ation of X_t from the ensemble mean $E(X_t)=0$. Consequently, the sample variance

$$\sum_{i=1}^{t} (X_i-\bar{X})^2/(t-1)$$

as a time average tends to be smaller than the theoretical variance in (1.44) as an ensemble average. Consequently, the slope of regression lines in Fig. 1.10 tends to be steeper than indicated by the theoretical coefficient in (1.45).

1.7 EFFECTS OF DENSITY-INDEPENDENT FACTORS

In this section, I shall elaborate on the effects of density-independent factors by classifying them into three categories, namely, vertical, lateral and nonlinear perturbation effects. [I shall elaborate on the effects of densities in Chapters 2 and 4.] The discussion of the last two categories leads to the parameterization of competition as a conditional density-dependent factor.

For simplicity without loss of generality of the argument here, I assume that there is no time delay in the effect of any ecological factor involved. Also, the set of density-independent factors Z is treated as a single factor. Thus, the set X consists only of X_t, and Z can be written as Z_t in (1.24), i.e.

$$R_t=f(X_t, Z_t). \tag{1.46}$$

1.7.1 Vertical perturbation effect

Consider that the effect of density-independent factor, say z_t, is a function of the measurement Z_t only, i.e. there is no interaction between z_t and the density X_t, such that we can write:

$$z_t=g(Z_t). \tag{1.47}$$

So, the general model (1.46) takes the linear form:

$$R_t=f(X_t)+z_t. \tag{1.48}$$

This model was illustrated in Fig. 1.6 in the context of the robust regulation in section 1.6.5. It showed that the reproduction curve, plot of R_t against X_t, is determined by the function $f(X_t)$, but the curve's relative position in the (R_t, X_t) plane is shifted up or down as z_t changes; hence, the term 'vertical perturbation effect'.

Because no animal can produce an infinite number of offspring, there must be an upper bound in R_t in (1.48). This implies, of course, that the vertical perturbation effect, z, must have a maximum somewhere across the entire spectrum of the measurement Z. An example is the effect of temperature as a density-independent factor. The factor can be measured by Z°C, and its effect z on reproductive rate is the function $g(Z)$ as in (1.47) (dropping the time subscript t). Now, look at Fig. 1.6 again. Model (1.48) shows that the effect of an extremely low temperature brings down the reproduction curve so low that the log reproductive rate (R) cannot be positive, i.e. no equilibrium density exists (see the curve in which $z=z_3$ and the equilibrium point $X^{***} \to -\infty$). As the temperature rises, the reproduction curve is shifted up so high that the curve can now have an equilibrium point (e.g. X^{**} of the curve in which $z=z_2$). As the temperature continues to rise, the reproduction curve will be raised to a maximum level. A further rise in temperature will have an adverse effect and the reproduction curve will be shifted down. Eventually, under an extremely high temperature, the curve is brought down so low again that no equilibrium density can exist.

In Fig. 1.11, I plotted the effect $z=g(Z)$ against the measurement Z(°C). It shows that a population can persist only within a certain interval of temperatures, (Z_n, Z_m), outside which the effect z causes the log reproductive rate (R) to always become negative so that a population has no chance to persist. As Z rises above the critical temperature (Z_n), the effect z raises the reproduction curve so that persistence becomes probable. For a further rise in temperature, its effect reaches a maximum (the probability of persistence is the greatest) and, then, declines. It so declines that, above the other critical temperature (Z_m), the probability of persistence will become nil again.

Thus, under the environmental conditions that exert vertical perturbation effects, a population can persist (because robust regulation is possible) only within the interval (Z_n, Z_m). The marginal environmental conditions,

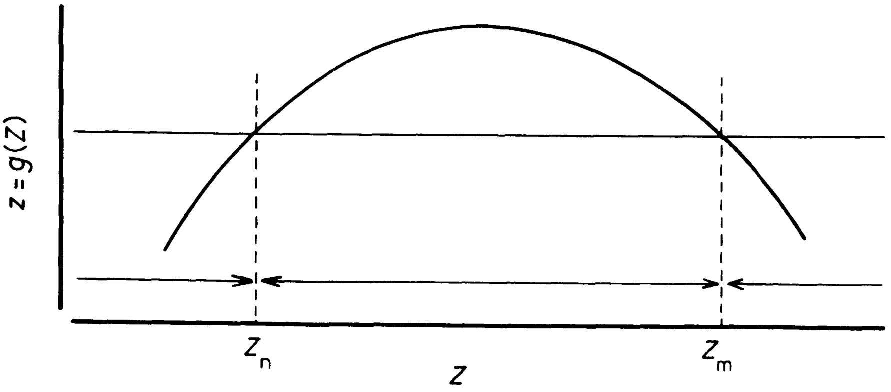

Figure 1.11 The effect $z=g(Z)$ plotted against Z. The interval (Z_n, Z_m) defines the range in which the population has a chance to persist.

Z_n and Z_m, mark the boundaries (a tolerance range) of a potential distribution of the animals concerned.

Vertical perturbation is the simplest type of perturbation by density-independent factors in that we can evaluate its effect completely independent of population density. In the following, I shall consider two other classes of density-independent factors – 'lateral' and 'nonlinear' perturbations – whose effects on reproductive rate cannot be evaluated independently of population density.

1.7.2 Lateral perturbation effect

Some hole-nesting birds, such as certain titmice of the genus *Parus*, do not excavate holes by themselves. Hence, their average breeding success depends on the supply of suitable holes in the woods. The number of holes, if much in excess of the number of breeding pairs, would practically have no effect on their nesting success. As the bird population increases, however, some degree of competition occurs sooner or later. Less competitive individuals might have to settle in holes which are comparatively poor in quality so that they might breed less successfully. Some individuals may not even be able to obtain a hole. Thus, given the supply of holes, the intensity of competition increases as population density increases and lowers the average breeding success of the population. The following simple model explains the principles in the process involving competition for the density-independent resource.

Suppose that Z' holes are distributed at random over x breeding territories. Suppose further that a pair can breed successfully if its territory contains at least one hole; otherwise, no breeding. Then, assuming a Poisson distribution with the parameter Z'/x (the mean number of holes per pair), only $1-\exp(-Z'/x)$ proportion of the population can breed. In other words, the realized reproductive rate r_t is equal to the potential rate r_m reduced to the above proportion at time t, i.e.

$$r_t = r_m[1-\exp(-Z'_t/x_t)]. \qquad (1.49)$$

We see that the effect of nest holes as a density-independent factor can only be evaluated jointly with the effect of bird density.

A logarithmic transformation of (1.49) can be written in the general form:

$$R_t = f(X_t - z'_t) \qquad (1.50)$$

in which $R \equiv \log r$, $X \equiv \log x$ and $z' = \log Z'$. It shows that the parameter $-(X_t - z'_t)$, the log per-capita share of the resource, characterizes competition as a conditional density-dependent factor. Graphically, competition determines the conditional curve $R_t = f(X_t | z'_t)$, and z'_t translates the coordinates (R_t, X_t) of the curve laterally along the X_t axis (Fig. 1.12). A large supply of holes would shift the equilibrium density to the right, and a small supply to the left.

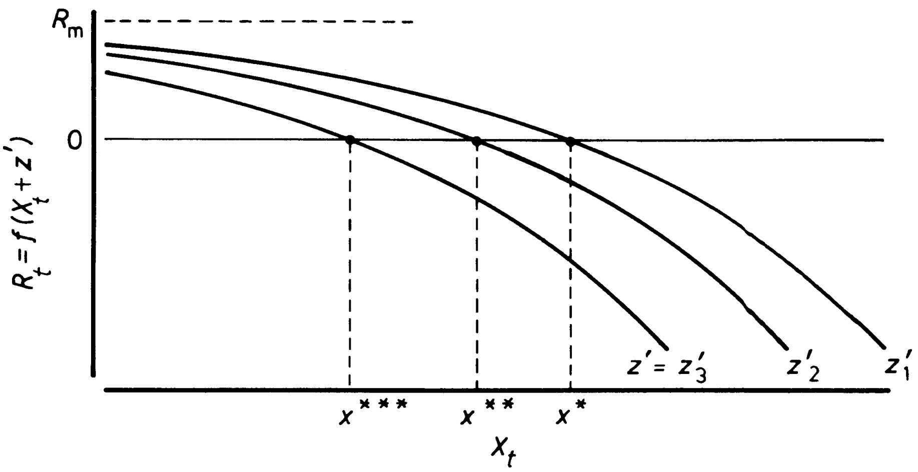

Figure 1.12 Lateral perturbation of the reproduction curve by (1.50). As z' varies from z'_1 to z'_3, the log equilibrium density shifts from X^* to X^{***}, although the maximum (potential) log reproductive rate R_m remains unchanged. All curves will coincide with each other if laterally translated along the X_t axis.

Both vertical and lateral perturbations can be called linear perturbations inasmuch as changes in z and z' do not influence the relative shape of the conditional reproduction curve, $R_t = f(X_t | z, z')$. Vertical and/or lateral translations of the coordinates (R_t, X_t) can bring all curves with different values (z, z') into one. In the following nonlinear perturbation, this cannot be done.

1.7.3 Nonlinear perturbation effect

Let Z'' be the measure of a density-independent factor. Suppose that changes in Z'' change the relative shape of the conditional reproduction curve, $R_t = f(X_t | Z'')$, so that curves with different values of Z'' cannot be brought into one by linear translations of the (R_t, X_t) coordinates. Then, this density-independent factor acts as a nonlinear perturbation.

As I mentioned in section 1.6.2, a food supply may be uninfluenced by density of the animals which feed on it. For instance, in some localities in Britain and Europe, the beech (*Fagus sylvaticus*) yields a good crop of mast in some years and a poor crop in other years. The great tit, *Parus major*, utilizes the beechmast in winter. When other types of food are scarce, the bird tends to survive better in a year of good crop than in a poor year (Perrins, 1979; Balen, 1980). The annual beech crop, though, is uninfluenced by the abundance of the animals which feed on the mast in the winter time. Therefore, the annual beech crop is a density-independent factor. However, like the nest hole example, its effect on the reproductive rate of the birds can only be evaluated jointly with the bird density. Simply, competition for the crop depends on the number of birds, given the crop.

Here, again, competition is characterized by the per-capita share of the resource, i.e. the quantity of mast each bird can consume through the winter. However, unlike the availability of nest holes, consumption per bird cannot be measured by a simple crop-to-bird ratio at the onset of the winter, because the food will be gradually depleted through the winter. Thus, the consumption per bird must be a more complicated function of both the annual crop, Z'', and the log bird density, X. I shall not attempt to find a probable function here.

However, without resorting to a particular model of consumption, we can readily see that changes in Z'' would influence the relative shape of the conditional reproduction curve $R_t = f(X_t|Z'')$. For a given X, competition will be more intense for a small Z'' than for a large Z''. As a result, the negative slope of a conditional reproduction curve for a small Z'' would become steeper more quickly as X_t increases, than it would for a large Z''. Hence, the beech crop acts as a nonlinear perturbation (Fig. 1.13).

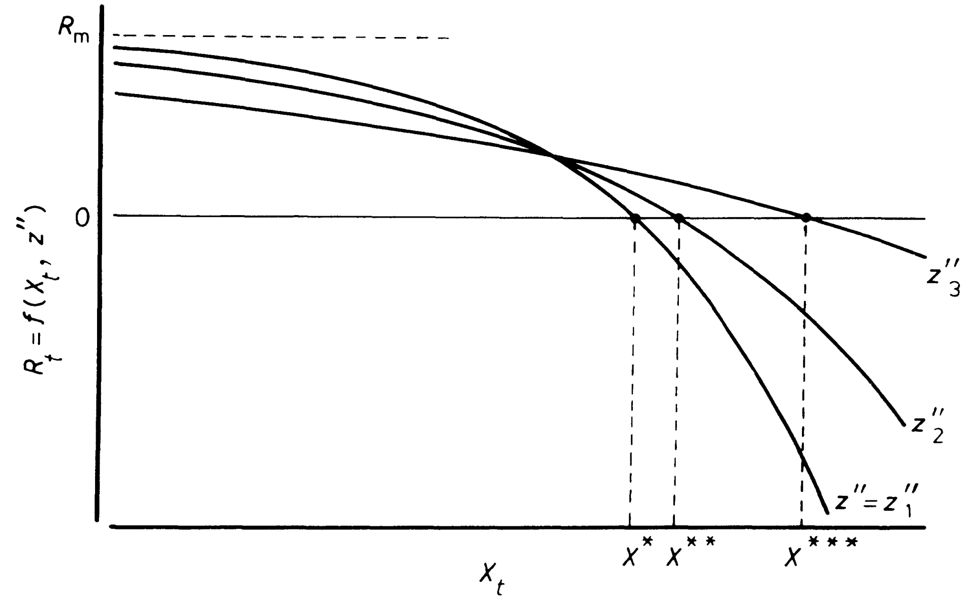

Figure 1.13 A nonlinear perturbation of a reproduction curve. The curvature of the reproduction curve changes as z'' changes from z''_1 to z''_3, causing the log equilibrium density to shift from X^* to X^{***}.

Several more examples are conceivable. (1) A multivoltine parasitoid, which requires alternate hosts, may act as a nonlinear perturbation factor on a given host, if the parasitoid density is largely governed by the densities of other alternate hosts. (2) A predator which feeds on a given prey in summer may migrate to a winter quarter. The predator density, if governed by food supply at the winter quarter, would act as a nonlinear perturbation factor on the summer prey. I shall discuss the impact of these types of predation and parasitism on the outbreak processes of the spruce budworm (*Choristoneura fumiferana*) in Chapter 9. (3) The susceptibility of animals to a density-independent environmental factor, such as a drought, may also depend on their density. The drought may reduce the production of foods for the animals. If so, the animals would suffer more severely when their density is high than when it is low. Such a weather factor would act as nonlinear perturbation.

A population process could be subject to all of these types of perturbations by density-independent factors simultaneously. Thus, letting z, z' and z'' be, respectively, vertical, lateral and nonlinear perturbation effects, we can write:

$$R_t = f[(X_t - z'_t), z''_t] + z_t. \tag{1.51}$$

Keep in mind, however, that a quantitative analysis of a process involving lateral or nonlinear perturbation is not easy. Thus, provided that their effects are comparatively small, we may – as in Chapter 2 – resort to an approximation by the simplest vertical perturbation scheme. Nonetheless, the conceptual distinction between the three types of perturbation would still be useful for qualitative understanding of population dynamics, such as the mechanism causing an insect outbreak (Chapter 9), even if a quantitative analysis is difficult.

In this section, the production of resources was assumed to be independent of the density of the animal which utilizes them. The production of some resource may be governed by the density of the animal, as in a predator–prey interaction. This topic will be discussed in Chapter 4.

1.8 CONCEPT OF DENSITY DEPENDENCE

In section 1.6.2, I remarked that my concept of density-dependent and density-independent factors differs from common usage. I now discuss the pragmatic signficance of the difference.

1.8.1 Connotations of 'density dependence'

The concept of **dependence** carries wide and narrow connotations. In the wide sense, it refers to a statistical correlation and, in the narrow sense, to a causal connection.

For instance, in describing a relationship between certain parts of the body, one might say that arm length **depends** on leg length. Here, obviously, one is speaking of a correlation between the two parts, rather than implying a functional influence of one part on the anatomy of the other. On the other hand, when we say that crop yield **depends** on precipitation, we are primarily speaking of the causal dependence of the crop on precipitation. It would sound rather silly if one said that precipitation depends on the crop. Nonetheless, the word dependence may still be used in its wide sense inasmuch as the information on the crop at hand can be used as an indicator of the amount of rainfall received during the season. The situation is so obvious that there is no danger of confusion.

In the context of population dynamics, the popular terminology 'density dependence' may likewise be used in the wide or narrow sense. However, the distinction is often so subtle that it must be made clear or confusion might result.

As already mentioned in section 1.6.2, standard text books use the term in the wide sense. Thus, any attribute of an ecological factor – be it the measure of its physical state (e.g. degree of temperature or population density) or its effect on a given population parameter (e.g. birth, death or dispersal rate) – is said to be density-dependent if it is **correlated** with the population density of the animal concerned. Conversely, it is said to be density-independent if uncorrelated.

Now a non-zero correlation between population density and the effect of a given factor on the density may result from several different situations: (1) when the physical state of the factor determining the net reproductive rate $r_t(=x_{t+1}/x_t)$ is, by itself, influenced by the density x_t, i.e. the correlation is due to a feedback between the population and the factor determining it; (2) when the state of the factor is autocorrelated, even if it is uninfluenced by population density, i.e., no feedback from population density, as demonstrated in section 1.6.7; (3) when the effect of the factor can be evaluated only jointly with the effect of population density, even though the factor itself is uninfluenced by the density, e.g. when the factor acts as lateral or nonlinear perturbation in section 1.7; (4) when the observed population series is short, even if the state of the factor is neither influenced by density nor autocorrelated (to be explained in section 3.3.3).

Evidently, the term 'density-dependent factor' used in the wide sense cannot distinguish between these situations as they all give rise to a non-zero correlation. Using it in the wide sense, we would be unable to describe the effects of those factors that cause lateral or nonlinear perturbation. We would be unable to distinguish those factors that regulate populations in the fragile manner from those that regulate in the robust manner. If we identify a factor by **effect**, we might place structurally similar mechanisms in different categories, and put different mechanisms in the same category, thereby making it difficult to identify the process structure. In other words, although a proper evaluation of the effects of the factors involved is ultimately a key to the analysis of population dynamics, it would defeat our purpose if the factors were identified in the wide sense.

Thus, as I suggested in section 1.6.2, we should use the term 'density-dependent or density-independent factor' in the narrow sense: excluding all but the first of the above four different situations from which a non-zero correlation results. Only then would we be able to describe the structure of a population process mathematically by representing the effect of a density-dependent factor as a function of density and that of a density-independent factor as vertical, lateral or nonlinear perturbation as in (1.51).

I do not imply that the expression 'density-dependent or density-independent' should always be used in the narrow sense. It is sometimes useful and convenient for describing some ecological relationships in the wide sense, if so understood. But, as a specific term to label a factor determining a population process, it must be used in the narrow sense.

To summarize my categorization of ecological factors developed in this section for the purpose of analysing population processes:

> A factor influencing net reproductive rate of an animal population is said to be density-dependent if the measure of its state of existence (or the parameter that characterizes the state) – but not necessarily its effect on the reproductive rate (section 1.6.5) – is, in turn, influenced by (and, in that sense, dependent on) the population density. Conversely, a factor is said to be density-independent if its measure (parameter) is uninfluenced by (and, hence, independent of) the population density, even if its effect on reproductive rate is correlated with density.

1.8.2 Density-dependent processes and density-dependent regulation

If, as discussed in section 1.6.3, a density-dependent factor (in the narrow sense) is involved in a process which determines the net reproductive rate, let us call it a 'density-dependent process' and, otherwise, a 'density-independent process'. Then, as discussed in section 1.6.5, robust population regulation can be achieved only by the **particular class** of density-dependent processes that ensures an equilibrium state of a population within a suitable range of density-independent environmental conditions.

Accordingly, we should use the term 'density-dependent regulation' as meaning robust regulation (section 1.6.5) by a density-dependent process belonging to the above class, as opposed to fragile (hence, only theoretically possible) density-independent regulation by a density-independent process (section 1.6.4).

Note also that the distinction between **density-dependent** and **density-independent regulations** is meaningful only in the narrow sense. In the wide sense, regulation by any type of process – including the density-independent process (1.33) – would always be density-dependent. As demonstrated in section 1.6.7, a correlation between net reproductive rate and population density (after the removal of population trend, if any) is necessarily negative in every regulated population no matter what regulates it. Therefore, in the wide sense, density-independent regulation cannot exist by definition, and the term density-dependent regulation is tautological and meaningless.