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## 5 *Bird population dynamics, management, and conservation: the role of mathematical modelling*

J.-D. LEBRETON and J. CLOBERT

### *Introduction*

In the real world animal populations rarely show simple patterns of growth such as the exponential or logistic model: most of the time complex mechanisms interact over time in an intrinsically multiplicative process. This complexity limits the value of intuitive reasoning or of simple models. In a parallel way, biological goals in studies of the dynamics of bird populations are very diverse, ranging e.g. from deciding if a population is stable in numbers, to assessing the effects of dispersal at various levels in time and space. This might be used equally to fight a pest as to predict the risk of extinction of an endangered population.

Thus, it would be a formidable task to attempt to review all the modelling approaches that might be valuable in such studies. For example, the modelling of species-environment relationships using multivariate methods is an important field which has been the subject of several recent reviews (see e.g. Verner *et al.* 1986; Ter Braak 1986, 1988; Sabatier *et al.* 1989). Therefore, we will confine ourselves to demographic models concerned with flows and rates of change rather than on population size *per se*: 'Since population is a changing entity, we are interested not only in its size and composition at any one moment, but also how it is changing. A number of important population characteristics are concerned with rates' (Odum 1971). From this point of view, as noted by Reddingius (1971a), 'there is no sharp borderline' between models built for either theoretical or practical purposes. We will however emphasize realism and precision as well as generality, three classical attributes for model judgment (Levins 1968; Walters, in Odum 1971, p. 278).

Wherever possible, we will cite primarily papers in biological rather than mathematical or statistical journals. For the sake of clarity we will cite for biological examples reviews rather than particular papers. Estimation of demographic parameters is reviewed in another paper (Clobert and Lebreton, this volume).

Initially we consider models with constant parameters. Then we

introduce environmental variability over time and density dependence. Finally we consider complex approaches incorporating density dependence, spatial effects, and various kinds of stochasticity.

### Models of population dynamics with constant parameters

#### The Leslie matrix model

Sizeable differences in demographic parameters according to age seem to be so general in birds that their incorporation in population models should be given priority (survival: see e.g. Coulson and Wooller 1976, for *Rissa tridactyla*; fecundity: see Ricklefs 1973). Demographic models arising from age-specific demographic rates considered as constant over time represent a starting point in population modelling. In the case of seasonal breeding it seems natural to consider a discrete time scale to model the long-term behaviour of the population: the formulation most commonly used is that of matrix models (Leslie 1945, 1948). The Leslie matrix model (for a detailed study, see Cull and Vogt 1973) is presented in Table 5.1 with a parameterization particularly suitable for birds, incorporating age-specific probabilities of breeding.

It is well known that, under mild conditions, this model leads to asymptotically exponential growth: exponential growth is reached only simultaneously to a stable age structure. This is the price to pay for taking into account differences in demographic parameters according to age. The asymptotic population *multiplication* rate is obtained as the largest eigenvalue of the Leslie matrix, traditionally denoted as  $\lambda$ .

Table 5.1 The Leslie matrix model with a parameterization suitable for bird population

$$\begin{matrix} \begin{bmatrix} N_1 \\ N_2 \\ N_3 \\ \vdots \\ N_m \end{bmatrix} \\ t+1 \end{matrix} = \begin{bmatrix} 0 & \dots & s_1 a_n f_n & \dots & s_1 a_m f_m \\ s_2 & 0 & 0 & \dots & 0 \\ 0 & s_3 & 0 & \dots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ 0 & \dots & 0 & s_m & s_{m+1} \end{bmatrix} \begin{bmatrix} N_1 \\ N_2 \\ N_3 \\ \vdots \\ N_m \end{bmatrix} \\ t \end{matrix}$$

$N$ , age at first reproduction;  $m$ , age of stabilization of parameters or maximum age;  $a_i$ , age-specific probability of reproduction;  $f_i$ , reproductive output (in *females per breeding female*);  $s_i$ , age dependent survival,  $s_{m+1}$ , 0 if  $m$  is maximum age;  $s_{m+1} > 0$  if survival remains constant for individuals older than  $m$ ;  $s_1$  and  $f_i$  should have coherent definitions so that there is no gap in the life cycle. For example if  $f_i$  is expressed as a number of newly hatched young,  $s_1$  must include fledging success.

$r = \text{Log}_e \lambda$  is the asymptotic *growth* rate of the modelled population. The ratio of the modulus of the second largest eigenvalue of the Leslie matrix to the first one provides a straightforward index of convergence speed to this asymptotic age distribution. Lewis (1976) illustrates this underused approach for the Herring Gull *Larus argentatus*. In this instance, the value of this ratio (0.536/1.0886) indicated a fairly rapid convergence, as is usually found.

Reasoning directly from flows of individuals leads to a renewal equation for  $\lambda$ , known as the Lotka equation (for some particular cases see Capildeo and Haldane 1954):

$$\sum a_i f_i s_1 \dots s_i / \lambda^i = 1$$

The renewal equation and the matrix approaches are strictly equivalent formulations of the (discrete time) stable population theory (Keyfitz 1968), which would more appropriately be called stable structure population theory.

Various age structures arise from the model:

- (a) the longitudinal one, i.e. that of a cohort over time, proportional to  $(s_1, s_1 s_2, s_1 s_2 s_3, \dots)$ ;
- (b) the transversal one, i.e. the stable age structure of the model, proportional to  $(s_1 / \lambda^1, s_1 s_2 / \lambda^2, s_1 s_2 s_3 / \lambda^3, \dots)$ ;
- (c) the transversal structure of breeders, proportional to  $(a_1 s_1 / \lambda^1, a_2 s_1 s_2 / \lambda^2, a_3 s_1 s_2 s_3 / \lambda^3, \dots)$ ;
- (d) the transversal structure of breeders, corrected for fecundity, proportional to  $(a_1 f_1 s_1 / \lambda^1, a_2 f_2 s_1 s_2 / \lambda^2, a_3 f_3 s_1 s_2 s_3 / \lambda^3, \dots)$ .

The last structure is made up of the terms of the Lotka equation, which sum up to 1: considered as a frequency distribution, it is the asymptotic distribution of the ages of mothers of newly born young, taking into account multiple births. Its mean  $\sum i a_i f_i s_1 \dots s_i / \lambda^i = T$  is a particularly meaningful definition of generation time (Leslie 1966). The stable age structure of the whole population and that of breeders of a Black-headed Gull *Larus ridibundus* population (Lebreton 1987) are shown in Fig. 5.1.

Ratios of numbers observed in the age classes can provide estimates of survival rates for the longitudinal age structure: this is the basis for the longitudinal life table techniques. This is also possible for the transversal (stable) age structure if and only if  $\lambda$  is equal to 1, i.e. if the population is stable (see Chapman and Robson 1960). Moreover, for many birds, only counts of breeders will be available, and nearly always relative to original numbers ringed since ringing is usually the only way to determine the age of a bird. Specific models are needed (Clobert and Lebreton, this volume).

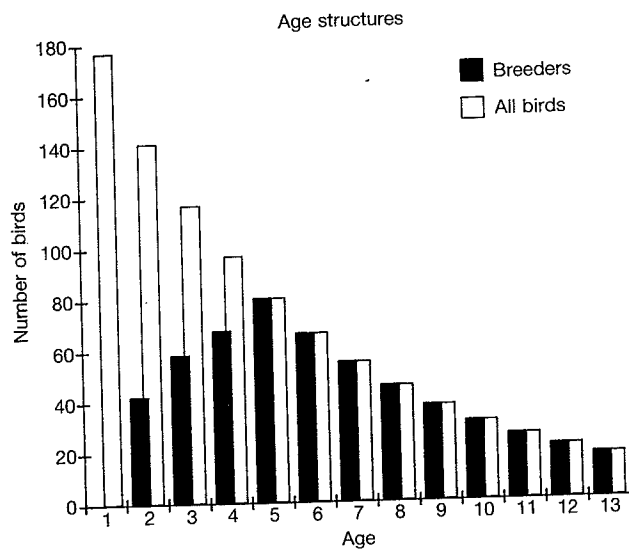


Fig. 5.1. Asymptotic age structures of the total population and of breeders, predicted by a Leslie matrix model of a Black-headed Gull *Larus ridibundus* population (parameter values from Lebreton 1987).

### Sensitivity of population multiplication rate to parameters

Various authors noticed the strong sensitivity of the multiplication rate to adult survival and the limited role of fecundity in simulations of populations of long-lived species (Lebreton and Isenmann 1976: *Larus ridibundus*; Eberhardt and Siniff 1977: marine mammals; Kosinski and Podolski 1979: *Rissa tridactyla*). The same conclusion, contrasted with heavy sensitivity to fecundity of short-lived species had been obtained by Young (1968) considering hypothetical populations of Robin *Turdus migratorius* and Bald Eagle *Haliaeetus leucocephalus*. Explicit results on sensitivity for individual parameters have been given by a number of authors (e.g. Goodman 1971). The generation time  $T$  (see above and Leslie 1966) plays a central role which is particularly striking when sensitivity is expressed as the relative sensitivity to changes in all fecundity rates, or all survival rates after age one (Fig. 5.2, from Lebreton 1981; see also Houllier and Lebreton 1986). This role has not been emphasized by human demographers, working on populations with fairly homogeneous generation time. However, it is of primary importance in our case since it means that in any sharp change of population growth rate for a long-lived species, one should first suspect a change in adult survival. Among outputs of the model, generation time is therefore as important as the multiplication rate.

Stable age structures are much less sensitive than multiplication rate to permanent changes in parameters. The most extreme case is that an overall change of all survival rates,  $s_i$ , in a same proportion:  $\lambda$  will also change in the same proportion, and the stable age structures will not be affected at

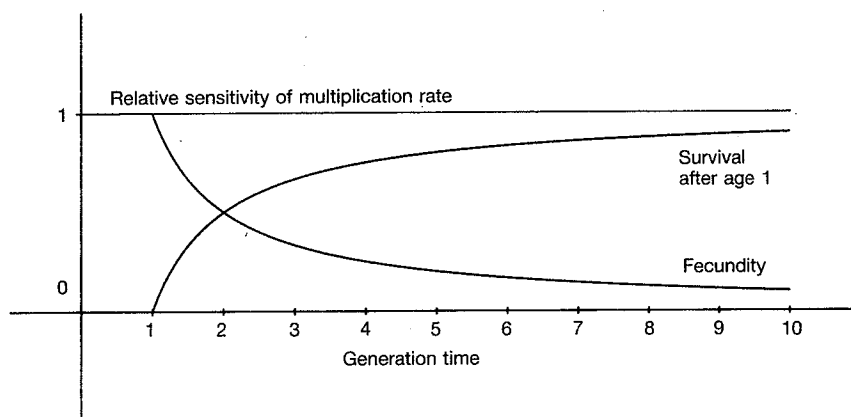


Fig. 5.2. Relative sensitivity of the asymptotic population multiplication rate to survival after 1st year and to fecundity, as functions of generation time (see text for details).

all. This is the first reason which limits possible inferences on population dynamics from estimates of age structure (Caughley 1974). Slow changes in demographic rates have been considered by Artzrouni (1986) who gives approximations to the transient age structures occurring during such changes.

### Uncertainty in parameters

In the ideal case where estimates of all parameters are available, the population multiplication rate  $\hat{\lambda}$  obtained from them can be viewed as an estimate of a true unknown  $\lambda$ . A linear approximation of  $\hat{\lambda}$  as a function of parameters  $\theta_i$  leads to an approximation of its sampling variance (Daley 1979):  $\text{var}(\hat{\lambda}) = \sum (\partial \lambda / \partial \theta_i)(\partial \lambda / \partial \theta_j) S_{ij}$ , where  $S_{ii} = \text{var}(\theta_i)$ ,  $S_{ij} = \text{cov}(\theta_i, \theta_j)$ . This approximation includes the simultaneous influence of the uncertainty of parameter estimates on  $\lambda$  through the sensitivity coefficients. The role of the various parameters can be examined separately as components of the variance. Although this expression slightly underestimates the true variance, a cumbersome second order approximation does not improve it appreciably (Houllier *et al.* 1989).

The multiplication rate can also be estimated from counts, under the hypothesis of exponential growth and of measurement error; various estimates are possible, according to the structure of the error variance (Lebreton 1982a). Most can be considered as weighted means of the indices of population changes in successive years  $N_{t+1}/N_t$ . If the imprecision in counts is expressed as  $\text{var}(N_{t+1})$  and  $\text{var}(N_t)$ , standard approximation formulas lead to an approximation of the variance of  $N_{t+1}/N_t$  (Sen 1983) and then to an approximation of the variance for the other estimates (Lebreton, unpublished). Another good estimate of  $\log \lambda$ , especially in the case of irregularly distributed censuses is the slope of a regression of  $\log N_t$  over  $t$ . Plotting  $\log N_t$  against  $t$  is always useful. When stochasticity is more complex (see below) and causes autocorrelation between counts, fitting a similar equation taking account of the autocorrelation can provide a more satisfactory estimate (see an example in Binkley and Miller 1988).

There are thus two kinds of estimates of the multiplication rate: those arising from estimates of parameters through a demographic model, and those arising from counts under the hypothesis of exponential growth. As noted by Nur (1987) these two kinds of estimates have not always been clearly separated in the literature. When both are available and accompanied by estimates of their variance, a formal comparison is possible under the hypothesis of normality of these estimates, by comparing  $(\lambda_1 - \lambda_2)/\sqrt{(S_1^2 + S_2^2)}$  to a standardized normal random deviate. It tests consistency between the external approach (counts) and the internal one (demographic mechanisms). The demographic estimate can also be compared with the theoretical value 1, to test stability. For example Lande (1988) shows for *Strix occidentalis* that the observed  $\hat{\lambda} = .961$ , with a standard error of .029, does not depart significantly from stability (1 is within the interval  $.961 \pm 2 \times .029$ ). Because of possible skewness and bias it might be useful to work out such comparisons after transformation (e.g. to log) (Sen 1983, p. 711). In the first test, rejection of the hypothesis of equality indicates a bias in demographic estimates (e.g. an underestimated survival; overestimated proportions of breeders . . .), a failure in assumptions of the model (e.g. variable parameters, immigration, and emigration . . .), or a bias in counts.

### The application of LESLIE matrix models

Possible strategies for using a Leslie matrix model range from such a formal comparison to simply running scenarios when estimates of some of the required parameters are missing (e.g. Mertz 1971). In the latter case, it is still worthwhile to calculate the generation time and to perform sensitivity analyses. Between these two extremes, many intermediate uses are possible.

Whatever the degree of sophistication, the model should be used as a tool, and not as a perfect representation of the population under study. From this point of view, even running it with estimates from other populations, neighbouring species, or parameter predictions obtained from comparative studies may be worthwhile. Estimates of unknown parameters can also be deduced from a matrix model by equating the multiplication rate to a fixed value (see e.g. Henny *et al.* 1970; O'Neill *et al.* 1981). This leads to moderately biased estimates because of the nonlinearity of  $\lambda$  as a function of the unknown parameters. In many cases such estimates will nevertheless provide an interesting order of magnitude, e.g. for juvenile survival.

As noted by Henny *et al.* (1970), Lebreton and Isenmann (1976), and Eberhardt (1985), matrix models for seasonally breeding populations appear to be valid on their own without having to be considered as approximations of homogeneous continuous time models. The only correct continuous time approach would involve cumbersome periodic rates: 'the matrix approach is both compact and efficient and permits a great deal of exploration and special analysis not so readily done in other ways' (Eberhardt 1985). On the other hand, biases and shortcomings of matrix models are obvious. For example, the population is supposed not to be affected by emigration and immigration; the scale in space should thus account for recruitment dispersal. The parameters are supposed to be constant; this might be an acceptable hypothesis for a short time-scale for some populations. Although conclusions in terms of sensitivity make these models a necessary—and underused—step, they are clearly inadequate for any precise assessment of population resilience (in the meaning of Holling 1973) because they do not consider stochasticity and density dependence.

More generally, any graphical model of flows over seasons between classes of individuals leads to a generalized matrix model if parameters are assumed to be constant (Lebreton and Isenmann 1976; Lewis 1976); this is another underused possibility. Rogers and Castro (1973) gives examples of such models for human populations interconnected by migration. In species with demographic rates dependent on the duration of breeding experience or the time since the pair-bond was established (e.g. *Rissa tridactyla*, Coulson 1966) models with stages rather than age classes might be preferable (Houllier and Lebreton 1986; Crouse *et al.* 1987).

### *Effect of variations of parameters over time*

#### Models for random environment

Year-to-year random environmental variation can be modelled in a straightforward way as a succession of random Leslie matrices (Sykes



1969). Since these matrices are positive, population numbers are positive; this kind of model does not consider population extinction. Numerical simulation has been and still is heavily used. However, under mild conditions log population size becomes asymptotically normal and grows or decreases linearly with an expected rate,  $a$  (Tuljapurkar and Orzack 1980); population growth is then best characterized by  $\Lambda = \exp(a)$ . When environmental variations are independent over the years this multiplication rate can be approximated as (Tuljapurkar 1982):

$\Lambda \approx \lambda \exp(-\frac{1}{2}\text{var}(\lambda)/\lambda^2) \approx \lambda (1 - \frac{1}{2}\text{var}(\lambda)/\lambda^2)$ , where the previous linear approximation for  $\text{var}(\lambda)$  can be used; Lande (1988) show for *Strix occidentalis* that reasonable environmental variation leads to  $\Lambda = .98\lambda$ .

If variability in a single parameter  $\pi$  is considered,  $\Lambda/\lambda \approx 1 - \frac{1}{2}(\partial\lambda/\partial\pi)^2 \text{var}(\pi)/\pi^2$ . The effect of the variability in  $\pi$  can be viewed in terms of the increase  $\delta\pi$  in the average  $\pi$  needed to compensate for variability, given by  $\delta\pi/\pi = \frac{1}{2}(\partial\log\lambda/\partial\log\pi) \text{var}(\pi)/\pi^2$ . The relative increase required to compensate for variability is thus higher for sensitive parameters. Reducing the variability is thus a way to reach a higher average multiplication rate.

### Environmental variability and population counts

Simultaneously to detecting variability over time, a common goal is to attribute its origin to some external variables (weather...). Regression of any index of population change, such as  $N_{t+1}/N_t$ , on an environmental variable  $x_t$  (for example see Hafner *et al.* 1987) should be used with extreme caution. While the usual estimator of slope is not biased, its variance is; usual tests of significance for the regression will thus be biased, in a direction depending on the sign of the autocorrelation of the environmental variable. This effect jeopardizes all classical key-factor analyses, and will be even more dramatic when density dependence is considered (see next paragraph). If key-factor analysis is defined as looking for parameters of which variability induces the largest changes in numbers (Manly 1977), it reduces to sensitivity analysis.

### Density dependence

After the early discussions on density dependence (for review see Royama 1977), the problem is still challenging because, as in general in cybernetics (Wilbert 1970), the existence and intensity of negative feedbacks governs the stability of the system (Holling 1973) and its ability to withstand perturbations.

### Modelling density dependence

Modelling techniques are straightforward: one or several parameters in the Leslie matrix are considered as functions of one or several components of population numbers. After an early proposal by Leslie (1948), Beddington (1974) gave a general formulation and studied dependence on the *total* number in the population. A stable equilibrium is reached under mild conditions. For this equilibrium level, the largest eigenvalue of the Leslie matrix is equal to 1. Density-dependent Leslie matrix models can thus be considered as multivariate discrete time analogues to logistic growth. Beddington's results can be easily extended to dependence on any linear compound of components of population size (Lebreton 1981): this covers dependence on total breeding population (cf. Fig. 5.1) or on total biomass as particular cases. In a particularly clear paper Smouse and Weiss (1975) investigate density dependence in fecundity, prereproductive survival, or adult survival. The differences obtained in the stable age-structure under these different regimes of regulation are limited if the intrinsic growth rate ( $\log \lambda$  at density 0) is low, which is the case for bird populations. The stable age structure is reached earlier than the plateau in numbers; both results cast further doubt on inferences about population mechanisms drawn from age structures. Although discrete time density-dependent models exhibit complex behaviour (periodic, chaotic; see May 1975), especially in multivariate models, such effects are mostly irrelevant here, again because of low maximum growth rates of bird populations.

### Detecting density dependence

The unreliability of naive statistical approaches based on regression in detecting density dependence has been emphasized by many authors (Salt 1966; Eberhardt 1970; St-Amant 1970; Ito 1972; Slade 1977). Considering for example the regression of  $\log N_{t+1}/N_t$  on  $N_t$ , one can see that errors in  $Y_t = \log N_{t+1}/N_t$  and  $X_t = N_t$  are not independent, as well as those in  $Y_t = \log N_{t+1}/N_t$  and  $Y_{t-1} = \log N_t/N_{t-1}$ . Estimates of slope and of its variance are biased. All other kinds of stochasticity will affect the slope in the same way (St-Amant 1970). All these methods tend to detect density dependence too often. Despite contrary claims by their authors, the same problem exists in recently proposed *ad hoc* methods and reviews (Vickery and Nudds 1984; Pollard *et al.* 1987; Cuperus and de Bruyn 1987). Time-series techniques are the logical tool (Bulmer 1975; Lebreton 1989). However, measurement error should be accounted for by the Kalman filter technique as noted by Poole (1978) and Brillinger (1981), and proposed in the second model of Bulmer (1975, p. 903). Both Poole and Brillinger review time-series approaches potentially relevant for population studies,

with an emphasis on forecasting in Poole's paper. Although appealing, especially with reference to management, such techniques will rarely be powerful with the number of points usually available in population dynamics, especially because the effect of environmental variables has to be accounted for simultaneously (Lebreton 1982*b*). Their best use seems to be as approximations of mechanistic models rather than as descriptive forecasting models on their own.

Fortunately enough, the problem is much more to measure the intensity of density dependence, locate the concerned parameters and assess the consequences, rather than simply detect density dependence. Our advice is to look for effects of population density on parameters such as survival or fecundity (see Clobert and Lebreton, this volume), and to include environmental variables and density as explanatory variables to limit confounding between sources of variation. To avoid the pitfalls of key-factor analysis, the estimates of parameters used in such an approach should be independent of the estimates of density.

### Model use

In view of these problems, using density-dependent models is clearly difficult. Evidence for density dependence is usually limited, although it is supposed to play a major role in determining the stability of bird populations. Numerical simulation, easy with a desk computer, is of great help, particularly to achieve a sensitivity analysis of equilibrium level. Patterns of sensitivity are roughly similar to those of multiplication rate in density-independent models with a main role of survival in long-lived species (Lebreton 1981).

### Density dependence and seasonality

Up to now seasonality and age structure seem not to have affected the general pattern of growth. They seem to have been included for the sake of realism only. However results depart from the standard logistic growth when we look at the consequences of simultaneous seasonality (or random environment) and density dependence. Figure 5.3 gives numbers over time in a model alternating a good and a poor season (or year). The population never reaches at time  $t$  the carrying capacity for the conditions prevailing at this time, but an equilibrium level depending on the overall dynamics of the system. Although this role of seasonality in regulated populations has been well studied (Fretwell 1976; May 1976), is not usually realized how weak it makes the concept of carrying capacity (see e.g. Caughley 1976). This paradoxical effect is more pronounced for populations with low maximum growth rate, i.e. in practice for long-lived species. The numbers

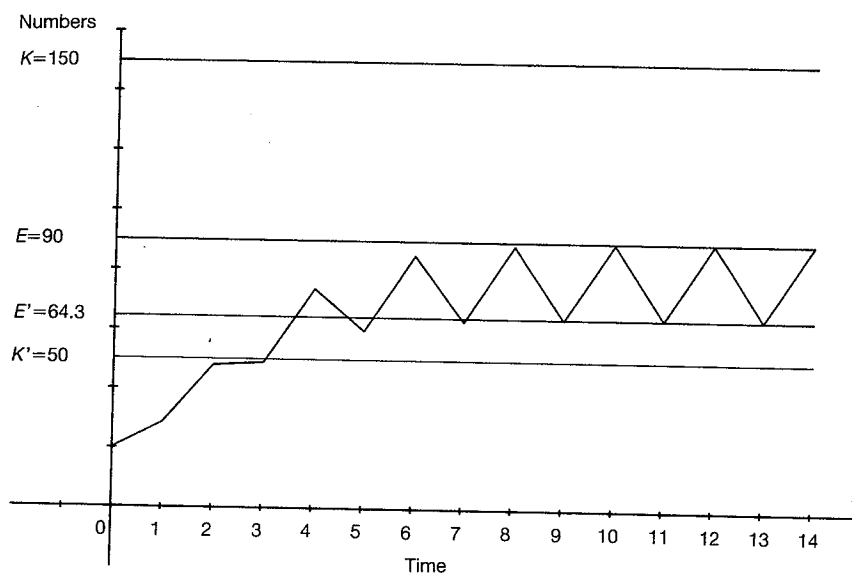


Fig. 5.3. Population size over time in a model alternating good and poor seasons (or years), according to equations:  $N_{t+1} = 2N_t / (1 + N_t/150)$  (good) and  $N_{t+1} = 2N_t / (1 + N_t/50)$  (poor). Asymptotic population size does not oscillate between the poor year model ( $K' = 50$ ) and the good year model ( $K = 150$ ) carrying capacities, but between two equilibrium levels ( $E' = 64.3$  and  $E = 90$ ), both well below the average carrying capacity ( $(K + K')/2 = 100$ ).

in populations of such species do not track environmental variability as narrowly as those of shorter-lived species. This has two consequences. Firstly, it is better to examine the influence of environment on population dynamics at the level of population mechanisms, i.e. at the parameter level, because species-environment relationships may appear to be weak when considered on the basis of population numbers. Secondly, a regulating factor in spring may determine the *existence* of an equilibrium level, while the *value* of this equilibrium level will be determined by internuptial survival. For migratory species in particular, ecological factors on the wintering grounds may determine what is usually called the carrying capacity of the breeding habitat (see Lebreton 1981; *Larus ridibundus*).

### Harvesting

Another approach to model stability which is relevant to conservation and management is concerned with optimizing harvesting. The basic literature on the subject (see full account by Getz and Haight 1989) comes from exploited fish populations (e.g. Deriso 1980; Reed 1980) where the goal is to maximize the sustainable yield. One could also look for maximum

efficiency against a pest (Murton and Westwood 1976), with guidelines from sensitivity analysis. Doubleday (1975) studied optimal harvesting in the density-independent case, which is however of restricted practical interest, as noted by Mendelssohn (1976).

Optimal harvesting is in general studied in models with density dependence in fecundity (or survival in the first year or any other 'immature' parameter) (density-dependent recruitment). The shape of the 'stock-recruitment curves', i.e. of the density-dependent relationship (see e.g. Eberhardt 1977), and the sustainable yield (Winters 1978; Eberhardt and Siniff 1977) are concepts of general validity. However, they appear difficult to use with realism and precision for bird populations in the present state of the art, since they suppose widescale information on mechanisms of density dependence. In exploited fish populations it is commonly found or assumed that the proportion of immature animals that recruit to the breeding part of the population (called the breeding stock) is density dependent. The extent to which this is true in bird populations is unclear (Duncan 1978; Coulson *et al.* 1982; Brown 1969; Klomp 1972; Patterson 1980). This question requires a discussion of more complex phenomena such as spatial heterogeneity and dispersal.

### *Incorporating more spatial and temporal heterogeneity and stochasticity*

#### Variability between habitats and dispersal

Building population models that include dispersal does not raise particular technical difficulties. Spatial cells can be considered to have the same status as age classes. Such models have been developed in both density-independent (Rogers and Castro 1976) and density-dependent cases. Gurney and Nisbet (1975), Kot and Schaffer (1986), and Den Boer (1971) show that oriented dispersal from high densities to low densities tends to stabilize numbers.

This is probably the best example of a problem for which a good array of modelling techniques exist, but for which data are extremely difficult to obtain because of the complexity of the time and space scales in bird populations. Developing studies integrating modelling of meta-populations and field evidence is obviously one of the present challenges in population dynamics.

#### Demographic stochasticity

Demographic stochasticity, or within individual stochasticity (Chesson 1978) is the residual variability that affects the demographic results of a

given individual, under fixed conditions: for example, death with probability  $p$  is viewed as a coin-tossing process. This type of variability, both in survival and in fecundity, can easily be incorporated in a process together with age structure and seasonality. Such 'multitype discrete time branching processes' have been heavily studied by mathematicians (see e.g. Jagers 1975). Average numbers are described by a Leslie matrix model and the probabilistic structure relies on the hypothesis of independence between individuals. Although the relative role of demographic stochasticity is negligible in a large homogeneous population, it may be important in a small or subdivided one (Chesson 1978; Mode and Pickens 1986). Models including subunits and dispersal should thus consider demographic as well as environmental stochasticity.

### Extinction

With branching processes, possible extinction is now under concern: the ultimate probability of extinction is lower than 1 if and only if the population increases ( $\lambda > 1$ ), i.e. goes to infinity rapidly enough to avoid the trap of extinction. The next step considers simultaneously demographic and environmental stochasticity with parameters of the branching process varying from year to year in a random way. Such models (Branching Processes in Random Environment = BPRE) have been used for theoretical purposes (Heyde 1978; Mountford 1973). Moreover, BPRE can incorporate realistic features of seasonal age-structured populations (Mode and Jacobson 1987a), since they have a Leslie matrix model as mean equation. They constitute a natural tool to study extinction phenomena.

Decreasing populations coming close to extinction present, as modelled by branching processes, a particular behaviour of convergence to what is called a *quasi-stationary distribution*. Once reduced to a few individuals, the population can become extinct next year, or survive. In the latter case, it will include on average more than one individual; conditional on non-extinction, there is thus a small residual population. This conditional residual population tends to stabilize. This means that when this quasi-stationary distribution is reached, the population behaves in terms of survival like a single individual, dying with probability  $1 - p$ , or surviving next year identical to itself (on the average in the case of the population) with probability  $p$ . Extinction time then follows a geometric distribution. A striking result is that  $p = \Lambda$ , which depends not only on the average parameters but also strongly on the environmental process, in particular on its autocorrelation (Mode and Jacobson 1987b). In the case of the decreasing population of White Stork of the Alsace area (Lebreton 1982b), a BPRE leads to a quasi-stationary distribution with about 7 individuals (about 1.5 breeding pair), with a yearly probability of extinction of .15.

Results become scarcer when density dependence is mixed with seasonality, age structure, discrete time, demographic stochasticity, and environmental stochasticity. In some simple models it is possible to prove the certainty of extinction (Lebreton 1981). When an equilibrium distribution is reached, extinction in a single step of time is always possible with an extremely small probability (Lebreton 1982b), and such an equilibrium distribution can only be a quasi-stationary distribution, of which formal existence is difficult to prove (see however De Angelis 1976; Lebreton 1981; Lande and Orzack 1988); simulation is often the only possible tool. De Angelis (1976; Canada Goose *Branta canadensis* population) and Lebreton (1981; Great Tit *Parus major*) provide examples of quasi-stationary distributions for discrete time density-dependent models.

The convergence between studies of mathematical processes (Branching Processes in Random Environment have mainly been developed since 1970) and the concept in conservation biology of Minimum Viable Populations (MVP) (Soule 1986, 1987; Frankel and Soule 1981) is thus very striking, and is explicitly pointed out by Mode and Jacobson (1987a, b). One can speak with Gilpin and Soule (1986) and Burgman *et al.* (1988) of extinction models. Extinction models in continuous time (Pettersson 1985) are highly questionable because they neglect the seasonal structure of the population (De Angelis 1976). The variations are buffered by the continuous role of density dependence, and the predictions of extinction seem likely to be optimistic. Burgman *et al.* (1988), who emphasized the theoretical character of extinction models, focused on continuous time models (e.g. pp. 17-18) and neglected the wide literature on discrete time branching processes published mainly in probability journals. Discrete time branching models built as generalizations of demographic models bring some more realism to the general concept of MVP. However, the sensitivity of predictions to variations in the environmental process and to the amount of density dependence makes them very difficult to validate.

It seems striking to us that the effects of parameter uncertainty, on which rapid progress has been made for the Leslie model in the last ten years, have still to be investigated in extinction models. This difficulty must always be borne in mind for small populations where a reasonable precision on demographic parameters is unattainable. More realistic models would also include genetic (Schonewald-Cox *et al.* 1983) and behavioural aspects (e.g. mate selection, social stimulation). As a rule, it seems wise in the present state of the art to consider MVP obtained from models as being underestimated.

In conclusion, such complex phenomena are probably easier to model than to assess. Models can be used with caution to test some hypotheses in an informal way, but the robustness of the conclusions will usually be

limited by the absence of replication (Hurlbert 1984). It seems dangerous for conservation and management purposes to use complex models developed in an *ad hoc* way by incorporating all potential mechanisms and effects (see e.g. McKelvey *et al.* 1980).

### Discussion

Modelling of population dynamics for seasonal populations with constant parameters has reached a stage of maturity. Demographic stochasticity, environmental stochasticity (Chesson 1978), and density dependence have progressively been brought together in parallel in a common probabilistic framework. Such a framework, already advocated by Reddingius (1971*b*) provides a sound basis for studies of regulation, harvesting, and extinction, and more generally of resilience of populations. The application of these approaches to practical problems will take time, as is to be expected for a multidisciplinary endeavour. There are no major differences in modelling approaches for fundamental research or conservation and management goals. It seems likely that in the future the diversity of interest in population dynamics modelling will maintain the same balance between theoretical and practical approaches.

General models of population regulation have been developed less extensively and less rapidly for bird populations than for exploited populations such as fish, marine mammals (Eberhardt and Siniff 1977), or large terrestrial mammals (Caughley 1976). However the information on demography and on mechanisms of regulation is usually much greater for birds. This has probably inhibited the broad generalizations which have been made, perhaps unjustifiably, for fish populations.

While some generality and realism have already been reached, precision will frequently remain out of reach, for reasons of cost, or for intrinsic reasons in the case of small populations. Models of adaptive management (Holling 1978) might in this case be helpful, as well as arrays of methods in monitoring programs (Aebischer 1986).

The 'new frontier' of population modelling—which hopefully will develop simultaneously with refined designs in field studies—is in modelling meta-populations *sensu lato*, i.e. in focusing on dispersal phenomena. We also emphasize the need for flexibility: models should be seen as constantly developing tools, which should be periodically re-evaluated.

### Summary

This paper reviews, in four steps, mathematical models of the dynamics of bird populations which are relevant to conservation and management.



- (1) demographic models with constant parameters, with an emphasis on sensitivity analysis and on the comparison of model results with population censuses;
- (2) environmental variability and its effect on population growth rate;
- (3) density-dependent models, with comments on the difficulties to assess density dependence using censuses;
- (4) models incorporating density dependence, spatial aspects, and various kinds of stochasticity.

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