are measured in terms of probabilities, we can compare them against the background risks in the absence of conservation efforts. The difference (which we hope is a decrease in the risk of decline) is a measure of the effectiveness of the conservation effort.

The probability of extinction or explosion of a population in a given time period is one way we can describe the chances faced by natural populations. Another way is to use the expected time to extinction or explosion. These statistics are the average time it takes for a population to fall below or to exceed specified population thresholds. We will discuss this further under the heading Additional topics (Section 2.5.1).

2.1.2 Variation and Uncertainty

We saw in Chapter 1 that the change in size of a population is governed by births, deaths, immigrants, and emigrants. Births and deaths may be governed by environmental parameters. Variation in the environment leads to variation in survival and fecundity rates, and results in variation in population size that is independent of the average growth rate of the population. "Good" years are those in which the population produces more offspring and experiences fewer deaths. Species respond to environmental variation in different ways. The time scales of impact and response are related to the ecology of populations. Some species will resist environmental change and others will respond to it, depending on its severity and duration.

The picture is further complicated by the fact that estimates of population size will vary from one time to the next, even in the absence of any real change, because of measurement errors. Further, some populations will fluctuate in a regular fashion, following diurnal, seasonal, or longer term weather patterns, or because of their interactions with predators or competitors. Natural variation in the environment and measurement error will overlay any other natural or human caused patterns, trends, or cycles in population size. The consequences of this variation are that we cannot be certain what the population size will be in the future. In addition, there are other factors that may cause population sizes to vary unpredictably, and there are other reasons why our predictions may be uncertain. However, if we can characterize this uncertainty, we may be able to provide an indication of the reliability of any estimate that we make. We will explore these concepts below and introduce ways of dealing with them in circumstances where predictions are necessary for resource and wildlife management and species conservation.

2.1.3 Kinds of Uncertainty

Uncertainty may be considered to be the absence of information, which may or may not be obtainable. Uncertainty encompasses a multiplicity of concepts including:

incomplete information (what will the population size be in 50 years?)

disagreement between information sources (what was the population size last year?)

linguistic imprecision (what is meant by the statement "the population is threatened"?)

natural variation (what will be the depth of snowfall this winter?)

relationships between variables (does resistance to cold in winter depend on the amount of food available in the preceding summer?)

the structure of a model (should emigration be represented as a number or a rate?)

Models are simplifications of reality. Uncertainty may be about the degree of simplification that is necessary to make the model workable and understandable. It may be about the decision we should take, even if all other components of the problem are known or understood. Different types and sources of uncertainty need to be treated in different ways. Probability may be a useful means of describing some kinds of uncertainty. Others are more appropriately handled with decision theory, or even with political process. There are numerous classifications of the kinds of uncertainty and variability. Decomposing uncertainty into its different forms allows us to use available information together with appropriate tools to make predictions. These predictions may then be qualified by a degree of uncertainty.

2.2 Natural variation

2.2.1 Individual Variation

Individual variation is the variation between individuals within the same population. It is the term used to describe the variation within a population due to genetic and developmental differences among individuals that results in differences in phenotype. Individual variation also includes genetic variability. Each individual has a different genetic makeup that results from the combinations of genes in its parents, and the random selection of those genes during meiosis. The rate of change in the genetic makeup of a population is inversely proportional to the number of adults that contribute to reproduction. In small populations, the genetic composition of the population may change significantly because of these random changes, a process known as genetic drift.

Inbreeding is mating between close relatives. In small populations, mating between relatives becomes more frequent. If the parents are related to one another, rare recessive genes are more likely to be expressed and genetic variation may be lost. These processes may alter the survival and

fecundity of individuals, and reduce the average values of these rates in the population as a whole. The loss of variation may also reduce the ability of the population to adapt to novel or extreme environmental conditions.

Other differences among individuals contribute to this kind of uncertainty. For example, in species with separate sexes, uneven sex ratios may arise by chance and have an enhancing or a detrimental effect on further population increase. While these processes are relatively well understood, it is not possible to say if, and to what extent, these effects will be felt in any given instance. The process is inherently unpredictable.

2.2.2 Demographic Stochasticity

Demographic stochasticity is the variation in the average chances of survivorship and reproduction that occurs because a population is made up of a finite, integer number of individuals, each with different characteristics. Consider the following example. The Muskox population on Nunivak Island began in 1936 with 31 individuals and had an average growth rate of 1.148. On the basis of this average, we might expect the population in 1937 to be 35.6, but there is no such thing as 0.6 of a Muskox. The growth rate we specified is an average based on observations. What this result says is that, 4 to 5 more births than deaths are expected in the Muskox population between the 1936 census and the 1937 census. Exactly how many, we cannot be sure.

The people who conducted the censuses of the Muskox population on Nunivak Island recorded the number of calves produced each year. Over the years the average number of calves per individual (f) was 0.227. Given that

$$R = f + s$$

the average survival rate was

$$s = 1.148 - 0.227 = 0.921$$

The parameters in the models we developed in Chapter 1 do not vary, so they are termed deterministic models. They provide a single estimate of population size at some time in the future. We could add an element of realism to these models by following the fate of each individual. For example, rather than multiplying the whole population by a survival value of 0.921 to calculate the number of survivors, we could decide, at each time step, whether each individual survives or dies. We do this in such a way that, in the long term, 92.1% of the individuals survive. One way to do this is to choose a uniform random number between 0 and 1 for each individual. ("Uniform" means that each number in that range has an equal chance of being sampled; see the exercises section for ways of choosing random num-

bers.) If the random number is greater than the survival rate of 0.921, then the individual dies. Otherwise, the individual lives. We ask the question for each individual in the population, using a different random number for each. Thus, if there are 31 individuals in the population, there is no guarantee that 29 will survive, although it is the most likely outcome ($31 \times 0.921 = 28.6$). There is some smaller chance that 28 or 30 will survive and some still smaller chance that 27 or 31 will survive. This kind of uncertainty represents the chance events in the births and deaths of a real population, and is what we mean when we talk of demographic uncertainty.

We could add a further element of reality by treating the births in the population in an analogous fashion. Like deaths, births come in integers (no Muskox will produce 0.227 offspring; rather, most will produce none, some 1). We can represent this in our model by following the fate of individuals in the same way as we did for survival. That is, choose a random number for each individual. If the value is less than 0.227, the animal has an offspring. Otherwise, it does not.

A time step of a year seems appropriate because reproduction in this species is seasonal and the environment is highly seasonal. We treat the population as composed of an integer number of individuals and we sample the survival and reproduction of members of the population, using the observed population size and the population average fecundity and survival rates. The result is that our predictions will no longer be exact. As in a real population, our model reflects how a run of bad luck could lead to the extinction of any population, no matter how large the population size or how large the potential growth rate.

Each time we tally the population and we ask "Does this animal die?" and "Does this animal produce offspring?", the answer may be different. To gain some idea of the expected outcome, and the reliability of that outcome, we need to run a series of trials. We need to repeat the experiment a number of times and calculate the average and the variability of the outcome. Variability of a set of numbers is often expressed as their variance or standard deviation (variance is equal to the standard deviation squared). Histograms showing the frequencies of different possible population sizes one year after the introduction of Muskox to Nunivak Island are shown in Figure 2.1. The larger the number of trials, the more reliable will be our knowledge of the average and the variance. This approach is most effectively implemented on a computer.

Formulating demographic stochasticity in this way makes a number of assumptions about the ecology of the population. It assumes that a female can have no more than one offspring per year. More efficient and more general methods are available that involve sampling the binomial and Poisson distributions, but learning how to use them is beyond the scope of this book

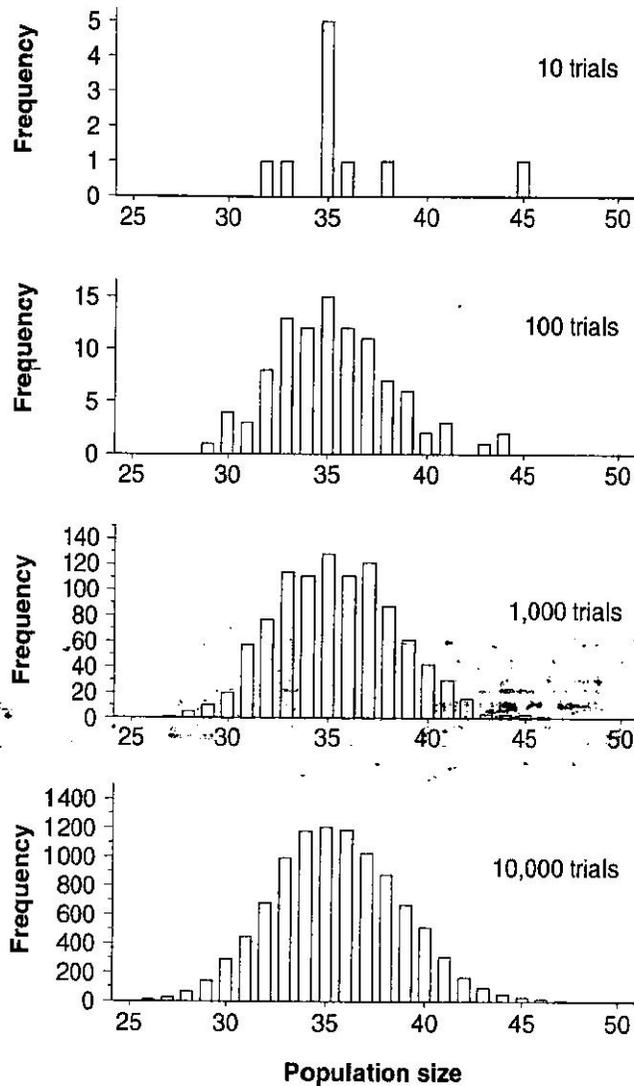


Figure 2.1. Histogram of population sizes for a Muskox population model with demographic stochasticity.

(the computer program that comes with this book implements these more advanced methods). Our approach here assumes further that births and deaths are independent events. We choose different random numbers to represent the survival and reproductive success of each individual. If an animal dies in 1937, it may also have offspring before it dies that year. We could, if we wanted, preclude reproduction if an animal dies, or make it less likely for an animal to survive if it reproduces.

It is clear that demographic stochasticity can have an important effect on estimates of population size. From a starting population of 31, the population quite reasonably could increase to 46 animals, or decrease to 27 animals after one year, just because of the random chances associated with giving birth and surviving from one year to the next. This kind of variability is present in every population. The deterministic expectation of 35.6 is just one of many possible outcomes. The mean predicted by the model including demographic stochasticity (Figure 2.1) is similar to the number predicted by the deterministic model (35.6). By carrying out a great many trials, we can be reasonably certain that we know the mean and the variation in expected population sizes. The uncertainty arises because real populations are structured, composed of discrete individuals, and because the individual occurrences of births and deaths are unpredictable.

By developing forecasts in this way, we can ask different kinds of questions. For example, we could ask "How likely is it that there would be less than 31 animals in 1937?" or "What is the chance that the population will increase by 30% or more, rather than the average 14.8%?" To answer these questions let's count the number of trials that met the stated criteria and divide by the total number of trials. For example, to answer the first question, we tally the number of trials that reached 30 animals, 29 animals, etc., down to the smallest recorded number (which was 24). The result is given in the second column of Table 2.1. The third column shows the cumulative frequencies, i.e., the number of trials predicting a given number or fewer individuals. Each row of this column is calculated by adding up the numbers in the second column up to and including the current row. Adding up the first 7 numbers gives 548, which is the number of trials in which the predicted number of animals was 30 or less. The last column gives the same (cumulative number), divided by the total number of trials (10,000 in this example). Note that this table contains only part of the data represented by the last histogram in Figure 2.1; the dots ("...") at the end of table are to remind you that the maximum population size was 49, and the table could have another 18 rows.

Table 2.1. Number of trials (out of the total of 10,000 trials) that predicted 24 to 31 animals in 1937.

Population level (N_c)	Number of trials that reached a level $\leq N_c$	Cumulative number of trials (that reached a level $\leq N_c$)	Probability of decline to N_c
24	3	3	0.0003
25	2	5	0.0005
26	11	16	0.0016
27	29	45	0.0045
28	67	112	0.0112
29	142	254	0.0254
30	294	548	0.0548
31	449	997	0.0997
..

According to the table, 548 trials out of 10,000 predicted a population size of 30 or less, so the chance is 548/10000 or 0.0548. Thus, even though the deterministic model tells us the population will increase, and the stochastic model tells us the population will probably increase, there is a better than 5% chance that the population will actually decline from 1936 to 1937.

We can answer the second question posed above in a similar way. The question was "What is the chance that the population will increase by 30% or more?" An increase of 30% is equal to a population size of 40.3. The number of trials that predicted a population size greater than 40 was 669. The chance of exceeding 40 is therefore 0.0669, or about 6.7%. Note that you cannot find this answer in the table above. The above table shows the probability of reaching a level *less than or equal to* N_c , whereas this question was expressed in terms of reaching a level *greater than or equal to* N_c .

The task of wildlife managers is to implement plans to manage both the expected population size and the probabilities of extreme outcomes. Wildlife management questions that may be answered by population forecasts come basically in two forms. The first is: "What is the chance that the population will exceed some threshold?" (for control problems) and the second is "What is the chance that the population will fall below some threshold?" (for conservation problems). The management of natural populations may require ensuring that the populations remain within prespecified levels, so that both the upper and the lower bounds are important. For example, large herbivores in parks or reserves frequently must be maintained within upper and lower limits so that they persist indefinitely within the confines of the reserves without becoming so numerous that they displace other herbivores.

Alternatively, it may be important to manage various ecological processes and human impacts to maintain a population, to keep it from becoming extinct.

To address these questions, we may redraw the histograms in Figure 2.1 as cumulative frequencies. As we demonstrated above, if the cumulative frequencies are divided by the number of trials, they may be interpreted as probabilities. Thus, the curve in Figure 2.2 represents the chances that the population which began as 31 individuals in 1936, will be equal to or less than various threshold population sizes in 1937. The x-axis of this curve is the threshold population size (first column of Table 2.1), and the y-axis is the probability that the population size will be less than or equal to the threshold (last column of Table 2.1).

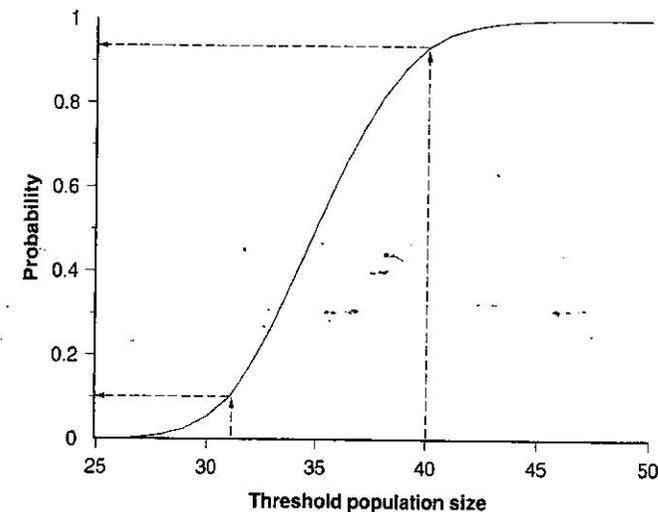


Figure 2.2. Cumulative frequencies from Figure 2.1, divided by 10,000 (the number of trials), and plotted against population size.

To interpret the figure above, let's use the two sets of arrows on the figure to answer a couple of questions: What is the chance that the population will be equal to or less than 31 individuals in 1937 (in other words, what is the chance of no increase)? Looking at the figure, we see that the curve predicts a probability of about 0.1, or 10% for a threshold population size of 31 (see also the last column of Table 2.1, which shows a probability of 0.0997, or about 10%, of declining to 31 or below). What is the chance that the pop-

ulation will be less than or equal to 40 individuals in 1937? The answer is about 0.93. The curve represented in Figure 2.2 is called a risk curve. More specifically, it is a quasi-extinction risk curve. It provides answers to questions phrased as follows: "What is the chance that a population with current size N will fall below some critical threshold population size, N_c , within the next period, t ?" Thus, it is useful for questions concerning the lower bound of population size.

Demographic stochasticity, as well as phenotypic variation of all kinds, has most important consequences in small populations. This is because the effects are inversely related to population size. We can see the qualitative effect of population size by considering the survival probability for the Muskox, 0.921. Assume some catastrophe affects the population and only two animals remain. What is the chance that both will die before the following year? The chance due to demographic uncertainty is $(1 - 0.921)^2 = 0.0062$. When there are 31 animals, the chance is $(1 - 0.921)^{31}$, which is a very small number. In general, the chance of loss of the entire population (p) in a single time step is

$$p = (1 - s)^N$$

where N is the population size. As N increases, p decreases. Nevertheless, even for medium-sized populations, there remains some chance of important deviation from the deterministic model and some small chance of loss of the population through nothing more than bad luck.

Questions such as those posed above are particularly relevant to wildlife managers and environmental scientists who have to manage populations within limits. They are phrased and answered quite naturally in terms of the probabilities of different outcomes. Common sense tells us that we can never predict exactly the size of the population next year. Models that include elements of randomness may be designed to cope with the uncertainty that is part of all environmental prediction and decision making. Such models will allow us to target both the expected size and the risk of decline or expansion of a population. We will see below that, to some extent, these properties are independent. The management strategies to maximize the expected population size may be different than those that are required to minimize the risk of decline.

It is important to remember that, even though the models we developed in this section allowed variability in the number of survivors or the number of offspring, they did not allow the survival rates and fecundities to vary. We demonstrated that *even when these rates remain the same*, demographic stochasticity introduces randomness and unpredictability in the estimated population size. In the next section, we will add more realism to our models by allowing their parameters (survival rates and fecundities) to vary.

2.2.3 Environmental Variation

2.2.3.1 Temporal variation

Environmental variation is unpredictable change in the environment in time and space. It is most often thought of as temporal variation at a single location. An obvious example is rainfall. Even in circumstances in which we know precisely the average annual rainfall of a location based on records going back centuries, it is difficult to say if next year will be relatively wet or dry, and even if next week will be rainy or not.

In circumstances in which the vital rates of a population depend on environmental variables, the rates will likewise be unpredictable. The concept of a niche implies that a set of biotic and abiotic variables limits the distribution of a species. It is usually assumed that a set of environmental parameters will affect the rate of growth of a population within the niche that a species occupies. Environmental variation that results in variations in population size is seen as a mechanism that is extrinsic to the population. Environmental variation is not the sole determinant of fluctuations in population size. We will explore intrinsic causes of population change in subsequent chapters.

Environmental variation results in fluctuations in population size when environmental variables affect the number of survivors and the number of offspring in a population. There are many examples of relationships between environmental variables, and the survival and fecundity of individuals within populations. For example, population numbers of the California Quail are influenced by climate. High winter and spring rainfall is associated with high reproduction in semi-arid regions (Figure 2.3). The mechanisms for this dependence may be based on the quality and quantity of plant growth or the availability of free drinking water. If water is scarce in the region inhabited by the California Quail, fewer juveniles survive than if water is plentiful.

The causes of interactions between population dynamics and environmental variables such as rainfall may be less direct than in the example above. The fecundity of Florida Scrub Jays, expressed as nest success, is likewise dependent on rainfall (Figure 2.4). However, the researchers speculate that the direct cause of variation in nest success is variation in nest predation rates. Rainfall could influence nest predation by affecting the density or activity of predators, the availability of alternative food items, the nest vigilance of the Jays, or the protective vegetation cover surrounding nests.

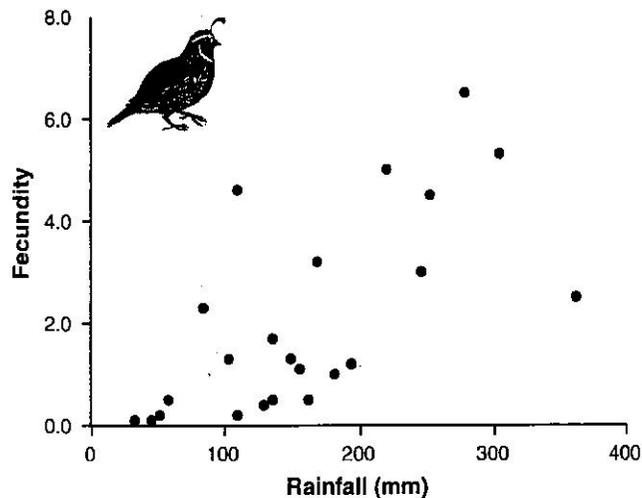


Figure 2.3. The relationship between rainfall (December to April precipitation) and fecundity in the California Quail (*Callipepla californica*) for a population in the Panoche Management Area, California (after Botsford et al. 1988). The correlation coefficient for these (log transformed) data was 0.68. Fecundity was expressed as the number of juvenile birds per adult.

There are many causes of death in the Muskox population on Nunivak Island, some of which are directly related to environmental variables. Over the 20-year period that observations were made, animals fell from cliffs, became lost on sea ice, were mired in a bog, drowned, were otherwise injured, were shot by humans, or died during winter snow falls. There were almost certainly deaths due to starvation in years of heavy snowfall, during which it was harder to find food. A relatively common event in this population was for small groups of animals to wander onto pack ice around the island during winter. The ice floes broke up or melted, blocking the animals' return to land. These animals either starved or were drowned at sea. It would be impossible to predict the number of animals that might suffer such a fate in any year, because it depends on the propensity of groups to wander over the ice, and the chance environmental events that lead to the break up

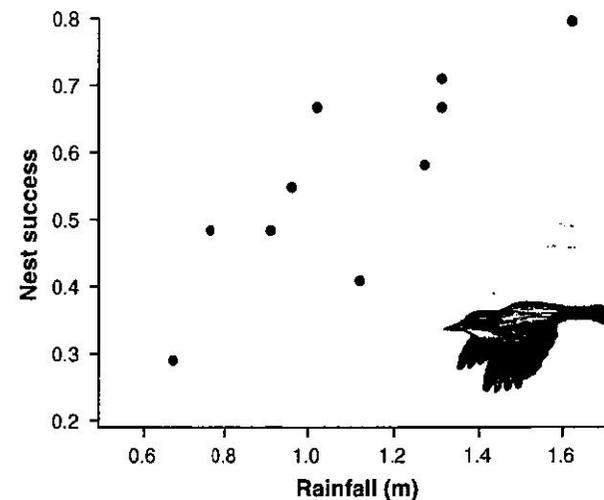


Figure 2.4. Nest success in Florida Scrub Jays (*Aphelocoma c. coerulescens*) as a function of total rainfall in the preceding 10 months (June to March) (after Woolfenden and Fitzpatrick 1984). Nest success is the proportion of nests that survive to fledgling. The correlation between rainfall and nest success is 0.78.

of the pack ice. Weather conditions are thought to be the single most important factor determining year to year variation in population growth of Muskox on other islands (see Gunn et al. 1991).

If we wanted to predict the population size next year, and in making this prediction take into account the variation due to some environmental factor, we would need to know three things: (1) which environmental factor is important, (2) how it affects the population dynamics, and (3) what the value of that environmental factor will be in the future. In other words, even if the dynamics of a population are directly related to an environmental variable (and we knew exactly what this relationship is), we still cannot make precise predictions because it is impossible to say what the value of the environmental variable will be next year.

We noted in Chapter 1 that the growth rate of the Muskox population was not fixed through the period of observation. It varied from a maximum of 1.27 to a minimum of 0.94. Having taken note of the fact, we estimated the mean growth rate and then made some predictions for population sizes that

ignored the fact that growth rates are variable. The results of our predictions were made without any estimate of how reliable they were. For example, we predicted that the population size in 1968 should have been 778 animals. It turned out to be 714 (or 762 if you include removed animals). Was the prediction within the bounds of probability, given the variable nature of the population's growth rate?

We may rewrite the equation for exponential population growth as follows:

$$N(t+1) = N(t) \cdot R(t)$$

where $R(t)$ is the growth rate for time step t . Writing $R(t)$ instead of R indicates that the growth rate varies from one time step to the next. When we use this equation, we sample the growth rate from some distribution for each time step, rather than use a fixed value. We may, for example, use observed distribution of growth rates for the population (Figure 2.5). This distribution shows that between 1947 and 1964, there was one year when the growth rate was between 0.90 and 0.95 (indicated at the mid-value of this range, 0.925), one year when it was between 1.00 and 1.05, etc.

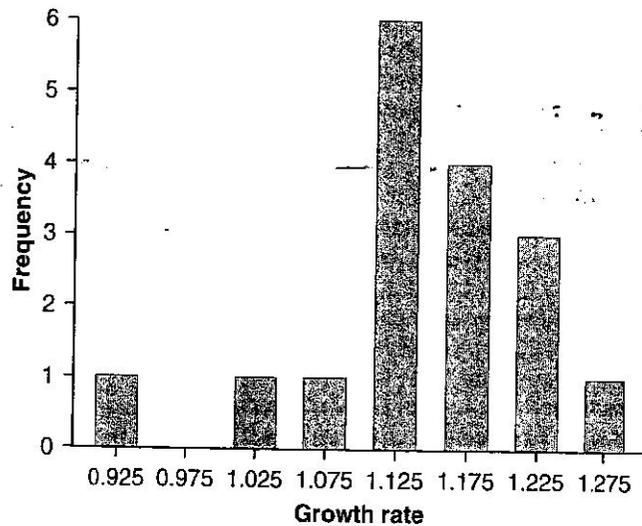


Figure 2.5. Frequency distribution of growth rates observed in the Muskox population on Nunivak Island between 1947 and 1964 (see Figure 1.4 in Chapter 1).

By sampling randomly from this distribution, we assume that the properties of the random variation that we have observed in the past will persist in the future. By properties, we mean characteristics such as the mean, variation, and shape of the distribution. Why do we sample randomly, instead of using the correct sequence of growth rates between 1947 and 1964? We cannot use the exact sequence of growth rates because there is no guarantee that the environmental factors between 1947 and 1964 will repeat themselves in exactly the same order in the future. It would be a very strong assumption (meaning very likely to be wrong) to assume that they would. Instead we make a generalization based on this observed distribution: We assume that the distribution of growth rates in the future (their mean, variation, etc.) will remain the same as the observed distribution, even if the growth rates do not repeat themselves in the same order as in the period from 1947 to 1964.

Of course, even if we sampled randomly, the set of growth rates we chose will probably be different from what actually will happen in the future. To account for the inherent uncertainty of the future growth rates, we do this many times. We randomly select a set of growth rates for, say, 20 years, and estimate the population's future with these 20 growth rates. This gives one possible future for the population. Then we select another 20 random numbers, and repeat the process. By undertaking repeated trials we may predict the population size into the future, accounting for the effects of the environment on the population. In order to get a representative sample of possible futures of the population, we have to repeat this hundreds of times. This procedure is most easily implemented on a computer (actually, it is next to impossible to do without a computer).

The procedure may be further generalized by sampling the growth rates from a statistical distribution that has the same properties as the variations that have been observed in the past. For example, we may sample the distribution known as the normal distribution, with the same mean and standard deviation as the observed distribution. This approach has the advantage of recognizing that values of R more extreme than those observed in the past are possible in the future. For instance, if we observed the population for 100 years instead of 17, perhaps there would be a year with a growth rate of 0.8 or 1.4.

Before we proceed, we need to define some terms we will use frequently in describing stochastic models. A time series of population abundances is called a population trajectory. When we estimated the population's future with 20 randomly selected growth rates, we produced a population trajectory. Each trial or iteration that produces a population trajectory is called a

replication. Finally, running the model with many replications is called a stochastic simulation. A deterministic simulation produces a single population trajectory without any variation in model parameters.

The Muskox population in 1936 was begun with 31 animals. Applying our current knowledge of the population, we can make predictions for the population over the period before regular sampling, between 1936 and 1948. The results of 1,000 trials for the Muskox population are shown in Figure 2.6. This figure shows, for each year, the average expected size (dashed curve), plus and minus one standard deviation (vertical lines), and the maximum and minimum values recorded for that year (triangles). These statistics (mean, standard deviation, minimum and maximum) are calculated over the 1000 replications (trials) of simulated population growth. The five observed values for the Muskox population size made between 1936 and 1948 are also shown (black circles). The model includes both demographic and temporal environmental variation. The growth rate, R , is 1.148, the survival rate, s , is 0.921, and the standard deviation in the growth rate is 0.075 (based on the observed variation in Figure 2.5).

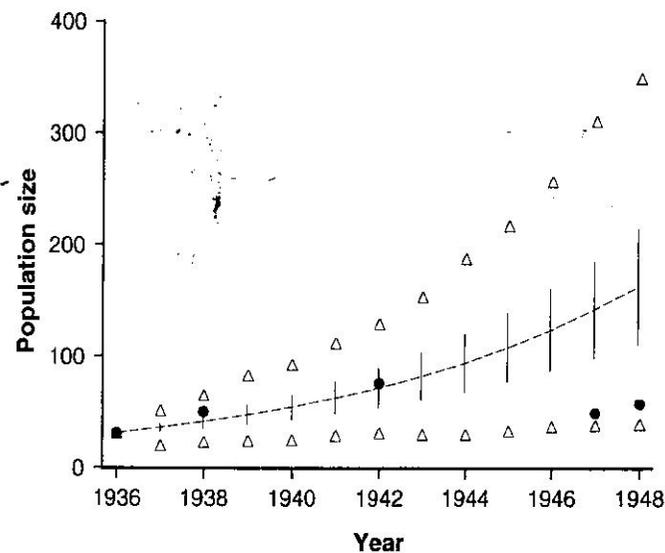


Figure 2.6. The size of the Nunivak Island Muskox population, based on 1,000 replications.

The population grew much as could have been expected between 1936 and 1942. However, between 1942 and 1947, the true population was markedly reduced, compared to growth in periods before and after that interval. In 1947, the population numbered just 49 animals. The observers suggested that the losses were due to groups of animals wandering onto sea ice during winter and being lost, other accidental deaths, and shooting. The observed population size in 1947 was within the limits of what could have been expected, once the random variations due to demographic and environmental uncertainty were included in the prediction.

The variation in the predicted abundance increases as time goes on (Figure 2.6). Our predictions become less and less certain, the further into the future we make predictions. This characteristic is a general result common to all predictions that include uncertainty. It makes good intuitive sense. One can be more certain of predictions that are made in the short term. Long-term judgements are subject to many more uncertain events, and the bounds on our expectations must increase, the further into the future that we make projections.

It is possible to construct a quasi-extinction risk curve based on the projections that are summarized in Figure 2.6. One simply records the smallest size to which the population falls during each trial. There will be 1,000 such records from 1,000 trials. These numbers are then used to create a cumulative frequency histogram. The frequencies, rescaled between 0 and 1, and plotted against population size, become the risk curve (Figure 2.7a).

If one collects the smallest value recorded at any time during each trial, the risk curve has a specific meaning. It tells us the chance that the population will fall below the specified threshold at least once during the period over which predictions are made.

Of equal interest is the creation of explosion risk curves. It is possible to construct a curve representing the chances that the population will be greater than or equal to a specified threshold population size. The procedure is much the same. One records the largest size to which the population rises during each trial. These numbers are used to create a cumulative frequency histogram. The frequencies, rescaled between 0 and 1, and plotted against population size become the explosion risk curve (Figure 2.7b). Extinction risk curves are useful for questions related to the likely lower bound of a population. Explosion risk curves are useful for questions related to the likely upper bound of a population.

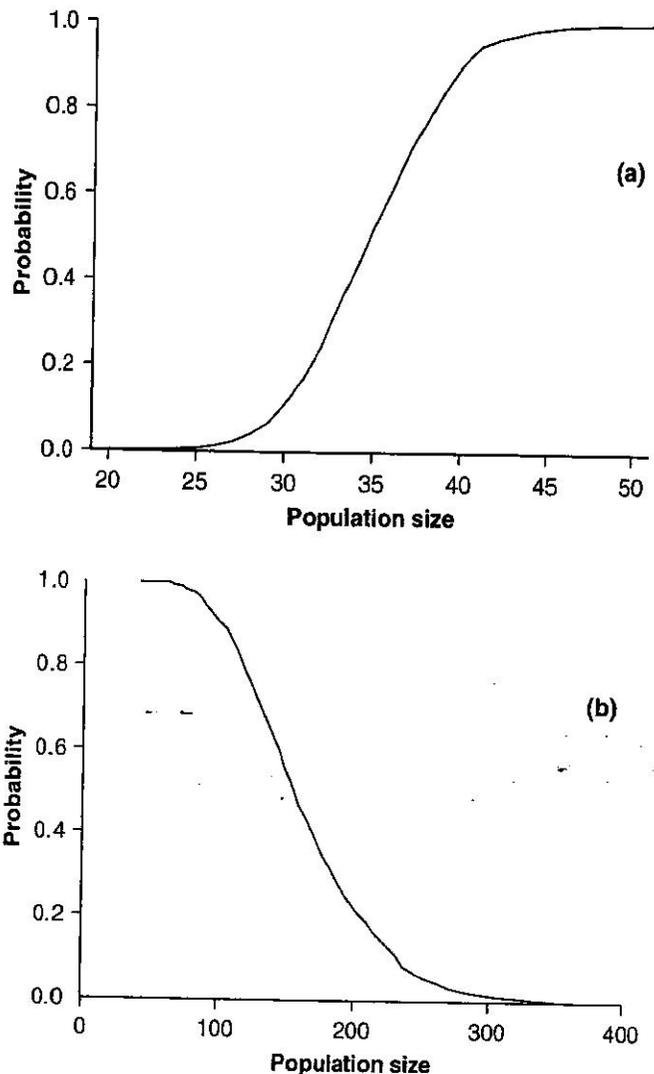


Figure 2.7. Risk curves for the Nunivak Island Muskox population for the 12-year period between 1936 and 1948: (a) quasi-extinction risk curve and (b) quasi-explosion risk curve, for the population based on an initial size of 31 individuals.

2.2.3.2 Spatial variation

The environment varies in space as well as in time. Changes in environmental conditions are related to distance. Two butterflies living in an oak forest in New York are more likely to experience the same kind of weather from day to day than are butterflies that live on opposite sides of the continent. Anyone who has dived in the ocean will have noticed a smooth transition from light to darkness with increasing depth. If survival or fecundity depend on environmental conditions, then they too will vary in space in response to the variation in environmental conditions.

One way of looking at spatial variation in the environment is to think of it as your ability to predict the conditions in some other place, knowing the conditions where you are. It is not possible to predict exactly the rainfall at one location, knowing the current rainfall at another location. The degree of reliability in the prediction from one place to another will depend, at least in part, on how far the two points are apart. The association between the recorded values of an environmental variable at different places is termed spatial correlation.

Spatial variation may also be thought of as the variation in environmental conditions between spatially separate patches of habitat, the different conditions experienced by each of several populations. Many species consist of an assemblage of populations that occur in more or less discrete patches of habitat. We can ignore the differences in the environment experienced by these populations only if these patches are identical in composition and close enough that they experience the same environmental conditions. In most real populations, at least one of these conditions will be violated. All of the populations will experience some environmental changes in common (such as the average summer temperature) and some will experience local environmental changes uniquely in a given patch (such as the local water hole drying out). The pattern of change in local population size in response to unique environmental conditions can have profound effects on our expectations of future population sizes. The interactions between these processes and the role of migration of individuals between patches will be explored more fully in Chapter 6.

2.2.3.3 Catastrophes

Catastrophes are extremes of environmental variation, including natural events such as floods, fires, and droughts. Any environmental change that has a relatively large effect on the survival or fecundity of individuals in a population compared to the normal year to year fluctuations may be considered a catastrophe. Thus, it is somewhat arbitrary to single out and label such environmental conditions as extreme. The category is useful only insofar as some ecological processes are driven by relatively infrequent, cat-

astrophic events. In many ecosystems, disturbances such as fire, windstorms, or snowstorms are an important or even the dominant ecological process determining the structure and composition of populations and communities. Often, we may know quite a lot about the characteristics of these events such as their average frequency and the distribution of intensity of the events. With field data it is possible to specify the effects of catastrophes on the parameters of a population. If so, then there will be better understanding of the relationship between the population and the environment incorporated in the expressions that we write.

Explicit modeling of unique catastrophic events may even be essential for circumstances in which species are specially adapted to the effects of the catastrophe. For example, seeds of many plant species in the genus *Acacia* require a fire to germinate. In the absence of fire, adults produce seeds that mostly fall to the forest floor and remain dormant. Fires stimulate the germination of dormant seeds and kill adults, which have life spans of 10 to 100 years in the absence of fires. Thus, recruitment of new individuals into the population occurs in pulses following the fires that stimulate germination and eliminate adults. Fecundity is a binary condition: either there is none (in years without fire) or most seeds in the soil-stored seed bank germinate (in years with fire). Such dynamics could only be modeled by writing expressions that include the chance of a fire.

2.3 Parameter and model uncertainty

2.3.1 Parameter Uncertainty

In all of the above discussion, we have assumed that the quantities obtained from field observation including mean survival, fecundity, growth rate, and the variation in these parameters, are known exactly. Effectively, we have assumed that the observed variation in population parameters comes from sources including demographic and environmental variation. Anyone who has attempted to measure the simplest parameter more than once under field conditions knows that this is a false assumption. All measurements involve error.

Parameter uncertainty is the variation in our estimate of a parameter that is due to the precision and accuracy of the measurement protocol. The assumption that sampling error is absent is particularly suspect when data are limited. Smaller samples are subject to relatively large sampling errors. If sampling variation is included in a model, projected variability will be much larger than in the true population. The Muskox of Nunivak Island provide an example. Aerial census techniques were used to estimate population size between 1949 and 1968. These data were used to calculate all of the parame-

ters in the examples used up to the present. However, between 1964 and 1968, independent estimates were made based on ground samples (Table 2.2).

Table 2.2. Counts (from ground samples) and estimates (from aerial samples) of the total population size of Muskox on Nunivak Island.

Year	Count	Estimate	Bias (Count/Estimate)
1965	532	514	1.035
1966	610	569	1.072
1967	700	651	1.075
1968	750	714	1.050

After Spencer and Lensink (1970).

The aerial "estimates" of population size were consistently lower than the ground-based counts. If we assume that the counts are correct (and there is no absolute guarantee of that), then the estimates were consistently biased, but the magnitude of the bias varied from year to year, from 3.5% to 7.5% (Table 2.2). Bias may be defined as systematic error, the difference between the true value and the value to which the mean of the measurements converges as more measurements are taken. Precision is the repeatability of a measurement made under the same conditions. Unfortunately, we do not have any estimates of Muskox population size made in the same year using the same method. Such data would allow us to quantify the precision of the population estimates.

Often, subjective judgment is involved in the choice of a method for measuring a parameter. Similarly, judgment may be made in assuming a correspondence between one variable and another. For example, we may observe that rainfall varies by 10% each year, and assume that population growth varies by the same amount. Even more subtle is the assumption that the levels of variation that we have observed in the past will persist in the future. There is nothing wrong with such judgments; often they are unavoidable. However, it is wrong to ignore the uncertainty inherent in such judgments.

2.3.2 Model Uncertainty

The structure of a model relates the parameters to the dependent variable, in this case future population size. If our ideas concerning the population's dynamics and ecology are wrong, or if we have not been careful in translating our ideas into equations, our predictions may be astray. Uncertainty

concerning the form and structure of the expressions we use to describe the population is known as model uncertainty. Thus, even if the parameters that describe the dynamics of a population were known exactly, and the variation associated with each parameter was decomposed into demographic uncertainty, environmental uncertainty and measurement error, we could still make mistakes in predicting future population size.

Model structure is a simplification of the real world. It represents a compromise between available data and understanding, and the kinds of questions that we need to answer. It is difficult to know the degree of simplification that is both tractable and adequate to the task at hand, but that is not so simple that it misses some important ecological processes. Competing model structures may provide as good, or almost as good, explanations of past observations as one another, but generate quite different expectations. The only way to deal with model uncertainty is to compare predictions of models with different structures and (if they make different predictions) to analyze the models in detail to understand which assumptions led to the differences. Such an analysis may guide further field observations or experiments to decide which model structure is more realistic.

2.3.3 Sensitivity Analysis

Both parameter uncertainty and model uncertainty may be explored using a process known as sensitivity analysis. Sensitivity analysis measures the change in a model's predictions in response to changes in the values of parameters, or to changes in the model structure. To illustrate sensitivity analysis, consider the model in which a population's growth rate is related to several environmental variables. For example, variation in the growth rate of a population of Shrews (*Crocidura russula*) that inhabit suburban gardens in Switzerland is related to weather variables by

$$\Delta R \approx 0.73 \cdot P - 0.78 \cdot S + 0.50 \cdot T_s - 0.83 \cdot T_w$$

where P is mean monthly precipitation in spring (m), S is winter snow fall (m), and T is average monthly mean temperature ($^{\circ}\text{C}$) in summer (T_s), and winter (T_w). We know that summer rain averages about one meter and that winter snow fall averages about the same value. The coefficients for the two parameters are similar. Thus, the growth rate will be equally sensitive to variations in snow fall and rainfall. The coefficients for temperature are about the same magnitude. However, the values for temperature vary more (they are around 10°C in summer and around 5°C in winter), so that R is

effectively more sensitive to variations in temperature. A 10% increase in summer temperature will increase R by 0.5, whereas a 10% increase in snow depth will decrease R by only 0.08.

The object of sensitivity analysis is to tell us which parameters are important and which are not. If a 10% change in a parameter results in a small change in the dependent variable (say, less than 1%), the model is insensitive to the parameter. If the change in the dependent variable is large (more than 10%), then the model is highly sensitive to the parameter. Such information is useful because it may guide the direction of research effort. It is more important to eliminate measurement errors from parameters to which our predictions are sensitive than to eliminate it from parameters that contribute little to our predictions.

Sensitivity analysis may also be used to explore alternative model structures. For example, our model for the growth rate of a population above may have the best explanatory power in a statistical sense. However, our biological intuition may tell us that the following model is likely to be a better predictor of future population growth:

$$\Delta R \approx 0.15 \cdot P \cdot T_s - 0.7 \cdot S$$

In this version, P and T_s are multiplied because we treat the effect of rainfall and summer temperature as an interaction. We may fix the parameter values and explore the consequences for predictions of one model versus the other. In some cases, the model structure will make little difference to expected outcomes. In other cases, it will make an important difference. If the latter is true, it would be advisable to perform experiments or acquire more data to discriminate between the competing models. If the acquisition of data or experimental results are impossible, then predictions may be made with both models, and the most extreme upper and lower bounds may be used to place limits on the predictions. In this way, predictions can incorporate model uncertainty that is not reducible without further field work.

The above example was based on a statistical relationship between population growth rate and environmental variables. Sensitivity analysis may be based on other variables as well. It is important to evaluate both the deterministic and the probabilistic components of a prediction. Thus, the dependent variable against which we judge model sensitivity may be the risk of population extinction within a specified period of time, or the risk of the population increasing above some specified upper bound. The independent variables would be model parameters and their variation. If an increase in a parameter (say, average growth rate or the standard deviation of growth

rate) results in more than a 10% increase in risk, then the model may be considered to be sensitive to that parameter. We will further explore this type of sensitivity analysis in the exercises of this section.

Sensitivity analysis is perhaps one of the most important tools in quantitative population ecology. It allows us to explore the consequences of what we believe to be true (in terms of the model parameters and their ranges). It provides a measure of the importance of parameters and model assumptions. It may be used to place bounds on predictions that subsume both model and parameter uncertainty, providing a relatively complete picture of the reliability of a prediction.

2.4 Ambiguity and ignorance

In natural resource management, rare and unexpected events may be termed "surprises" (see Hilborn 1987). Ignorance leads to surprise. It may result from unawareness of unexpected events, or from false knowledge or false judgments. That does not mean that surprise itself is rare, only that each event is essentially unexpected. It includes anything we do not expect, anything that is unaccounted for by our model or by our intuition.

Some surprises are avoidable because the ignorance they spring from may be reducible. That is, it may be amenable to study or learning. One may be ignorant of a process or a predictable outcome, but could overcome that ignorance by learning or research if the information or the methods of study were available. There are direct and indirect costs of such ignorance. For example, ignorance of past experiments or observations may lead to the tacit acceptance of hypothetical results, without empirical testing. It may cause disciplines such as wildlife management to lose credibility with people with a vested interest in wildlife.

Other surprises may be unavoidable. We may be unaware that we are unable to make predictions accurately, if the structure of the system were to change. That is, we would be faced with novel circumstances. For example, the demographers studying the human population as recently as 60 years ago predicted that the population size would be 3 billion by the end of the century. It will probably be over 6 billion. They were wrong by a factor of two, in part because of unavoidable surprises. They could not have foreseen the decrease in mortality caused by the invention of antibiotics, or the increase (albeit temporary) in food production as a result of widespread use of pesticides.

Uncertainty may arise from disagreement, even amongst scientists interpreting the same information. Interpretations are colored by a person's technical background, expertise, and understanding of the problem. Things

are further complicated by the fact that people, decision makers and scientists included, frequently hold direct or indirect stakes in the outcome of a question. Judgments are influenced by motivational bias.

Linguistic imprecision may be responsible for important components of uncertainty. The statement "the population is not threatened by what we plan to do" is ill-specified. To interpret it, we need more information. Would the statement be true if the probability of decline of the population to half its current size was 10% in the presence of the impact, and 2% in the absence of the impact? Even so, many more specifics are needed.

A quantity is called well specified when there is a single true value that is measurable, at least in theory. The test for clarity of specification of a problem is whether it can be unambiguously defined, given a description. For example, the phrase "Provide a management plan that results in an acceptable risk of decline of a population" is an ambiguous request. Risks include both a probability and a time frame, so one must first ask, What is the time horizon over which one wishes to estimate the risk? Secondly, the term "acceptable" is undefined. The concept of an acceptable risk will vary depending on the magnitude of the decline, whom you ask, and what it is they have to gain or lose by various management strategies. Thus, ambiguity in the specification of a problem may create kinds of uncertainty that are beyond any kind of quantitative or qualitative analysis, and it may be resolved only by political or social processes. We will explore these concepts further in the final chapter of the book.

2.5 Additional topics

2.5.1 Time to Extinction

The quasi-extinction risk curves we examined focus on probability of falling below certain levels anytime during a fixed interval of time (thus we call them "interval" risk curves). For example, we used a 12-year period or interval in the Muskox example (Figure 2.7a). A different way to express the results of the simulation is to keep a record of the time it takes each replication of the simulation to become extinct (or fall below a critical threshold abundance). If we ran the simulation for a long time and recorded the year of extinction for each of the 1000 replications, we could use these data to construct a time-to-extinction curve, the same way we used minimum abundances to construct risk curves. A time-to-extinction curve (Figure 2.8) gives the probability that the population will have gone extinct by the time a given number of years (x -axis) have passed.

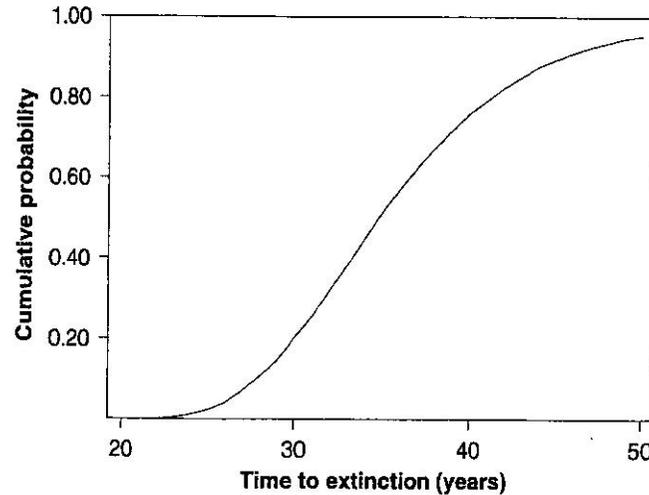


Figure 2.8. Time-to-extinction curve (the number of years that will pass before a hypothetical population falls below a fixed threshold).

Note that the curve looks similar to the quasi-extinction risk curve, but it has a very different meaning. In this case (Figure 2.8), the x -axis gives the number of years, and the threshold of extinction is fixed. In the case of the risk curve above (Figure 2.7a), the x -axis gives the threshold, and the time interval is fixed. In this book we will mostly use the risk curves, but briefly come back to the time-to-extinction curve in a later chapter.

2.5.2 Estimating Variation

Very often, estimates of population size through time are used to calculate parameters for population growth models. In Figure 2.6, the standard deviation representing variation around the mean population size was predicted by a simple population model that included both demographic stochasticity (see Section 2.2.2) and environmental variation (see Section 2.2.3). In this model, the environmental variability was modeled by a population growth rate that varied randomly from one year to the next. The amount of variation in the growth rate is measured by its standard deviation. In this case, the standard deviation was 0.075. This estimate was based on the observed,

year-to-year variation in growth displayed in Figure 2.5. In other words, the number 0.075 is the standard deviation of the 17 yearly growth rates from 1947 to 1964.

There are some problems with this approach. The observed variation in growth rate (Figure 2.5) has several sources, including environmental change between years, demographic stochasticity, and sampling (measurement) error. Even if the environment was constant, demographic variation and sampling error would ensure that the rate of change in the size of the population changes (or appears to change). When estimating the standard deviation of the growth rate (which we used in the model that produced Figure 2.6), we assumed all of the variation is due to environmental change.

This assumption may be reasonable if the population is large (so that demographic variation is negligible) and the size of the population is known with a high degree of reliability (so that sampling error is negligible). In other circumstances, to assume that all observed variation in growth rates is due to the environment alone will overestimate the true variation in the population.

We should subtract the sampling variance and the demographic variance from the total variance estimate. The difference would be variance due to the environment. In general, this is difficult to do correctly and it is a topic of ongoing, active research. In the meantime, assuming that all variation is due to the environment generally will tend to result in estimates of extinction and explosion probabilities that are too high. It is important to remember this fact when interpreting the results of a study, and to explore the consequences for the results of relatively small values for environmental variation.

2.6 Exercises

Before you begin this set of exercises, you need to install the program RAMAS EcoLab, if you have not yet done it. Read the Appendix at the end of the book to install RAMAS EcoLab on your computer.

Exercise 2.1: Accounting For Demographic Stochasticity

In this exercise, you will predict the change in population size of the Muskox population between 1936 and 1937, accounting for demographic stochasticity. For this exercise you will need to choose uniform random numbers. Some calculators give a uniform random number every time you press a key. If you have one of these, you can use it (skip "Step 0" and go to "Step 1"; you will need two such numbers for each repetition of this step). If you don't have such a calculator, you can use RAMAS EcoLab (see "Step 0").

Step 0. Start RAMAS EcoLab, and select "Random numbers," which is a program that produces random numbers. The program will display two uniform random numbers (between 0 and 1) on the screen. To get another pair of random numbers, click the "Random" button. (To quit, select "Exit" under the File menu, or press **(Alt-X)**.)

Step 1. The Muskox population consisted of 31 individuals in 1936. Write down this number ($N = 31$) on a piece of paper. Repeat the following steps 31 times, once for each Muskox on Nunivak island in 1936. For each repetition, use a new pair of random numbers.

Step 1.1. Use the first random number to decide if the animal produces an offspring or not. If the first random number is *less than* the fecundity value ($f = 0.227$), then *increase* N by 1, otherwise leave it as it was.

Step 1.2. Use the second number to decide if the animal survives or dies. If the second random number is *greater than* the survival rate ($s = 0.921$), then *decrease* N by 1, otherwise leave it as it was.

Step 2. After repeating the above steps 31 times, record the final N . This is your estimate of the Muskox population size for 1937.

Step 3. Repeat Steps 1 and 2 four times, for a total of five trials. You will have 5 estimates for the Muskox population size for 1937. Comment on the amount of variation among the results of the five trials.

Exercise 2.2: Building a Model of Muskox

In this exercise, you will use RAMAS EcoLab to build and analyze a stochastic model of Muskox on Nunivak island.

Step 1. Start RAMAS EcoLab, and select the program "Population Growth (single population models)" by clicking on its icon. See the Appendix at the end of the book for an overview of RAMAS EcoLab. For on-line help, press **(F1)**, double click on "Getting started," and then on "Using RAMAS EcoLab." You can also press **(F1)** anytime to get help about the particular window (or, dialog box) you are in at that time. To erase all parameters and start a new model, select "New" under the Model menu (or, press **(Ctrl-N)**).

Step 2. From the Model menu, select **General information** and type in appropriate title and comments (which should include your name if you are going to submit your results for assessment).

Enter the following parameters of the model.

Replications:	0
Duration:	12

Setting replications to 0 is a convenient way of making the program run a deterministic simulation, even if the standard deviation of the growth rate is greater than zero. Note that the last parameter of this window, whether to use demographic stochasticity, is ignored (it is dimmed and is not available for editing). This is because when the number of replications is specified as 0, the program assumes a deterministic simulation. This parameter is ignored because it is relevant only for stochastic models.

After editing the screen, click the "OK" button. (Note: Don't click "Cancel" or press **(Esc)** to close an input window, unless you want to undo the changes you have made in this window.) Next, select **Population** (under the Model menu). Recall that the Muskox population on Nunivak Island began in 1936 with 31 individuals and had an average growth rate of 1.148. Based on these, enter the following parameters in this screen.

Initial abundance:	31
Growth rate (R):	1.148

The parameter "Standard deviation of R" is not available for editing because we will first run a deterministic simulation, in which standard deviation will not be used. Similarly, "Survival rate (s)" is used only to model demographic stochasticity, so it is also ignored by the program when the simulation is deterministic.

For this exercise, you can ignore the last two parameters in this window (density dependence and carrying capacity); we will discuss density dependence in a later chapter. The default selection for "Density dependence type" is "Exponential," which refers to exponential growth with no density dependence. The last parameter is ignored because it is related to other types of density dependence. When finished, click "OK" and press **(Ctrl-S)** to save the model in a file.

Step 3. Select **Run** from the Simulation menu to start a simulation. The simulation will run for 12 time steps; you will see "Simulation complete" at the bottom of the screen when it's finished. For a deterministic simulation, this will be quite quick. Close the simulation window.

Step 4. Select "Trajectory summary" from the Results menu. Describe the trajectory you see. What is the final population size?

Step 5. Close the trajectory summary window. Select **General information** and change "Replications" to 100 by typing the number. Next, click the little box next to "Use demographic stochasticity" This will add demographic stochasticity to the model. The parameters should now be as follows:

Replications:	100
Duration:	12
<input checked="" type="checkbox"/> Use demographic stochasticity	(checked)

Click the "OK" button and select **Population** (again, under the Model menu). Recall that the survival rate of the Muskox population was 0.921 and that the observed standard deviation in the growth rate was 0.075. Based on these, enter the following parameters in this screen.

Initial abundance:	31
Growth rate (R):	1.148
Survival rate (s):	0.921
Standard deviation of R:	0.075

Click "OK," and select **Run** to start a simulation. While this stochastic simulation is running, after the first five replications, the program will display each population trajectory it produces (the program cannot display the population trajectories produced by the first five replications, because it uses them to scale the graph). Describe the trajectories in comparison with the deterministic trajectory. Do any of these trajectories look similar to the deterministic trajectory? What is the cause of the difference?

Step 6. After the simulation is completed, close the simulation window and save the model by pressing **Ctrl-S**. Then, select "Trajectory summary." You will see an exponentially increasing population trajectory. Describe the trajectory summary. What is the range of final population sizes? You can try to read the range from the graph, or if you want to be more precise, you can see the results as a table of numbers. To do this, click on second button from left ("show numbers") on top of the window. The first column shows the time step, the others show five numbers that summarize the abundance for each time step: (1) minimum, (2) mean - standard deviation, (3) mean, (4) mean + standard deviation, and (5) maximum.

Step 7. Select "Extinction/Decline" from the Results menu. What is the risk of decline to 31 individuals based on this curve?

It might be difficult to read the precise value of the risk from the screen plot. Do the following to record this number precisely:

Click the "Show numbers" button, and scroll down the window to where you see "31" in the first column. Record the probability that corresponds to this threshold level.

Exercise 2.3: Constructing Risk Curves

In this exercise you will construct an interval decline risk curve based on the Muskox model. If you have exited the program after the previous exercise,

first open the file you saved at Step 6 in Exercise 2.2 (press **Ctrl-O**) and choose the file you saved). If you did not save the previous model, then enter the parameters as described in Step 5 of the previous exercise.

Step 1. In the next step we will generate single trajectories. To prepare for this, select **General information**, and change "Replications" to 1. Also, change "Duration" to 5. Make sure that "Use demographic stochasticity" is checked. Click OK. (Note: If you want to save the model in this exercise, use "Save as" and give the file a different name, so you keep the original file.)

Step 2. Generate a single random trajectory based on the model in Exercise 2.2. To do this, run the model and display the trajectory summary as a table of numbers (see Step 6 in the previous exercise). Record the smallest value that the population trajectory ever reached during time steps 1 through 5 of this single replication. (Note: Ignore time step 0, for which the abundance is always 31.)

Step 3. Repeat Step 2 a total of 20 times.

Step 4. You now have 20 minimum population sizes from 20 runs. Sort these in increasing order, and use the table layout below to generate frequencies from the records of minimum population sizes. In the first column of the table, write the population sizes you have in increasing order. You are likely to get some population sizes more than once. Write these down only once. You will most likely use only some of the rows in this table. In the second column, write how many of your numbers is the population size in column one. In the third column, cumulate the numbers of the second column (see Table 2.1). In the fourth column, calculate probabilities by dividing the cumulative frequencies (third column) by the number of trials (20). Note that this table is similar to Table 2.1, but your numbers will be different because you have only 20 trials or replications, whereas Table 2.1 was constructed based on 10,000 trials.

Step 5. Plot the probabilities against population size in Figure 2.9.

Title:	Explosion/Increase
<input checked="" type="checkbox"/> Autoscale (<i>checked</i>)	
X-Axis Label:	Threshold
Minimum:	46
Maximum:	456
Y-Axis Label:	Probability
Minimum:	0.00
Maximum:	1.00

First, uncheck the box next to "Autoscale" by clicking on it. (This makes the program use the values entered in this screen instead of automatically rescaling the axes.) Second, change the maximum value of the x-axis to the threshold (in this case, 150). Third, click OK.

Scroll down the table. The last line of the table will give the threshold (150), and the probability of reaching or exceeding that threshold. Record this probability below.

Probability of increasing to 150 =

Step 2. Create eight new models based on the standard model. For each model, increase or decrease one of the four parameters of the model (see below) by 10%, and keep all the other parameters the same as the standard model. Note that there are some restrictions. For example, the survival rate (s) cannot be less than 0 or greater than 1. And the initial abundance must be an integer. Make necessary adjustments or approximations for these parameters. Save each model in a separate file. Record the low and high value of parameters, and filenames that contain them.

Initial abundance:	31
Growth rate (R):	1.148
Survival rate (s):	0.921
Standard deviation of R:	0.075

Parameter:	low value and filename	high value and filename
Initial abundance		
Growth rate (R)		
Survival rate (s)		
Stand. deviation of R		

Step 3. Run stochastic simulations with the eight models you created in the previous step. After each simulation, view the quasi-explosion results, and record the probability that the Muskox population will increase to 150 individuals within the next 12 years. Record the results in the table below.

Parameter:	Probability of increasing to 150		
	with high value	with low value	difference
Initial abundance			
Growth rate (R)			
Survival rate (s)			
Stand. deviation of R			

Step 4. For each parameter, subtract the probability with low value from the probability with high value of the parameter. Discuss the results.

- In which direction did each parameter affect the result? (In other words, does higher value of the parameter mean higher or lower probability?)
- Which parameter affected the outcome most, when the change was 10%? What should this result tell about field studies which attempt to estimate these parameters, or about future projects similar to this one?

Note that sensitivity of the result to $\pm 10\%$ of survival rate, or growth rate, or its standard deviation can be interpreted in terms of accuracy in the estimation of these parameters, or in terms of the value of these parameters in other places where a similar project will be implemented. However, sensitivity of the result to $\pm 10\%$ of initial abundance cannot be interpreted in terms of accuracy: It is probably not very difficult to count 31 animals. However, it might be interpreted in terms of the effect of the initial number of individuals on the success of the project.

2.7 Further reading

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- Shaffer, M. L. 1987. Minimum viable populations: coping with uncertainty. In M. E. Soulé (Ed.). *Viable populations for conservation* (pp. 69-86). Cambridge University Press, Cambridge.