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**Démographie animale
et biologie des populations**

modélisation et applications à la gestion d'espèces sauvages

par
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Soutenue le 27 octobre 1994 devant le Jury composé de :

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Estimation de la *fitness* ou du statut démographique dans les populations animales


Hn objectif majeur en biologie évolutive ainsi qu'en gestion de la vie sauvage est de prédire le statut futur des populations. Le taux de multiplication λ (ou son équivalent, le taux intrinsèque d'accroissement r) exprime, pour un groupe homogène d'individus, l'équilibre dynamique entre sa capacité de croissance dans un environnement donné et les facteurs limitants du milieu. Calculés pour un groupe homogène d'animaux ou de plantes partageant le même phénotype, ces taux estiment leur *fitness* (Fisher 1930, Charlesworth 1980, Caswell 1989).

Bien que l'on puisse présenter les modèles démographiques sous différentes formes, le taux d'accroissement asymptotique et le taux de multiplication, s'obtiennent respectivement comme la première racine de l'équation d'Euler-Lotka (Euler 1760, Lotka 1924) ou comme la première valeur propre de la matrice de Leslie (1945, 1948).



Ces équations n'ont pas de solution explicite, sauf dans des cas particuliers. Des modèles *ad hoc* ont donc proliféré bien que les résultats qu'ils permettent d'obtenir soient en général biaisés, voire erronés (Danchin 1992). Cependant, on les utilise largement dans les études de dynamique de populations sauvages (exemples dans Clutton–Brock éd. 1988). En outre, le modèle démographique original, les hypothèses sous-jacentes et les divers résultats sont oubliés ou méconnus.

Le présent Chapitre contient un article (Danchin, González–Dávila & Lebreton, à paraître dans *Journal of Avian Biology*) présentant la critique du modèle *ad hoc* utilisé souvent par les ornithologues pour obtenir un estimateur de λ (e.g. Harris 1983, Newton 1989, Vermeer & Devito 1989, Brooke 1990). La mise en page de la version ici présentée différera de la version publiée ainsi qu'en quelques corrections de l'anglais, quelques précisions des formulations mathématiques et que l'on a discuté (parmi les autres résultats démographiques d'intérêt pour la gestion de populations) les concepts de *valeur reproductive* et de *convergence*. Bien que les concepts des modèles démographiques aient été présentés dans le Chapitre 1 (dans le cadre de la démographie *strictu sensu*), ici, l'intérêt est centré sur leur application en biologie animale et gestion de populations sauvages. Il est vrai, qu'une partie de la argumentation pourrait s'avoir épargnée si le Chapitre 2 avait été rédigé comme un chapitre et non comme la base d'un article, mais l'intérêt d'une présentation à part entière avec l'orientation précisée ci-dessus nous semble nécessaire.

Les objectifs sont donc, d'abord rétablir les bases des modèles démographiques indépendants de la densité, puis rappeler les statistiques que l'on peut obtenir explicitement et celles qui requièrent un calcul plus sophistiqué, et ensuite présenter les sorties d'intérêt général pour les biologistes de populations. Un graphique illustre l'ordre de grandeur du biais des estimations issues du modèle *ad hoc*. Enfin, nous montrons que les modèles démographiques permettent d'établir un lien entre les approches empiriques et théoriques 



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Estimating bird fitness correctly by using demographic models

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ABSTRACT

One aim of studies in evolutionary biology is to estimate the fitness of a phenotype within a population. One of the most natural estimates of fitness is λ , the multiplication rate, or finite rate of increase, which results from the demographic parameters of that particular phenotype. Even though *ad hoc* computations of λ may be strongly biased, they are still widely used, in particular in bird population biology. We compare *ad hoc* computation of the multiplication rate and exact ones using demographic models. The magnitude of the discrepancy increases sharply with the departure of λ from unity. This may alter our perception of population functioning. Other outputs of demographic models, which play a prominent role in bird evolutionary biology and population management, are briefly discussed. As a whole, demographic models provide a link between empirical and theoretical approaches.



INTRODUCTION

A main objective in evolutionary biology and in wild population management is to forecast the future status of populations. The growth rate, or equivalently, the multiplication rate, expresses, for a phenotype, the dynamic balance between limiting factors and growth capacity in a given environment. Calculated for a group of animals or plants sharing the same phenotype, it measures their fitness (e.g. Charlesworth 1980, Caswell 1989, Charnov 1990, Murray 1992). Its calculation, from estimates of demographic parameters obtained in the field or in the laboratory, is thus a standard approach to evolutionary biology.

The exponential growth capacity of populations, first expressed by Euler in 1760 (republished 1970) is a well known result: if the demographic parameters are constant over time and depend only on age, the growth of the population is asymptotically exponential. Although demographic models may be presented in a number of slightly different forms, the asymptotic growth or multiplication rates of the population are obtainable as the first root of a compact equation, called the Euler–Lotka equation (Euler 1760, Lotka 1925), or as the first eigenvalue of the Leslie (1945, 1948) matrix.

In fact, except in some rare exceptions, there is no way of obtaining explicitly the multiplication rate and *ad hoc* formulas are in general wrong (Danchin 1992). However, they are still widely used, particularly in bird population studies (e.g. Harris 1983, Vermeer & Devito 1989, Brooke 1990, several examples in Clutton–Brock 1988 and in Newton 1989). Moreover, the underlying original model, its assumptions and its various outputs, tend to be forgotten.

The purposes of this paper are: first, to restate briefly the background of density independent demographic models, second, to delimit which statistics can be obtained explicitly and which ones require more sophisticated computation, and third, to give outputs of demographic models of general interest to population biologists, bird population biologists in particular. The magnitude of the bias that can be caused by erroneous computations is illustrated in some real and some hypothetical data sets. Finally, a series of references where to find complementary information is given.



DEMOGRAPHIC BACKGROUND

The basic demographic parameters to consider for a population with seasonal reproduction as birds may be noted (Lebreton & Clobert 1991):

- m_i = number of newborn females produced per female aged i per year;
- s_i = annual survival rate of an individual from age i to age $i + 1$.
- α = age at first reproduction in the population;
- ω = age of stabilization of parameters, or maximum age;

In practice, particularly when dealing with bird (and other vertebrates) populations, it is convenient to decompose m_i as the product of a_i (the age-specific probability of breeding) and f_i (the age-specific fecundity of breeders, i.e. the number of newborn females produced per breeding female aged i). Then $m_i = a_i f_i$ (Lebreton *et al.* 1990).

The parameters of fecundity (f_i , α and p_i) can be estimated by monitoring marked populations in the wild, and parameters of survival (s_i) can be estimated by using capture-mark-recapture models on individually marked animals in the field (Pollock *et al.* 1990, Lebreton *et al.* 1992). This paper deals with another topic: once these demographic parameters are estimated, how to compute their balance for a group of individuals sharing the same phenotype?

The changes in numbers of individuals over the years can be modeled following two equivalent approaches: the renewal (Lotka) approach and the matrix (Leslie) approach.

In the renewal equation approach, the number of births $B(t)$ at time t is obtained by considering one age over several time steps:

$$B(t) = \sum_{i=\alpha}^{\infty} B(t-i) s_0 s_1 s_2 \cdots s_{i-1} m_i$$

where $B(t-i) s_0 s_1 s_2 \cdots s_{i-1}$ is the number of individuals aged i alive at time t . If population growth is exponential, $B(t) = \lambda^i B(t-i)$. Hence, the above equation reduces to the Lotka equation (Lotka 1956 p 18):



$$1 = \sum_{i=\alpha}^{\infty} \lambda^{-i} s_0 s_1 s_2 \cdots s_{i-1} m_i \quad (2.1)$$

noted for short $\psi(\lambda) = 1$. In general, this equation has no explicit solution.

However, the changes in numbers can also be expressed by considering several age classes over one time step, as a system of linear equations:

$$\begin{aligned} N_1(t) &= \sum_{i=\alpha}^{\omega} s_0 m_i N_i(t-1) \\ N_2(t) &= s_1 N_1(t-1) \\ &\vdots \\ N_i(t) &= s_{i-1} N_{i-1}(t-1) \\ &\vdots \\ N_{\omega}(t) &= s_{\omega-1} N_{\omega-1}(t-1) + s_{\omega} N_{\omega}(t-1) \end{aligned} \quad (2.2)$$

where $N_i(t)$ is the number of individuals aged i at time t . N_{ω} is the number of individuals aged ω or more. Hence $N_1(t) = s_0 B(t-1)$.

These linear equations reduce to the matrix expression:

$$\mathbf{N}(t) = \mathbf{L} \mathbf{N}(t-1) \quad (2.3)$$

which leads to $\mathbf{N}(t) = \mathbf{L}^i \mathbf{N}(t-i)$. \mathbf{L} is the well known «Leslie matrix» when $s_{\omega} = 0$ (Leslie 1945; see appendix A).

Under mild conditions, in the long run, the proportions of age classes in $\mathbf{N}(t)$ tend to stabilize to a stable age-structure \mathbf{N}_s , such that $\lambda \mathbf{N}_s = \mathbf{L} \mathbf{N}_s$. The asymptotic multiplication rate λ of the population (Anderson 1975) can be obtained as the largest positive root of (Cull & Vogt 1973):

$$\det(\mathbf{L} - \lambda \mathbf{I}) = \phi(\lambda) = 0 \quad (2.4)$$

Because of $\phi(\lambda) = (-1)^{\omega} \lambda^{\omega} (\psi(\lambda) - 1)$, $\psi(\lambda) = 1$ and $\phi(\lambda) = 0$ yield the same λ .

Thus, the Lotka equation and the Leslie matrix are strictly equivalent formulations of the stable population theory (Keyfitz 1968 ch VIII), which would more appropriately be called «stable structure population theory» (Lebreton & Clobert 1991).



COMPUTING THE MULTIPLICATION RATE

One traditional computation assumes that the population has reached its stable age structure and that the gross growth rate a is then a good estimator of the multiplication rate λ , i.e. that $N(t) = a N(t-1)$. This has led to an *ad hoc* computation which supposes that the recruits to breeding status take the place of dead adults and to the erroneous statement that the number of individuals in one year can be expressed simply as the sum of the adult survivors from previous year $sN(t-1)$, plus the recruits $R(t) = \rho N(t-1)$, as

$$\begin{aligned} N(t) &= sN(t-1) + \rho N(t-1) \\ &= (s + \rho) N(t-1) \\ &= \beta N(t-1) \end{aligned} \tag{2.5}$$

where $N(t)$ is the total number of breeders in year t , s is the constant adult survival rate, and $\rho = ms_j$ is the fraction of recruits or constant adult fecundity m times the juvenile survival s_j .

$\beta = s + ms_j$ is then considered as an estimate of λ (Harris 1983, Vermeer & Devito 1989, Brooke 1990, several examples in Clutton-Brock 1988 and in Newton 1989). Unfortunately, even under the above restrictive conditions (stability, and s , m , and s_j constants), equation (2.5) is not true in general because (excepting the case of species with age of first breeding $\alpha = 1$) the new breeders $R(t)$ recruited in year t were not born at $t - 1$, but at $t - \alpha$. So that $R(t) = N(t - \alpha) m s_0 s_1 \cdots s_{\alpha-1}$. Accepting equation (2.5) would mean that the number of recruits in year t is the same as in year $t + \alpha$ for every t . This is never true excepting if population is *stationary*, even if the population structure has reached its stability. Therefore, **equation (2.5) is wrong** and should be restated as:

$$N(t) = sN(t-1) + N(t-\alpha) m s_0 s_1 \cdots s_{\alpha-1} \tag{2.6}$$

In contrast with equations (2.1) and (2.3), the latter model assumes that fecundity and survival are constant from age α onwards. Assuming exponential growth, $N(t) = \lambda^\alpha N(t-\alpha)$ and $N(t-1) = \lambda^{\alpha-1} N(t-\alpha)$, lead to:



$$\lambda^\alpha - \lambda^{\alpha-1}s - m s_0 s_1 \cdots s_{\alpha-1} = 0 = \phi(\lambda) \quad (2.7)$$

which is the Leslie equation (2.4) under the above restrictive hypotheses (appendix B). The largest real positive root of equation (2.7), or first eigenvalue, is an estimation of the multiplication rate λ . Equation 2.7 can be solved iteratively, for instance by the Newton–Raphson method (see Keyfitz 1968, or Anderson 1975).

$$\lambda_{**} = \lambda_* - \frac{\psi(\lambda_*)}{\psi'(\lambda_*)}$$

starting e.g. from $\lambda_* = 1$, iteration converges to five digits in less than five cycles.

Using β as an estimation of λ would for instance consider that birds recruited at age 3 have the same effect on the population turn over as birds recruited at age 7, which is obviously wrong. Furthermore, in most species, females recruit progressively from age α to age ω with an age-specific probability of breeding $a_i < 1$ (Lebreton & Clobert 1991, Croxall & Rothery 1991:288–289; see the Herring Gull and the Black-headed Gull in Table 1.1 for examples). Hence, in general, the polynomial $\phi(\lambda)$ is more involved than (2.7). In all cases, λ should be obtained using standard algorithms. That is what is done by the software as those listed in Table 2.2.

In practice, when using those models, one has to understand the meaning of each parameter carefully. A common mistake is to do the calculation with fecundity expressed as a number of young per pair (e.g. Brown 1972, and Gargett 1972). The model being restricted to the female segment of the population, the fecundity must be expressed in females per female. Frequently, one will assume a balanced sex ratio at birth and uses fecundity in young per females, divided by 2.

Another frequently used statistics is the «net reproduction rate» R_0 (Keyfitz 1968:21, Charlesworth 1980:32). It is the lifetime expected number of female offspring per new-born female, while the «lifetime reproductive success» is the mean number of offspring of both sexes produced by female that survives to breeding age (Clutton-Brock 1988, Newton 1989). R_0 can be obtained as:

$$\psi(1) = \sum_{i=\alpha}^{\infty} s_0 s_1 \cdots s_{i-1} m_i = R_0 \quad (2.8)$$

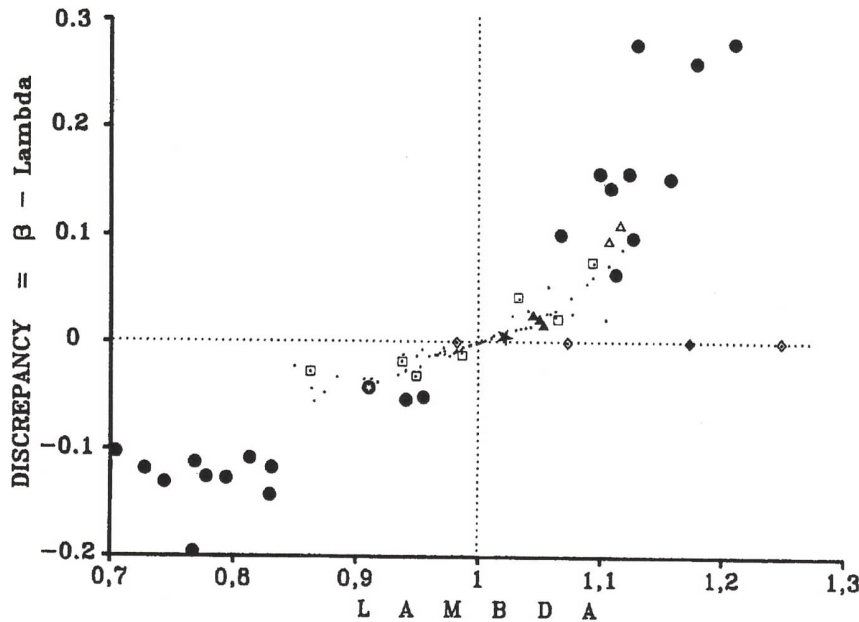


FIGURE 2.1. Discrepancy between λ and its estimation by *ad hoc* computation β , according to λ in 100 simulations. Δ : Herring Gull; \blacklozenge : House Martin; \blacklozenge : tits; \blacktriangle : Puffin; \star : Glaucous-winged Gull; \square : Kittiwake; \oplus : Manx Shearwater; -: biologically acceptable situations; \bullet : unlike situations (e.g. all demographic parameters from tits but first breeding at age of three).

Under the restrictive hypotheses $s_i = s$ and $m_i = m$, one obtains

$$R_0 = ms_0 \cdots s_{\alpha-1} + ms_0 \cdots s_{\alpha-1}s + ms_0 \cdots s_{\alpha-1}s^2 + ms_0 \cdots s_{\alpha-1}s^3 + \dots = \frac{ms_0 \cdots s_{\alpha-1}}{1-s}$$

i.e. the ratio between recruits and dead individuals, which reduces to $R_0 = \frac{\beta - s}{1-s}$.

RELATION BETWEEN λ , β AND R_0

The discrepancy between λ and β can be important and is unpredictable (Figure 2.1). There is no functional relation between λ and β because λ depends on α , while β does not. It can be shown that β always exaggerates the departure from stability (Figure 2.1, Appendix C).



TABLEAU 2.1. Computation of the fecundity that would be necessary to make λ reach the value of β calculated with the real fecundity of the species.

% Breeders (p_j)							Survival rates					Age of youngest breeders	Fecundity		Multiplication rate		References
2y	3y	4y	5y	6y	7y &+	s_0	s_1	s_2	s_3	s_4	s_5		Real ($2f_i$) [§]	necessary <u>a/</u>	β	λ	
<i>Rissa tridactyla</i>																	
		100				.70	.85	.85	.85	.85	.85	4	1.04	1.28	1.074	1.046	Danchin & Monat 1992
<i>Larus glaucescens</i>																	
		100				.41	.90	.90	.90	.90	.90	4	0.85	0.93	1.027	1.020	Vermeer & Devito 1989
<i>Larus argentatus</i>																	
	1	14	69	92	100	.71	.87	.91	.91	.91	.91	3	1.30	2.72 ^{b/}	1.201	1.106	Migot 1992
<i>Larus ridibundus</i>																	
45	61	55	100			.40	.82	.82	.82	.82	.82	2	1.50	2.20 ^{c/}	1.069	1.010	Lebreton <i>et al.</i> 1990
<i>Fratercula arctica</i>																	
			70			.83	.83	.83	.83	.83	.96	5	0.80	1.05 ^{d/}	1.070	1.051	Harris 1983
<i>Puffinus puffinus</i>																	
		100				.76	.76	.76	.76	.90	.90	4	0.70	0.74	1.017	1.012	Brooke 1990

§ 2 times f_i because f_i is the number of newborn females per breeding female aged i .

a/ Fecundity which would be necessary in order to force λ to reach β (computed with real fecundity).

b/ This value is much higher than highest fecundity ever observed in the species.

c/ This value is above the highest fecundity observed in the species.

d/ Impossible value because Puffins lay only one egg.

λ computed from demographic models using ULM software. As shown in Figure 2.1, the discrepancy tends to increase with the value of λ .

The fecundity needed to compensate for the discrepancy between β and λ can be out of biological range (e.g. Puffin in Table 2.1). It is thus of paramount importance to calculate λ properly (i.e. with demographic models) when estimates of the asymptotic multiplication rate are required. Furthermore, demographic models give other outputs which are of interest to the population biologist.

MEANINGFUL DEMOGRAPHIC OUTPUTS

Discrete time models for seasonally breeding populations are valid on their own, not only as approximations of continuous time models (Henny *et al.* 1970, Murray & Garding 1984, Eberhardt 1985), and projection matrix models are widely used in population biology (Groenendael *et al.* 1988). Some of the main outputs of discrete time models are detailed below.

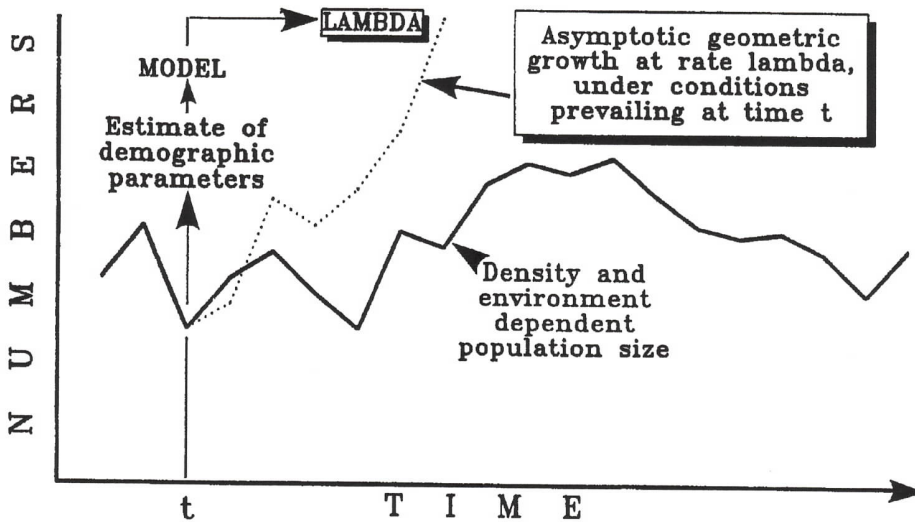


FIGURE 2.2. Meaning of the asymptotic multiplication rate calculated by demographic models. Full line: actual changes in number with time; Dashed line: changes in number that would occur if the demographic parameters, estimated at time t remain constant. Population growth would become exponential after only a few breeding cycles.

The multiplication rate

In practice, demographic parameters are estimated under particular environmental conditions and population numbers. λ calculated from such estimates would be the rate of multiplication if the parameters remain valid and after a stable age structure has been reached.

In this respect, λ is intuitively the rate of an exponential curve tangent to variation of the population at time t (Figure 2.2). Although it is derived from a model assuming constant parameters, it characterizes nevertheless growth under particular conditions even in the presence of complex variations in parameters, and even if it does not lead to a forecast of population size.

When estimates of all demographic parameters are available, the obtained value of λ can be viewed as an estimate of the true unknown λ and its sampling variance can be computed (Daley 1979, Lande 1989, Houllier *et al.* 1989, Alvarez-Buylla & Slatkin 1991). When the two kinds of estimates of λ (those obtained from estimates of demographic parameters using demographic models and those obtained from density-independent models from counts (eq. 6, see Nur 1987)) are available and accompanied by estimates of their variance, a formal



comparison is possible, assuming a normal distribution of estimates. Such comparisons can provide information on the emigration/immigration patterns (Danchin & Monnat 1992). Both estimates can also be compared with the theoretical value 1, as a test of stability (Lebreton 1989, Lebreton & Clobert 1991:110).

Age structure of the population

The asymptotic stable age-structure N_s of the population is proportional to: $s_0\lambda^{-1}, s_0s_1\lambda^{-2}, s_0s_1s_2\lambda^{-3}, \dots$. Owing to the ergodic property of populations, constant parameters always lead to the same N_s , whichever the original age-structure. This kind of output is helpful for managing exploitation rates by cohorts (Lande 1989). However, it is not very useful for demographic inference (Caughley 1974) because of a low sensitivity to permanent changes in parameters (Lebreton & Clobert 1991).

Reproductive value

Reproductive value V_s is a sequence of ω terms weighting the relative value of the individuals of each age-class as « seeds » for future population growth (Caswell 1989). The terms of this sequences are:

$$\begin{aligned}
 & s_0m_1 + s_0m_2s_1\lambda^{-1} + s_0m_3s_1s_2\lambda^{-2} + s_0m_4s_1s_2s_3\lambda^{-3} + \dots + s_0m_\omega s_1 \dots s_{\omega-1} \lambda^{-\omega+1}, \\
 & s_0m_2\lambda^{-1} + s_0m_3s_2\lambda^{-2} + s_0m_4s_2s_3\lambda^{-3} + \dots + s_0m_\omega s_2 \dots s_{\omega-1} \lambda^{-\omega+1}, \\
 & s_0m_3\lambda^{-2} + s_0m_4s_3\lambda^{-3} + \dots + s_0m_\omega s_3 \dots s_{\omega-1} \lambda^{-\omega+1}, \\
 & \dots \\
 & s_0m_\omega \lambda^{-\omega+1}
 \end{aligned}$$

where the first term sums up to unity while the other ones are smaller excepting, as a function of survival and fecundity, some of the subsequent ones. Hence reproductive value is an estimate of relative *fitness* per age-class and it is helpful in cohort analysis and management.

Coefficient of convergence

The *stable* age-structure can be reached with a relative speed depending upon the original observed structure of the population. The relative speed or convergence rate $\ln\rho$ is measured by the *damping ratio* $\rho = |\lambda_2|/\lambda$, and it allows to know the deviation of the asymptotic behavior from the actual behavior of the population, as illustrated in Figure 2.2.

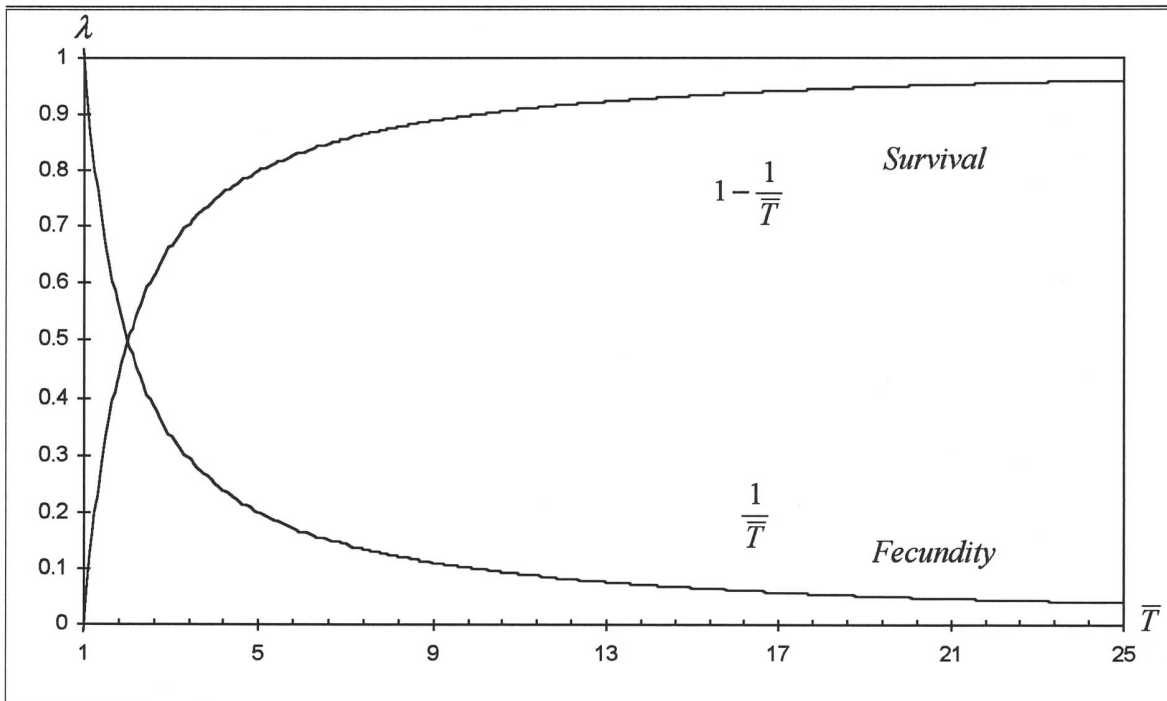


FIGURE 2.3. Relative sensitivity of the asymptotic population multiplication rate λ , to survival and to fecundity, as a function of generation time \bar{T} .

Generation time

The age-structure of breeders, multiplied by fecundity, is made up of the terms of the Lotka equation, which sum up to unity: $m_1 s_0 \lambda^{-1} + m_2 s_0 s_1 \lambda^{-2} + m_3 s_0 s_1 s_2 \lambda^{-3} + \dots$. It can be considered as the probability distribution of the ages of mothers when giving birth in the stable population.

The mean generation time $\bar{T} = \sum_{\alpha} i m_i s_0 s_1 \dots s_{i-1} \lambda^{-i}$ constitutes a meaningful definition of generation time.

Net reproductive rate

R_0 is often considered as a measure of fitness (Newton 1989). However, this is only true in species with no overlapping generations (which is not the case in birds) or in stationary populations (Charlesworth 1980, Lande 1982, Charnov 1986, 1990), i.e. when $R_0 = \lambda = 1$. In growing or decreasing populations R_0 cannot be a measure of fitness. Indeed two phenotypes with identical R_0 but different generation times should not contribute equally to the population turn over: the category with the shortest generation time would have the highest fitness in a growing population but the lowest fitness in a declining one.



Sensitivity analysis and generation time

Explicit results on the sensitivity of λ to changes in any demographic parameter can be obtained from a linear approximation of λ through the Lotka equation (see e.g. Goodman 1971), or through a matrix approach (Caswell 1978). In long-lived species (i.e. those with generation times higher than 2, which is the case of most birds) λ is more sensitive to changes in adult survival rate than to changes in fecundity (Eberhardt & Siniff 1977, Kosinski & Podolsky 1979, Figure 2.3). On the contrary, in short-lived species the opposite is true. The mean generation time \bar{T} (Leslie 1966) plays a prominent role, which is particularly striking when sensitivity is expressed as the relative sensitivity to changes in all fecundity or survival rates after first year (Houllier & Lebreton 1986, Lebreton & Clobert 1991, Figure 2.3). This role of generation time has not been clearly understood by human demographers who work on populations with a limited range of variation in generation time.

DISCUSSION

A discussion of methods for estimating demographic parameters is beyond the scope of this paper. However, it is fairly clear that the quality of the prediction of population asymptotic growth rate depends strongly on the quality of parameter estimates, whether in terms of bias or in terms of precision (Houllier *et al.* 1989, Alvarez-Buylla & Slatkin 1993). For instance, survival rates estimated solely from recoveries of birds marked as young can be subject to many biases and are thus suspect (Anderson *et al.* 1985). We strongly recommend to provide point estimates of demographic parameters, their estimated standard errors and correlations, and information on the statistical model used for estimation.

In most situations, among the known estimates of the *fitness*, the multiplication rate λ or equivalently the malthusian parameter $r = \ln\lambda$ is the best one for a phenotype (Charlesworth 1980, Stearns & Crandall 1981, Murray 1985, 1990, 1992, Caswell 1989, Charnov 1990). Comparing these parameters for different phenotypes in a population informs on their relative fitness in that particular environmental situation.



TABLE 2.2. Available softwares for computing the multiplication rate.

Name of Softwares	Kind of computer system needed	Reference or address for documentation
RAMAS/a	IBM PC or PS/2 compatibles	Ferson <i>et al.</i> 1987, 1989 Exeter Publishing Ltd. 100 North Country Road Setauket, New York 11733 USA
DERIVE	IBM PC or PS/2 compatibles	Rich <i>et al.</i> 1989 Soft Wharehouse Inc. Hawaii
SADE (Stand Alone Demography)	IBM PC or PS/2 compatibles	J.D. Lebreton (see address in heading)
CALMAT	IBM PC compatibles	R. Quris, CNRS University of Rennes I Biological Station of Paimpont, France
ULM (Unified Life Models)	IBM PC, PS/2 or SUN4	S. Legendre, Laboratory of Ecology, ENS 45 rue d'Ulm, 75230 Paris Cedex 05, France ULM was used to compute λ in Figure 2.1 and Table 2.1

TABLE 2.3. Relevance of demographic models outputs for evolutionary biology and management.

OUTPUTS	SIGNIFICANCE AND RELEVANCE
Multiplication rate λ	Best estimate of <i>fitness</i> . Comparison of different estimates of λ between themselves or against $\lambda = 1$
Age-structure N_s	Managing exploitation rates by cohorts (hunting, fisheries, forestry)
Reproductive value V_s	Estimate of <i>fitness</i> per age-class. Cohort management.
Damping ratio $ \lambda_2/\lambda$	Allows to estimate the coefficient of convergence toward the <i>stable</i> age-structure. Management of exploitation cycles.
Generation time \bar{T}	Provides information on the population turn over and calibrates the sensivity of λ to fecundity and survival. $1/\bar{T}$ is the rate of increase of the mean number of overlapping generations per breeding cycle.
Net reproductive rate R_0	Expected number of females born from a newborn female. Used as <i>fitness</i> estimator in <i>static</i> studies (life-history evolution)
Sensitivity of λ	Helps determining which parameters should be measured with greatest accuracy, and the best conservation decisions to be adopted.




As we showed, the multiplication rate cannot in general be obtained explicitly, and demographic models ought to be used. This is not always realized in the literature (for a critical reflection see Nur 1987, and Murray 1988, 1990). In practice, estimating various demographic characteristics of wild populations involves relatively complex methods in the field as well as for data analyses. It would not be worth measuring accurately the demographic parameters in the field if they are only used to estimate the multiplication rate with a rough and unpredictable biased method (Figure 2.1, Table 2.1). Only demographic models give the accuracy which is necessary to refined biological studies. Moreover, the use of demographic models is now simplified greatly by the existence of good computer programs (Table 2.2).

Furthermore, owing to their numerous outputs and their flexibility, demographic models make a link between empirical and theoretical approaches. Their outputs are of first importance for population management and evolutionary biology (Table 2.3). For example, in the White Stork, the Leslie model showed that the decrease of the population in Alsace (France) could be explained by a drop in survival rates after 1960 (Lebreton 1978). This involved the migratory phase. A deeper analysis of demographic parameters showed that this was due to environmental changes in North Africa (Kanyambwa *et al.* 1990). So, conservation measures on the breeding grounds might be ineffective. More generally, the role of generation time in sensitivity analysis shows that fecundity in short-lived species and adult survival in long-lived ones should be suspected in priority in any sharp and sustained change in the growth regime.

Discrete time density independent models can be used under much less restrictive hypotheses than those postulated for the explicit computation of λ . They can be generalized to more complex situations in which other approaches would fail. For example, if the biological situation is well documented, it is possible to take into account the variations of the demographic parameters in time and/or the existence of dispersion processes, i.e. when density-dependence and/or emigration/immigration are not neglected (Caswell 1989, Tuljapurkar 1990).

Moreover, under such complex situations, λ keeps its precise meaning. For instance, when density dependence is suspected it can be taken into account in the models by allowing some parameters to vary with density. The population dynamics can then be described by a sequence of instantaneous growth rates $\lambda(t)$ and a long run growth rate λ . The $\lambda(t)$ sequence describes the population growth between consecutive years. They can still be considered as the slope of



the tangent to the growth curve relating population size to time at time t (Figure 2.2) while the long run growth rate λ is uninteresting since equal to one (Ferrière & Clobert 1992, see Caswell 1989 and McDonald & Caswell 1993 for a review). However, it is possible to have a time-varying situation in which the population will, with probability one, grow even though the dominant eigenvalue of every matrix in the sequence is less than one (Tuljapurkar 1990). So, in such complex situations (which are likely to be the case of natural populations) the population may never reach a stable age-structure and the biological meaning of λ has to be questioned. This will depend on the other eigenvalues λ_i (for $i \geq 2$) of the matrix, particularly the second one λ_2 which allows to measure the rate of convergence $\ln(|\lambda_2/\lambda_1|)$ of the population structure towards the asymptotic stable structure N_s (Caswell 1989). This shows however, the conceptual limits of the interpretation of fitness as defined by demographic models, and it is obvious that under density dependence, the meaning of λ is not as clear as in density independent models 

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Appendix A

The synthetic matrix expression of the system of linear equations 2.2 is equation 2.3:

$$\mathbf{N}(t) = \mathbf{L} \mathbf{N}(t-1)$$

known as the **Leslie matrix** equation when $s_\omega = 0$. In a square-and-column matricial fashion:

$$\begin{bmatrix} N_1 \\ N_2 \\ N_3 \\ \vdots \\ \vdots \\ N_\omega \end{bmatrix}_t = \begin{bmatrix} s_0 m_1 & s_0 m_2 & s_0 m_3 & \cdots & \cdots & s_0 m_\omega \\ s_1 & 0 & \cdots & \cdots & \cdots & 0 \\ 0 & s_2 & 0 & \cdots & \cdots & \vdots \\ \vdots & \vdots & 0 & s_3 & 0 & \cdots \\ \vdots & \vdots & \vdots & 0 & \ddots & 0 \\ 0 & \cdots & \cdots & 0 & s_{\omega-1} & s_\omega \end{bmatrix} \begin{bmatrix} N_1 \\ N_2 \\ N_3 \\ \vdots \\ \vdots \\ N_\omega \end{bmatrix}_{t-1}$$

Birds are iteroparous species frequently presenting an age ω of stabilisation of parameters, thus $s_\omega > 0$. Under the hypothesis of a balanced sex-ratio, only half of the offspring produced in a given year are females, the number of newborn females produced per female aged i per year ($m_i = p_i f_i$) is only half the number of offspring produced per female aged i (or equivalently per pair) in a given year.

The solutions of the Leslie characteristic polynomial $\phi(\lambda)$ are obtained by the expansion of the determinant equation (2.4), and can only be solved iteratively as we show e.g. by the Newton-Raphson method (see Keyfitz 1968, or Anderson 1975). One may use any of the softwares available in the market (some listed in Table 2.2) to estimate λ and other demographic outputs.

Appendix B

Under the restrictive hypotheses $m_i = m \forall i \geq \alpha$ and $s_i = s \forall i \geq \alpha$, the Lotka equation (2.1 in the text) is:

$$\begin{aligned} \psi(\lambda) &= \sum_{i=\alpha}^{\infty} \lambda^{-i} s_0 m s_1 s_2 \cdots s_{\alpha-1} s^{i-\alpha} = 1 \\ &= \lambda^{-\alpha} s_0 m s_1 s_2 \cdots s_{\alpha-1} (1 + s \lambda^{-1} + s^2 \lambda^{-2} + s^3 \lambda^{-3} + \dots) \\ &= \lambda^{-\alpha} s_0 m s_1 s_2 \cdots s_{\alpha-1} \left(\frac{\lambda}{\lambda - s} \right) \\ &= \frac{\lambda^{-\alpha+1}}{\lambda - s} s_0 m s_1 s_2 \cdots s_{\alpha-1} = \frac{s_0 m s_1 s_2 \cdots s_{\alpha-1}}{\lambda^\alpha - \lambda^{\alpha-1} s} = 1 \end{aligned}$$

which leads to the Leslie equation (2.7): $\lambda^\alpha - \lambda^{\alpha-1} s - s_0 m s_1 s_2 \cdots s_{\alpha-1} = 0 = \phi(\lambda)$.



Appendix C

The relation between β and λ can be deduced from equation (2.5) and (2.6):

$\beta = \lambda \Leftrightarrow \alpha = 1$ and/or $\lambda = 1$ because

$$\alpha = 1 \Rightarrow \phi(\lambda) = \lambda - s - s_0 m = 0 \Rightarrow \lambda = s + s_0 m = \beta, \text{ and/or}$$

$$\lambda = 1 \Rightarrow \phi(1) = 1 - s - s_0 m s_1 s_2 \dots s_{\alpha-1} = 0 \Rightarrow 1 = s + s_0 m s_1 s_2 \dots s_{\alpha-1} = \beta,$$

$$\beta < 1 \Rightarrow s + s_0 m s_1 s_2 \dots s_{\alpha-1} < 1 \Rightarrow 0 < 1 - s - s_0 m s_1 s_2 \dots s_{\alpha-1} = \phi(1)$$

deriving $\phi(\lambda)$ shows that it is an increasing function:

$$\phi'(\lambda) = \alpha \lambda^{\alpha-1} - (\alpha-1) s \lambda^{\alpha-2} = \lambda^{\alpha-2} [\alpha \lambda - \alpha s + s]$$

the term in brackets is positive because $\lambda \geq s$

then as $\phi(1) > 0$ and $\phi(\lambda) = 0 \Leftrightarrow \lambda < 1$; and in the same way,

$$\beta > 1 \Rightarrow s + s_0 m s_1 s_2 \dots s_{\alpha-1} > 1 \Rightarrow 0 > 1 - s - s_0 m s_1 s_2 \dots s_{\alpha-1} = \phi(1)$$

then as $\phi(1) < 0$ and $\phi(\lambda) = 0 \Leftrightarrow \lambda > 1$

Furthermore, it can be shown that:

$$\beta = 1 \Leftrightarrow R_0 = \beta = \lambda = 1$$

in stationary populations,

$$\beta > 1 \Leftrightarrow R_0 > \beta > \lambda > 1$$

in growing populations, and

$$\beta < 1 \Leftrightarrow R_0 < \beta < \lambda < 1$$

in decreasing populations.

