7. Stochastic Population Models

Peter Chesson

Deterministic models dominated theory in ecology for much of its history despite recognition of the role of unpredictable environmental factors in population dynamics (Hutchinson, 1951, 1961; Andrewartha and Birch, 1954, 1984; Grubb, 1977, 1986; Sale, 1977; Wiens, 1977, 1986; Connell, 1978; Hubbell, 1979, 1980; Murdoch, 1979; Connell and Sousa, 1983; Sale and Douglas, 1984; Strong, 1984, 1986). Mathematical techniques for stochastic modeling were poorly developed and poorly understood. As a consequence, most ecological thinking about the role of stochastic factors was purely intuitive. Progress in stochastic population and community models has now allowed rigorous deduction to replace intuition. This progress has shown more complicated and intricate roles for stochastic factors than previously invisaged; but as is shown in this chapter, once elucidated, these roles can be understood intuitively.

The key to understanding stochastic factors is recognizing that even though they involve unpredictability they nevertheless have definable properties. For example, a stochastic factor such as rainfall has a frequency distribution characteristic of a locality. Moreover, there are a variety of ways in which any given stochastic factor may influence a population. For example, a stochastic factor might primarily affect the birth rate with little effect on the death rate; or it might not affect a given species directly but does affect the species' competitors or predators, thereby leading to an indirect effect on the species. Just as birth, death, competition, and preda-

tion are biologically distinct, each with their associated roles and theories, we have to expect that the role of a stochastic factor depends on which of these or other population processes it affects.

Another aspect of stochastic factors is scale. A stochastic factor may first appear or originate on one scale but have effects transmitted to other scales. We need to distinguish local phenomena, such as local thunderstorms, from regional phenomena, such as weather patterns over a large area. We must ask: Does this stochastic factor originate with individuals, local populations, or regional populations? Is its effect through time or over space? These questions of scale are basic when assessing stochastic factors.

However, the major scientific interest in stochastic factors is their effects on scales larger than their scales of origin. For example, one asks: Do stochastic effects seen at the level of an individual have an effect at the level of the total population? This question has two parts. First, do stochastic effects at one level (e.g., the individual level) lead to stochastic fluctuations at a higher level (e.g., the population)? Second, and more significantly, do stochastic effects at one level have systematic effects at a higher level? For example, do stochastic fluctuations on a short time scale lead to reductions in average population density on a long time scale, as has been suggested by some density-dependent population models (May, 1973)?

As used in ecology, the word "stochastic" has unfortunately taken on a rather mystical connotation. In mathematics, from which its ecological use is derived, a stochastic process is a function of time that is chosen with some probability from a set of possible functions of time. A stochastic process then is the appropriate description of population growth if we wish to consider the uncertainty of population trajectories. However, describing uncertainty is the least important attribute of a stochastic model. Rather, variation, which can be described by a frequency distribution but can be entirely deterministic in origin, is often key. From the population dynamic perspective of this review, stochastic factors are important because they generate variability. In contrast, in an evolutionary setting the unpredictability of stochastic factors can be the focus because it provides a problem for adaptation (Colwell, 1974).

Types of Variability

In 1978 I devised a classification of ecologically relevant variability based on its scale of origin. Any such classification is artificial to the extent that it imposes disjoint scales on a continuum. Nevertheless, such classifications have been useful. Three types of scale may be distinguished: spatial scale, temporal scale, and "population scale" (Chesson, 1982). Population scale relates to how large a population is or how many individuals are being considered. There may be few or many individuals in a given area, but

the number of individuals increases as the spatial scale increases. Thus although population and spatial scale are logically distinct, they are not independent in nature.

Within-Individual Variability

Even if two individuals have identical phenotypes, their future longevity and reproduction can be different. Chance processes may affect different individuals independently. For example, chance effects may lead to death by predation for some individuals but not others, mates for some but not others, and foraging success for only some individuals. There is no doubt that an individual's phenotype influences its success or failure, but variation remains after the effects of an individual's phenotype have been factored out. This residual variation is called within-individual variability (Chesson, 1978), or demographic stochasticity in earlier classifications (May, 1973). Within-individual variability involves purely chance phenomena that have nothing to do with an individual's phenotype.

Within-individual variability was the first kind of stochastic variation to be considered in population models and is the only variation included in the classic stochastic population models of mathematics (Feller, 1971). Within-individual variability works on the scale of an individual, because each individual experiences variation independently and on a temporal scale shorter than or equal to the lifetime of an individual.

A special case of within-individual variability is the sampling variation considered in population genetics, which leads to some copies of an allele, but not others, being transferred to the next generation. In the context of population genetics, within-individual variability leads to genetic drift (Roughgarden, 1979). In a similar way, it has been incorporated in community models to describe the possible drifting of species composition of a tropical forest in the case where it is hypothesized that species have identical niches and are average demographic equals (have equal average birth rates, longevities, and so on). In this setting, it has been possible to generate species abundance relations that resemble those of a real forest (Hubbell, 1979).

Within-individual variability also has an important role in discussions of population persistence: When populations are small, within-individual variability can lead to chance extinction, as discussed in more detail below in the section on population persistence. More generally, within-individual variability contributes to local population fluctuations and therefore contributes to the interesting effects of within-patch variability, also discussed below.

Between-Individual Variation

Individuals in a population usually vary phenotypically. Such variation has received only a little attention in ecological models, primarily within the

predator–prey and host–parasitoid framework. Variation in prey selection among individual predators gives frequency-dependent predation at the population level (Chesson, 1984b). On the other hand, between-individual variation in susceptibility of host to parasitism is able to stabilize the community-level interaction between parasitoids and hosts (Chesson and Murdoch, 1986). For systems of competitors, between-individual variation is a component of a species' niche breadth (Roughgarden, 1974). Milligan (1986) has taken this point further to investigate how heritable between-individual variation affects invasion and coexistence of competitors.

Between-individual variation has been found to have an important three-way interaction with competition and temporal environmental fluctuations (see below) and can play an important role in determining the outcome of interspecific competition in a variable environment. Between-individual variation occurs on the population scale of a single individual and on a temporal scale equal to or greater than the lifetime of an individual. The extent to which between-individual variation has a genetic basis determines the extent to which a phenotype is transmitted to an individual's offspring and therefore the temporal scale to which between-individual variation applies.

Within-Patch Variability

Within-patch variation is the analogue at the level of a local population of within-individual variability. Thus it is at a population scale greater than the individual but less than a closed population. It concerns stochastic fluctuations in population densities and environmental variables over time, locally in space (Chesson, 1981). If a population had only this sort of variation, and if there were no migration, each local population and the relevant environmental variables would fluctuate over time independently in different patches. Thus, the fluctuations in different spatial locations would be asynchronous. In nature, however, several sources of variation are present at any one time, and there is migration between patches. Rather than total asynchrony, there is some common element to the fluctuations. This common element is discussed below (see Pure Temporal Variation).

In the context of analysis of variance, within-patch variability is the space–time interaction, which may be partitioned out from other sorts of variation. Within-patch variability leads to asynchronous fluctuations in local population densities and local environmental parameters. For example, disturbance may affect some patches, but not others, in a way that is not predictable on the basis of the physical properties of a patch.

Asynchronous population fluctuations are at the heart of the verbal ideas of Andrewartha and Birch (1954) in their general theory of population regulation. General reasons for expecting within-patch variability to change the nature of population dynamics on the scale of a regional population consisting of many local populations are discussed by Chesson

(1981). Models and ideas about disturbance (Connell, 1979; Hastings, 1980) provide good illustrations. In these disturbance theories, catastrophes occur randomly in time and space, eliminating all organisms locally in space. Destruction of the organisms on a patch permits a successional process in which organisms with good colonizing abilities establish and grow for a while in the absence of later establishing competitive dominants.

Within-patch variability is especially important in these ideas on disturbance, as other patches are an important source of propagules for recolonization of a disturbed patch. The fact that only a portion of the patches is disturbed at any given time is critical.

Temporal fluctuations in mortality at a locality, which are a feature of disturbance, are critical too. One can imagine the same amount of mortality being spread uniformly through time. Can that additional mortality by itself promote coexistence without fluctuations in time or space? The first thing to note is that mortality does not eliminate linear hierarchies of competitive ability in resource exploitation (Armstrong and McGehee, 1980). At best, it changes the relative rankings of species favoring species with higher intrinsic rates of increase and so can merely alter the identity of the winner in competition. Thus mortality alone does not promote diversity in such a linear hierarchy of competitors.

Environmental fluctuations may be the cause of the local catastrophes involved in disturbance, or disturbance may be the result of predation. Discovery of patches by predators may vary in time and space, and so predators may disturb different patches independently. Although predation is more complicated than the simple effects of environmental variation, it nevertheless can work in principle in the same ways (Caswell, 1978; Hastings, 1978).

Spatiotemporal variation of discovery of local patches of habitat by different species of competitors, without invoking disturbance or predation, has also been regarded as having an important role in the maintenance of diversity on regional scales (Yodzis, 1978). More generally, one could simply consider within-patch variability of migration rates, which leads to spatially asynchronous fluctuations in the number of individuals colonizing different patches.

If fluctuating migration rates are less than perfectly correlated among species, chance fluctuations in the relative densities of competitors result. As a consequence, on average, individuals experience higher densities of conspecifics than heterospecifics. This statement is true for all species however, only when all patches are considered or when all time in a given patch is considered: It cannot be true for more than one species in a given patch at a given time. Thus the effect depends on spatially asynchronous temporal fluctuations, i.e., on within-patch variability.

This sort of fluctuating partial spatial segregation of species has the effect of increasing average intraspecific competition at the expense of interspecific competition on the spatial scale of many patches. The classic

consequence of this situation still applies: Species diversity is promoted (Atkinson and Shorrocks, 1981; Chesson, 1985; Comins and Noble, 1985; Ives and May, 1985; Ives 1988).

Within-patch variability in migration rates or parasitoid search rates can have a stabilizing role in host–parasitoid systems (May, 1978; Chesson and Murdoch, 1986). In this situation, variation in the numbers of parasitoids discovering patches has the effect of creating partial refuges for the prey. On a spatial scale consisting of many patches, this condition reduces over-shoot of the equilibrium and stabilizes the host–parasitoid interaction.

More generally, in predator–prey systems it has long been known that within-patch variability has a role stabilizing dynamics on a regional spatial scale. The time lag inherent in the dynamics of the predator–prey interaction in theory often leads to unstable oscillations. Predation that strikes different patches independently can stabilize such interactions and elim-inate oscillations for the system as a whole (e.g., Maynard Smith, 1974; Hastings, 1977). More recently, Crowley (1981) and Reeve (1988) have explored spatially asynchronous population fluctuations that result from spatiotemporal environmental fluctuations interacting with unstable local population dynamics. Within-patch variability arising in this way has also been found to lead to regional stability.

Between-Patch Variation

Different places may have essentially permanent environmental differ-ences. Such between-patch variation has long been appreciated in com-munity ecology, where in essence it allows niche differentiation and there-fore promotes coexistence. An example is Tilman's (1982) discussion of how between-patch variation in relative abundances of resources may per-mit high diversity in plant communities. Other discussions of between-patch variation explicitly taking into account migration between patches are those of Pacala and Roughgarden (1982), Shigesada and Roughgarden (1982) Shigesada (1984), Iwasa and Roughgarden (1986), and Pacala (1987).

Between-patch variation may also promote diversity without any in-volvement of habitat segregation when it is combined with pure temporal variation, as discussed in the next section. In predator–prey and host–parasitoid systems, between-patch variation can provide complete or par-tial refuges for prey or hosts, adding stability to the interaction between the species (Bailey et al., 1962; St Amant, 1970; Hassell, 1978).

Pure Temporal Variation

The weather, which is responsible for much temporal environmental varia-tion, is correlated over large areas of space. Such spatially correlated pat-terns are not covered by any form of variation discussed so far. Pure tem-poral variation is variation over time on a spatial scale sufficiently large to

contain essentially closed communities, i.e., communities in which migration has a negligible effect. Pure temporal variation is the variation remaining once all effects of space have been accounted for. Discussed here is the theory of temporal environmental variation in communities of competitors. This theory has been developed to the stage where broad generalizations are available. Some space is devoted to discussing them, as they may indicate the sorts of development that can be expected in other areas.

Stochastic Competition Models

When do stochastic fluctuations promote coexistence, and when do they hasten competitive exclusion? Two sorts of circumstance have been investigated. In the first case, population growth rates of different species are different nonlinear functions of the amount of competition the species experience: Thus the species differ in the range of competition to which they are most sensitive. For example, a species that exploits resources well when they are abundant but not so well when they are in short supply feels the effects of competition strongly while competition is still relatively weak. A species that is adapted to the situation of shortage of resources and that cannot increase its uptake rate even when resources are abundant would not respond to competition until it is severe. These nonlinear responses to competition are referred as negative and positive nonlinearities, respectively.

Fluctuations can promote coexistence of such species provided the species with the greater positive nonlinearity experiences smaller fluctuations in competition when it is at low density than the other species does when it is at low density. These ideas come mostly from models of deterministically varying factors (Levins, 1979; Armstrong and McGehee, 1980), but they hold up also in the stochastic case (Ellner, 1987a, Chesson, in preparation).

Models of disturbance (Chesson and Huntly, manuscript) can be formulated in this context. Disturbance was considered in the section on within-patch variability where asynchrony of disturbances on different patches was an important factor. Disturbance that is spatially synchronous is properly considered to be pure temporal variation. Naturally, such a disturbance must lead to less than 100% mortality. It can promote coexistence, provided organisms have complementary life histories as defined by Ellner (1987a).

Another broad class of models focuses not on differences between species in their response to competition but differences in their responses to environmental fluctuations. Most theoretical models do not deal with the environment directly, for example, temperature and rainfall usually are not variables. Population parameters that are presumed to depend on the environment serve instead and are referred to as environmentally dependent parameters. Examples are density-independent birth rates (Chesson

and Warner, 1981), survival rates (Chesson and Warner, 1981), seed germination rates (Ellner, 1984), and resource uptake rates (Abrams, 1984). Indeed, any parameter in a model that is not a function of density can be made an environmentally dependent parameter and a function of time.

Although environmentally dependent parameters themselves are not functions of density, it is nevertheless to be expected that their values affect the amount of competition that occurs in a system through their effects on population densities. For example, in models of annual plants the seed germination rate may be an environmentally dependent parameter that, together with the size of the seed bank, determines the density of plants that grow during a given year. Thus competition for resources needed by growing plants depends on the environmentally dependent germination fraction (Chesson, 1988).

In some models (e.g, Abrams, 1984) the environmentally dependent parameter is a resource uptake rate, and the involvement with competition is even clearer. The environmentally dependent parameter invariably has an indirect effect on population growth by altering the amount of competition, and it can be expected to have a direct effect as well. The indirect effect, however, depends on population density, whereas the direct effect is, by assumption, density-independent.

Variation of competition with the environmentally dependent parameter can be measured by a covariance, and this covariance is an important factor in the long-term dynamics of competing species. The direct and indirect effects of environment work in opposition, and the covariance between environment and competition indicates the extent to which environmental fluctuations are canceled out by opposing competitive effects. For example, in single-species models of organisms competing for space, fluctuations in the birth rate are exactly opposed by corresponding fluctuations in competition whenever space becomes saturated. Reflecting this situation, the measure of covariance between environment and competition is equal to the variance of the environmentally dependent parameter when the two are measured in the same standard units (Chesson, 1988). In several species models of space limitation (Chesson, 1984a), however, the covariance is usually less than the variance of the birth rate; and, as a consequence, a species' share of space fluctuates.

More generally, when a species is competing with others, the covariance between its environmentally dependent parameter and competition depends on the correlations between the environmentally dependent parameters of the different species and the absolute and relative densities of these species. For example, consider the case where the environmentally dependent parameters of different species are independent. When a given species approaches zero density, it experiences only interspecific competition, which is uncorrelated with its environmentally dependent parameter. The covariance between environment and competition is then zero.

When environmentally dependent parameters of different species are

positively correlated, the covariance between environment and competition does not drop to zero as a species approaches zero density but remains at some positive value. In general, however, this value is less than when the species is at high density unless there is a perfect correlation between the environmentally dependent parameters of different species or unless interspecific competition is stronger than intraspecific competition for all species pairs.

The final case, that of negative correlations between environmentally dependent parameters of different species, means that as population density decreases the covariance between environment and competition decreases from a positive to a negative value. *Density dependence* of the covariance between environment and competition means that the growth rate of a species at low density fluctuates more than that of a species at high density. Intuitively, we might expect that this fact is bad news and should hasten extinction. However, many organisms have traits that reduce the magnitude of negative fluctuations in the growth rate while allowing advantage to be taken of positive fluctuations (Chesson and Huntly, 1988). To see how it occurs we must consider the response of population growth rates to different environmental and competitive situations.

Because population growth is multiplicative over time, we take logs and define the growth rate as the change in log population size per unit time. This method is equivalent to considering the growth rate parameter, "r" of demography. On this log scale, changes in population size are additive over time. In certain simple circumstances the growth rate itself, applying for a given period of time (e.g., 1 year), is an additive function of the effects of environment and competition. It occurs if the effect of competition on survival and reproduction of an individual is independent of how that individual has been affected by the environment. For example, if environmental conditions lead to 60% survival, and of those individuals remaining competition permits only 40% survival, total survival is the product of these figures, or 24%. Taking logs, this product becomes a sum: $\log 0.24 = \log 0.6 + \log 0.4$. We say that the growth rate is additive over the effects of environment and competition.

The additive case seems to occur in only the simplest situations, although approximate additivity may be common. To see how deviations from additivity arise, consider a population subdivided into two types of individual, e.g., robust versus fragile, and for simplicity let them be equally abundant. Let environmental conditions yield 90% survival of the robust type but only 30% survival of the fragile type; competitive conditions lead to, respectively, 60% and 20% survival of the remaining individuals. Then total survival of the population as a whole is $\frac{1}{2}(90\% \times 60\%) + \frac{1}{2}(30\% \times 20\%) = 30\%$.

To see that environment and competition are not additive in this second case, note that when acting alone the average mortality due to the environment would be 60% as in the first example; and considered alone (i.e.,

without prior action of the environment), competition would lead to an average mortality that is also the same as the first example. Hence if we combine these average survival rates by taking a simple product (i.e., assuming additivity on a log scale) we get 24%, which is too low. Thus we see that the effects of environment and competition in this subdivided population are not additive.

In biological terms, the presence of "fragile" and "robust" individuals in the second example provides a buffer against the joint negative effects of environment and competition. Thus the growth rate of the population is not as severely affected by unfavorable environmental and competitive effects as predicted on the basis of the sum of their separate effects. Consequently, this sort of situation is referred to as *subadditive*.

Subadditivity due to population subdivision can arise in a number of ways. The example using robust and fragile individuals shows that it can result from between-individual variation. It can also arise from between-patch variation, as environmental and competitive factors may be more important in some patches than in others (Chesson and Huntly, 1988). For subadditivity to occur, some individuals must be more susceptible to environmental factors than others, and these same individuals must be more susceptible to competition than others. In the earliest models incorporating such population subdivision, the various classes of individuals were defined by stages of their life cycle, e.g., juveniles and adults (Chesson and Warner 1981) or dormant seeds and growing plants (Ellner, 1984). Differences in sensitivity to environment and competition in such cases can be expected to be large.

Superadditivity, the opposite of subadditivity, arises in situations where sensitivity to competition usually means insensitivity to the environment. For example, a species may occupy a mosaic of habitats, some of which provide benign environmental conditions but competition among many individuals, whereas other habitats may be exposed to harsh and fluctuating environmental conditions but have lower densities of individuals and little competition.

Subadditivity has the benefit of providing protection against unfavorable combinations of environmental and competitive events arising temporally. However, the preceding discussion of the covariance between environment and competition implies that the density of a species determines the extent to which it can take advantage of subadditivity. At low density, a species experiences more extreme fluctuations in environmental and competitive conditions. Subadditivity dampens the unfavorable extremes while permitting advantage to be taken of favorable extremes. As a consequence, a species at low density has an advantage when the results of all these fluctuations are combined over time. Competitive exclusion is thus opposed and species diversity promoted by environmental fluctuations.

These effects depend critically on subadditivity and the argument that a

species at high density has positive covariance between environment and competition. If positive covariance is combined with superadditivity, environmental fluctuations promote competitive exclusion (Chesson, 1989). Additive growth rates are neutral to coexistence in a fluctuating environment regardless of the covariance between environment and competition. Finally, if we consider negative covariance between environment and competition, all of the above conclusions about subadditivity and superadditivity are interchanged.

Models incorporating these effects have been reviewed elsewhere (Chesson and Huntly, 1988, 1989) together with various applications. There is much need for the development of models that apply in specific applications. Tools useful for developing and analyzing such models are also discussed elsewhere (Chesson, 1988).

Scale Transition

In all the models reviewed above, the interest is how variability on one scale leads to population and community phenomena on another. For example, questions of coexistence in the community models above involve density-dependent effects that appear when the results of fluctuations over many years are combined. Similarly, in the discussion of disturbance, we considered how large fluctuations locally in space contribute to a stable coexistence regionally.

Variability on one scale may or may not lead to significant variability on some larger scale. Variability on one scale, however, leads to different mean effects on a scale above it in most nonlinear systems (Chesson, 1981). Most of the results discussed above depend on this fact. To gain a better understanding of the subject, consider a single-species model exposed to pure temporal variation, such as that discussed by Turelli and Petri (1980).

$$X(t+1) = X(t)e^{r[1 - X(t)/K(t)]} \tag{1}$$

This equation is the Moran-Ricker model, which is a discrete time version of the logistic model. $X(t) =$ the population density at time t, and $K(t) =$ the carrying capacity, also a function of time representing stochastic factors. Assume for the purpose of this illustration that the values of the carrying capacity are independent from one time to the next and fluctuate within some finite range above 0. It is not difficult to see that this assumption implies that the fluctuations in $X(t)$ also are bounded within some finite range above 0.

Of the many interesting questions one may ask about this system, let us focus on the average of population density over time. The average over a time interval of length T is

$$\bar{X}_T = \frac{1}{T} \sum_{t=s+1}^{T+s} X(t) \tag{2}$$

It is shown in the Appendix that as we increase T (i.e., increase the temporal scale on which we are taking the average) the variance vanishes and $\bar{X}_T$ approaches a constant value $\bar{X}_\infty$ equal to the harmonic mean, $H(K)$, of $K(t)$, i.e.,

$$\bar{X}_T \to \bar{X}_\infty = H(K) = 1/E[1/K] \tag{3}$$

where E = the theoretical average or expected value of the random variable in the brackets. The scale or the value of T on which $\bar{X}_T$ is reasonably approximated by $\bar{X}_\infty$, which we call "long term," depends on the rate of decline of the variance of $\bar{X}_T$ as T increases. In general, the variance, $(V(\bar{X}_T))$ of $\bar{X}_T$ is given by the approximation

$$V(\bar{X}_T) = \sigma^2 c/T \tag{4}$$

where σ^2 = the variance of $X(t)$, measuring the magnitude of fluctuations on a yearly time scale, and the constant c is expressed in terms of the correlation $\rho(s)$ between the population size, $X(t)$, at time t, and the population size, $X(t+s)$, at time $t+s$, according to the formula

$$c = 1 + 2 \sum_{s=1}^{\infty} \rho(s) \tag{5}$$

Thus for T sufficiently large, the variance given by formula (4) is small. If we look at averages of population density over successive intervals of time of length T, we find that all of those averages are in fact close to $\bar{X}_\infty$. Thus on a time scale defined by this value of T, variation from year to year no longer causes fluctuations in population density on that scale.

In this model with $r > 2$, unstable deterministic dynamics can also cause fluctuations (May and Oster, 1976), but formula (4) still applies in that case, but with c as the limit of the Cesàro mean in formula (5), and indicates the time scale on which short-term fluctuations no longer propogate to long-term fluctuations.

Although we do not expect short-term fluctuations to cause fluctuations on a long time scale, they can nevertheless have an effect in the long run: They can affect the value of $\bar{X}_\infty$. Indeed, we found above that $\bar{X}_\infty$ is equal not to the arithmetic mean of $K(t)$ but to the harmonic mean. It is a general theorem of mathematics that the harmonic mean is less than the arithmetic mean (see below). Thus
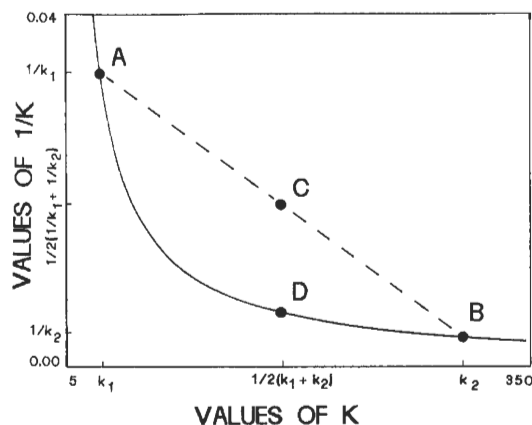
$$\bar{X}_\infty < EK \tag{6}$$

Figure 7.1. Plot of $1/K$ against values of K.

In other words, in a temporally stochastic environment, the long-term average population density is less than the ordinary mean or arithmetic average of the carrying capacity. We conclude that random fluctuations in the environment over time about a given mean carrying capacity lower the average population density.

This lowered carrying capacity comes from a generic property of non-linear stochastic models that is fundamental to many of the interesting conclusions derived from them. That the harmonic mean is less than the arithmetic mean can be rephrased as $E[1/K] > 1/EK$; i.e., the average of a reciprocal is greater than the reciprocal of the average. More generally, we can conclude that under most circumstances the average of a nonlinear function, $Ef(K)$, is different from the nonlinear function of the average, $f(EK)$ (Levins, 1979).

These ideas are illustrated in Figure 7.1, where the graph of $1/K$ is plotted. If K takes on just the two values k_1 and k_2 with probability $\frac{1}{2}$ each, EK is just $\frac{1}{2}(k_1 + k_2)$. $E[1/K]$ can be located similarly on the vertical axis at $\frac{1}{2}(1/k_1 + 1/k_2)$. It can be seen that the value of $E[1/K]$ is at point C on the straight line joining A and B; the value of $1/EK$ is at the point D below it. More generally, when k_1 and k_2 have different probabilities, $E[1/K]$ always lies on line AB, and $1/EK$ lies on the curve below it. With more than two values for K, the geometrical construction is more complicated, but the same principles apply. Moreover, the same construction can be done with any nonlinear function $f(Y)$ of a random variable Y, not just the reciprocal. When the function always curves in the same direction, as it does in the figure, the resulting difference between $Ef(Y)$ and $f(EY)$ is known as Jensen's inequality (Feller, 1971).

The example we have been studying involves a nonlinear function of

a parameter. More generally, nonlinear functions of population density arise. For example, consider the following modification of the Moran-Ricker model (Turelli and Petri, 1980).

$$X(t + 1) = X(t)e^{r\{1 - [X(t)/K(t)]^\theta\}} \tag{7}$$

In this case, there is no simple equation for the long-term average of $X(t)$, but there is an equation for the long-term average of $[X(t)]^\theta$.

$$\overline{[X_\infty]^\theta} = 1/E[1/K^\theta] \tag{8}$$

which means that

$$\left(\overline{[X_\infty]^\theta}\right)^{1/\theta} = \{1/E[1/K^\theta]\}^{1/\theta} \tag{9}$$

For θ more than 1, Jensen's inequality shows that $\bar{X}_\infty$ is less than the left-hand side of equation (9). Jensen's inequality also implies that the right-hand side of equation (9) is a decreasing function of θ. It follows that the long-term average density must decrease as a function of θ, at least for θ more than 1, although it need not do so monotonically.

This result depends on the presence of variation in K, as K is still the equilibrium value, regardless of the value of θ, and is stable for small $r\theta$ (Turelli and Petri, 1980). In this stochastic version, however, the value of θ affects the long-term average density in a way that depends on the variance of K, as the right-hand side of equation (9) can be expected to decrease more strongly as a function of θ for distributions with larger variance.

Although this second result follows from the same principle, i.e., the existence of differences between averages of nonlinear functions and non-linear functions of averages, this result differs qualitatively from the first. It shows how fluctuations can link properties of an equation (in this case the parameter θ and the outcome $\bar{X}_\infty$) that previously were independent. Such qualitative changes represent some of the most important effects of variability in ecological systems and are at the heart of many of the results discussed in this review.

A particularly clear example that reveals this effect is Ellner's (1987b) discussion of the evolution of dormancy in annual plants. In some equilibrium models, he found no advantage to between-year dormancy, where only a fraction of the seeds of an individual may germinate during any year. In the presence of fluctuations in the yield of germinating seeds, there is a selective advantage to between-year dormancy. Thus fluctuating yield in Ellner's models changes qualitatively the relation between fitness and dormancy.

This general mechanism by which short-term fluctuations translate into systematic effects on a longer time scale, if not treated carefully, can also be a source of confusion in stochastic models (Hastings and Caswell, 1979).

We illustrate this point by reparameterizing the Moran-Ricker model so that the carrying capacity (K) is replaced by its reciprocal, the intraspecific competition coefficient (α). Thus we get the equation

$$X(t + 1) = X(t)e^{r[1 - \alpha(t)X(t)]} \tag{10}$$

Both α and K are meaningful biologically, and it is not a priori obvious which one is best used in the analysis. However, a naive approach to the analysis gives strikingly different results. Because $\alpha = 1/K$, it follows that $E\alpha = E[1/K]$; and equation (6) now implies that

$$\bar{X}_\infty = 1/E\alpha \tag{11}$$

Because in a constant environment the equilibrium value of this model is $1/\alpha$, we might be tempted to conclude from equation (11) that fluctuations in α have no effect on the long-term average of $X(t)$, a result that appears to contradict the previous conclusions that fluctuations in the equivalent quantity K lower $\bar{X}_\infty$. In fact, both conclusions are correct; the key is to appreciate that they are based on different assumptions.

Parameterizing by K only leads to the conclusion that the fluctuations lower the mean because of the implicit assumption that EK, the arithmetic mean of K, remains constant as we alter the variance. However, if the mean changes with the variance, the conclusion that fluctuations in K lower the value of $\bar{X}_\infty$ is not valid. Similarly, the conclusion that fluctuations in α do not alter $\bar{X}_\infty$ depends on the assumption that $E\alpha$ remains constant as we increase its variance. Jensen's inequality implies that keeping $E\alpha$ constant is different from keeping EK constant. Indeed, keeping $E\alpha$ constant and increasing its variance almost always increases EK.

Another way of looking at this problem is to note that $H(K) = 1/E\alpha$. If when parameterizing with K we decide to use $H(K)$ rather than EK as the measure of location and keep it constant as we introduce variability, we would conclude that variation in K does not affect long-term average population sizes. Using EK as the measure of location of the distribution of K leads to the opposite conclusion. Thus the effects of fluctuations of a parameter, holding its location constant, may depend on the actual measure of location used.

These problems are not special difficulties with stochastic models. They simply reflect that determining the effect of some parameter in a model involves deciding whether it is linked with other parameters or can be varied independently in a meaningful way. In stochastic models, however, linkages among parameters are not always appreciated. Thus, if $V(K)$ means the variance of K, it is tempting to treat $V(K)$ and EK as equivalent to $V(\alpha)$ and $E\alpha$, with $EK = 1/E\alpha$. As we have seen, however, this assumption is not correct. Indeed, to a rough approximation, $EK = 1/E\alpha + V(\alpha)/(E\alpha)^3$.

A difficulty with stochastic models arises because it is not always easy to provide a rationale for keeping $E\alpha$ constant, EK constant, or some other mean value constant while a variance is changed. Rational criteria can be developed in some cases, however. For example, suppose the carrying capacity, $K(t)$, is proportional to food production during year t. Then keeping EK constant while changing its variance keeps the total food productivity in the system constant but shifts the way it is apportioned over time. Thus we can examine the effect of fluctuating food productivity without changing the overall amount. If we do not have a justification such as this one, we cannot say that fluctuations in the carrying capacity per se decrease long-term average population densities.

In the second model involving θ, more robust conclusions were obtained that did not require decisions about how to measure the location of the fluctuating parameter. That fluctuations in K make long-term average population densities dependent on θ is true regardless of whether we keep $E\alpha$ constant or EK constant. Such interactions between variability and some other factor are common and often lead to similarly robust results. Most of the conclusions from stochastic models we discussed in previous sections are of this nature. Some of the remaining difficulties can be dealt with by choosing standard parameterizations that have a common biological meaning in different models (Chesson, 1988). In general, however, one must be careful to avoid drawing conclusions from stochastic models that depend on arbitrary parameterizations (Hastings and Caswell, 1979; Bulmer, 1985).

Species Persistence

Most of our discussion has dealt with the way in which variability on one scale changes mean trends on a larger scale. Variability on one scale can also lead to variability on a larger scale. For example, Lewontin and Cohen (1969), using a density-independent population model, showed how pure temporal environmental variability on a short time scale translates into large population fluctuations on a long time scale. This situation contrasts with the density-dependent population model of the previous section in which such fluctuations on a short time scale do not lead to population fluctuations on a long time scale. Similarly, the competition models discussed in the section on pure temporal variation do not show variability on a sufficiently long time scale: There is always some finite period of time T such that the average density over such a period shows little fluctuation through time.

Some of the earliest concerns with stochastic models involve the expectation that stochastic variation may lead to extinction (May, 1973; Ludwig, 1976). Some discussions of biological conservation focus on this same

idea (Leigh, 1981; Gilpin, 1987; Lande and Barrowclough, 1987; Pimm et al., 1988). It is self-evident that large population fluctuations about a given mean must increase the likelihood of extinction because lower populations will be more frequent. Lower populations mean that it is easier to arrive exactly at zero—extinction—or that serious loss of genetic variability may occur, reducing long-term survival potential (Lande and Barrowclough, 1987).

Within-individual variability, which is usually referred to as demographic stochasticity in this literature, may be the cause of population fluctuations for populations consisting of relatively few individuals (May, 1973; Leigh, 1981; Pimm et al., 1988). For any reasonably large population, though, such variation generated on the individual scale does not lead to significant fluctuations on the scale of the whole population. Temporal environmental variability is different, however. Environmental variation generated on a large spatial scale affects all individuals in a population in a correlated way and therefore leads to population fluctuations on a log scale that are independent of population size or, more precisely, independent of population scale as defined in Chesson (1982). Thus it is generally believed that temporal environmental variability is more important than within-individual variability in causing population fluctuations.

It is tempting to conclude from this discussion that environmental variability is detrimental to species persistence. There are several reasons why this proposal is not likely to be true. First, Gillespie (1978) has pointed out that environmental fluctuations themselves, apart from causing population fluctuations, may play an important role in maintaining the genetic diversity of a population.

Second, in communities of interacting species, environmental fluctuations may be the mechanism of coexistence. Environmental fluctuations mean in this context that all species have times when they perform well. In this regard it is interesting to note that in some community models (Hatfield and Chesson, 1989), and perhaps fairly generally in the subadditive competition models discussed above, population fluctuations are not very sensitive to environmental fluctuations and approach an asymptote as environmental fluctuations become large. This seemingly paradoxical situation arises because environmental variability increases average low density growth rates and therefore increases the rate of recovery from low density. This situation opposes the intuitively disruptive effects of environmental variability at higher densities.

None of this discussion is to suggest that population fluctuations are not an important concern in biological conservation, especially when populations are small. It must be emphasized, however, that the results of this review show that population fluctuations, environmental fluctuations, and stochastic processes occurring on other scales have important functional roles in communities that often go beyond their seemingly disruptive

aspects. Understanding their sometimes subtle, sometimes counterintuitive, effects is critical to understanding community function and ultimately to the conservation of species.

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Appendix

To determine the behavior of the Moran-Ricker equation discussed in the text, we first take logs in equation (1) to get

$$\ln X(t+1) - \ln X(t) = r[1 - X(t)/K(t)] \tag{12}$$

Summing this equation from $t = 0$ to $t = T - 1$, and dividing by T, we obtain

$$\frac{\ln X(T) - \ln X(0)}{T} = r\left[1 - \frac{1}{T}\sum_{t=0}^{T-1} X(t)\cdot\left[\frac{1}{K(t)}\right]\right] \tag{13}$$

Because the fluctuations in $X(t)$ are bounded away from 0 and ∞ as $T \to \infty$, the left-hand side of equation (13) must converge to 0. In other words

$$\frac{1}{T}\sum_{t=0}^{T-1} X(t)\cdot\left[\frac{1}{K(t)}\right] \to 1 \tag{14}$$

Boundedness of $K(t)$ and $X(t)$ from 0 and ∞ imply that the convergence in relation (14) is mean square. The independent fluctuations of $K(t)$ over time mean that $X(t)$ and $1/K(t)$ are statistically independent, even though it is clearly not true of $X(t+1)$ and $1/K(t)$. Using this fact, routine calculations show that

$$\frac{1}{T}\sum_{t=0}^{T-1} X(t)\cdot K(t)^{-1} - EK^{-1} \tag{15}$$

coverges in mean square to 0; combining this result with equation (14) we see that $\bar{X}_T$ converges in mean square to $H(K)$, proving equation (3) in the text.

Equation (9) in the text has essentially the same derivation as equation (3).