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POPULATION MODELS FOR PASSERINE BIRDS: STRUCTURE, PARAMETERIZATION, AND ANALYSIS

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Abstract. Population models have great potential as management tools, as they use information about the life history of a species to summarize estimates of fecundity and survival into a description of population change. Models provide a framework for projecting future populations, determining the effects of management decisions on future population dynamics, evaluating extinction probabilities, and addressing a variety of questions of ecological and evolutionary interest. Even when insufficient information exists to allow complete identification of the model, the modelling procedure is useful because it forces the investigator to consider the life history of the species when determining what parameters should be estimated from field studies and provides a context for evaluating the relative importance of demographic parameters. Models have been little used in the study of the population dynamics of passerine birds because of: (1) widespread misunderstandings of the model structures and parameterizations, (2) a lack of knowledge of life histories of many species, (3) difficulties in obtaining statistically reliable estimates of demographic parameters for most passerine species, and (4) confusion about functional relationships among demographic parameters. As a result, studies of passerine demography are often designed inappropriately and fail to provide essential data. We review appropriate models for passerine bird populations and illustrate their possible uses in evaluating the effects of management or other environmental influences on population dynamics. We identify environmental influences on population dynamics. We identify parameters that must be estimated from field data, briefly review existing statistical methods for obtaining valid estimates, and evaluate the present status of knowledge of these parameters.

INTRODUCTION

We have chosen to review the state of population ecology of passerine birds in the context of age- and stage-structured population models (e.g., Caswell 1989). There is considerable interest in the use of population models to project a species' future population size, to determine the ultimate effects of current management decisions, and to gain insights into species extinction likelihoods under different management scenarios. These models require an in-depth understanding of the species' life history and precise and reliable estimates of birth and death rates (vital rates). Collectively, this information can be used to construct, and parameterize, a model of the life cycle of a species and to explore the demographic consequences of variation in the vital rates. The analysis of the life cycle allows projections of future populations, insights into the effects of management actions, and estimates of persistence likelihoods. Model construction requires understanding of: (1) technical aspects of the models, (2) basic demographic parameters and their estimation, and (3) interactions among demographic parameters over time; in brief, most of the interesting (in our opinion) topics in population ecology. Even a brief review of these topics would merit a volume on its own, so we will examine only a few selected topics in population modelling in this paper.

Even though population projection models are not new to ecology, there remains a significant gap between the theoretical structure and exploration of the models and their application to specific ecological questions and management problems. The limited application of these models to real-world problems has many explanations including: (1) confusion over the relationship among models, particularly between life tables and Leslie (1945, 1948*a*,*b*) matrix models, (2) unfamiliarity with population models by biologists conducting field studies, (3) failure by many mathematical ecologists to simplify model structure to reflect parameters that can actually be estimated from field studies, and (4) difficulties in parameterizing models with reliable estimates of a population's vital rates. In the context of life history studies of passerine birds, we propose to specifically address points (1), (3) and (4) and, in the process, make progress in addressing problem (2).

GENERALIZED MODEL STRUCTURE FOR PASSERINE BIRDS

When constructing general life cycle graphs for typical passerines, several simplifying assumptions to their life history can be made. First, most species usually produce one or more broods during a relatively short breeding season which allows them to be loosely characterized as birth-pulse populations (Caughley 1977:72). Second, reproductive periods occur at consistent intervals of 1 year, which allows separation of the population into discrete age classes. In our models, this allows us to redefine age-specific rates into class-specific rates because all reproduction in the interval occurs at a specific time. As a result, the projection interval, or time step, is of the same duration as the width of the age class. Third, in sexually reproducing species, particularly those that are monogamous, we often restrict our models to females. Collectively, these aspects of passerine life history allow us to use discrete, single-sex models formulated in terms of life tables or projection matrices (Leslie 1945, 1948*a*,*b*). A final simplification

is that it is possible to use stage projection matrices if the vital rates can be assumed constant and independent of age beyond a given age (e.g., an "adult" stage).

Model assumptions

To use simple population projection models for passerine birds we must assume, among other things, that: (1) males play no role in affecting survival and reproduction of females, other than their obvious role in sexual reproduction, (2) births occur during a limited portion of the annual cycle, (3) the values of the vital rates remain constant through time, and (4) no interactions occur among parameters and between parameters and population density. Male participation in preparation for and care of young varies greatly among passerines, so for at least some species assumption (1) is probably incorrect. Assumptions (3) and (4) are incorrect, although few analyses have addressed these issues for passerines (see below). Testing the appropriateness of simple models and possibly rejecting them in favor of more complex models is the essence of model fitting, and is probably the only appropriate framework for evaluating population dynamical questions about passerines. Several levels of model fitting exist, addressing: (1) the issue of structure of the population, and the issues of (2) time-specificity and (3) density-dependence of the vital rates. We discuss these issues later in the paper.

RECONCILING LIFE TABLE AND PROJECTION MODELS

Emlen (1984) categorized transition models as "bookkeeping" models, because they have a simple structure that is designed to account for changes in population size as a function of births and deaths. Unfortunately, application of these simple models has been greatly complicated by two alternative sets of terminologies (Table 1). Life table functions $l(x)$ and $m(x)$ are indexed by x, in continuous time, but projection matrix functions p_i and F_i are indexed by age class i in discrete time. Even if data are collected in continuous time, however, construction of the life table requires a discretization of age to form age classes. In this section we review how the life table functions can be placed into a Leslie matrix. Further, we demonstrate how timing of the census relative to the birth-pulse defines the components of the projection matrix functions, and demonstrate that projection matrices can be constructed using composite estimates of p_i and F_i.

There is an extensive literature on both parameterizing Leslie matrices and demonstrating the equivalence of Leslie matrix and life table approaches (e.g., Taylor and Carley 1988). Unfortunately, confusion still exists because many basic population ecology texts provide insufficient or in correct formulations of F_i (e.g., Pielou 1974, Begon and Mortimer 1981). As a result, the relationship between the projection coefficients p_i and F_i and the life table functions $l(x)$ and $m(x)$ remains confused because of: (1) different formulations regarding the relationship between the Leslie matrix model (Leslie 1945, 1948*a,b*) and the life table model (Cole 1954, Pielou 1974), (2) different formulations of common demographic parameters (e.g., Michod and Anderson 1980), and (3) failure to recognize the often subtle distinction between an animal's age-class and its calendar age. Most confusion has centered on the relationship between the recruitment

parameters F_i (Leslie) and $m(x)$ (life table) as a result of many factors including the time at which the population is censused relative to the birth-pulse, the specification of the time line, inconsistent definition of a recruit, and whether the first age class is labeled 0 or 1. Despite the confusion, it is possible to develop a consistent relationship between life tables and projection matrices.

TABLE 1. Terms commonly used in population ecology (see Caswell 1989).

Parameter	Symbol	Definition
Indexes		
Age	x	Continuous index for age
Age class	i	Discrete index for age categories $i = 0, \ldots, w\text{-}1$.
Life table components		
Survivorship	$l(x)$	Probability of survival from birth to age x
Reproduction	$m(x)$	Expected number of female offspring for each female of age x per unit time
Projection matrix components		
Survival rate	p_i	Probability of survival from t to t+l of females in class i.
Fertility	F_i	Expected number of female offspring at time $t+1$ per female in class i at t
Age class size	$n_i(t)$	Number of individuals in age class i at t

An algorithm for developing a Leslie matrix difference model of population change

A clear, practical algorithm for developing a Leslie matrix from life table functions does not exist in the literature. Here, we outline how $l(x)$ and $m(x)$ can be placed in a Leslie matrix formulation that is consistent with the original life table. There are two components that must be considered in this formulation. Life tables functions begin at the birth of individuals in a cohort and provide age-specific survival and reproduction throughout the individuals' lives. Leslie matrices group individuals into age classes and assume that survival and reproduction can be estimated for each age class from some specified time (the census) to another specified time occurring exactly one unit of time in the future. Leslie matrices therefore: (1) are indexed by time intervals that are of equal length to age classes but do not necessarily occur on the birth pulses, and (2) have functions p_i and F_i that are defined in terms of the time intervals.

1. Specifing the timing of annual events relative to the time of census and ages, and age classes of cohorts.

a. Set the time axis, in which the length of intervals from t to t+1 (the time

interval t) are the same as the length of age classes in the population to be studied. The time interval should contain just one birth pulse, and for passerine birds, the time interval will be one year. Each point t represents a time of census, which is the point from which parameters for all age classes must be indexed.

b. Establish an age axis x, at right angles to the time axis. Because of our assumption of a birth pulse, all individuals born during a time interval will be the same age, represented as a point on the age line which we call a cohort. Cohorts, indexed by the last integer value of age, are denoted by i and numbered from 0 (newborns) to w-1, where w is the maximum attainable age or age of reproductive senescence. Because the cohorts are only observed at census time, the number of individuals in each cohort at the censuses are indexed by age class i and census period t ($n_{i,t}$). The diagonal lines (Figs. 1-3) indicate the trajectory of a cohort as it ages over time.

c. In Fig. 1, time of birth-pulse occurs on the time-line at points located distance $1\text{-}k$ beyond the census points, and on the age-line at the time at which each cohort is exactly on integer values of the age axis, or where $i = x$. At the birth pulse, a cohort of age 0 (the newborns) is formed. Note that the proportion of time between the birth pulse and the next census in each time interval is denoted as k. The actual age of the animals in each age class i at the time of census is $i + k$.

2. The actual number of animals in the cohort at any location on these trajectories defined in (1) is a function of age and time of census (the axes). To convert the axes to a coherent framework for a demographic model, the transitions between age classes observed at each census must be defined. To do this, we use graphs, with nodes representing age classes and arcs representing paths between nodes. The nodes can be thought of as the number of animals in the cohort when censused at that age class and time, or $n_{i,t}$, and the arcs represent influences on each node at time t that change the values of the "target" nodes at time $t + 1$ (e.g., $n_{i+1,t+1}$). The product of the number of animals associated with the original nodes and the values associated with the intermediate arcs is the number of animals associated with the target nodes. Caswell's (1989) formulation also uses directed graphs, but does not explicitly incorporate time, which tends to obscure the transitions for those unfamiliar with graph theory. At this point, the alternative terminology between life tables and Leslie matrices must be reconciled.

We label the general graph (Fig. 1) with p_i and m_i. The critical assumption of a birth pulse allows us to set $m_x = m_i$, as all births occurring in an age class occur at time $t + (1 - k)$ (Fig. 1). Also, p_i can be defined for any age as $p_i = 1(i + 1)/1(i)$ (e.g., Caughley 1977:87). For this paper, we define each p_i as having two parts, p_i^{k-1} (the probability of surviving from census to time of birth pulse), and p_i^k (the probability of surviving from time of birth pulse to time of next census) where $p_i = (p_i^{k-1})(p_i^k)$.

Adults in age class i must survive from the time of census to birth time with probability p_i^{k-1} (that is, survive for the portion of the interval $1\text{-}k$ in age class i), then they produce young at rate m_{i+1}, then the young survive from birth to census time with probability p_n^k (the n indexes newborns, which are not seen before the census; note, $p_n^k = 1(k)$). So, in general, we define F_i as $p_i^{k-1} m_i p_n^k$.

These graphs can also be written out as difference equations or Leslie matrices. For the general case, the difference equations are:

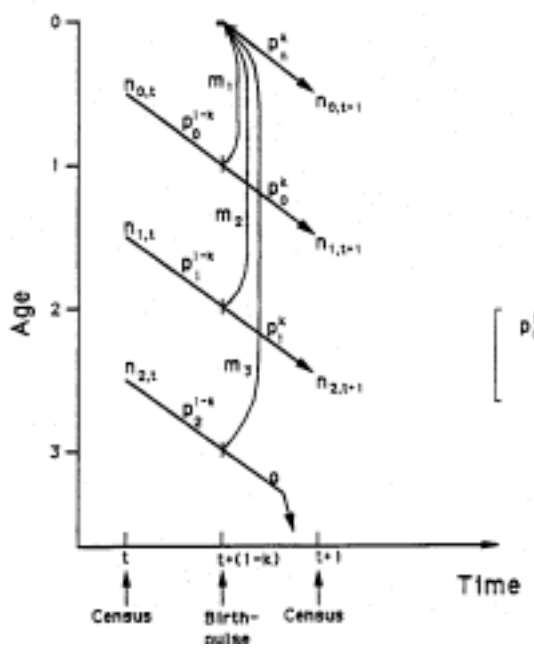
$$n_{o,t+1} = \sum_{i=0}^{w-1} n_{i,t}\, p_i^{1-k} m_{i+1}\, p_n^{k} \quad ,$$

and

$$n_{i+1,t+1} = n_{i,t}\, p_i$$

for $i = 0, \ldots, w\text{-}1$, which leads to the general Leslie matrix:

$$\begin{bmatrix} p_0^{1-k} m_1 p_n^k & p_1^{1-k} m_2 p_n^k & \ldots & p_{w-1} m_w p_n^k \\ p_0 & 0 & \ldots & 0 \\ 0 & p_i & \ldots & 0 \\ 0 & 0 & \ldots & 0 \end{bmatrix}$$



$$\begin{bmatrix} p_0^{1-k} m_1 p_n^k & p_1^{1-k} m_2 p_n^k & p_2^{1-k} m_3 p_n^k \\ p_0^{1-k} p_0^k & 0 & 0 \\ 0 & p_1^{1-k} p_1^k & 0 \end{bmatrix}$$

Fig. 1. A general time-by-age biplot illustrating cohort transitions between census periods. Symbols are: $n_{i,t}$, the number of age-class i individuals observed at census period t; p_i, the survival rate from age-class i to i+l; p_n^k, the survival rate of newborns from the birth-pulse to the next census at t+l; and m_i, the reproductive output of individuals of age-class i at the birth-pulse. The Leslie projection matrix, which summarizes the dynamics shown in the biplot, is given to the right of the graph.

A 4 age class example is presented in Fig. 1.

In practice the interval survival rates p_i^{k-1} and p_i^k are difficult to estimate, and almost all applications of this model fall into 2 special cases:

a. *Census just before the birth pulse.* -- If k approaches 1, animals have survived the time interval (and are therefore indexed in the higher age class), and immediately after the census produce young with reproduction associated with that age class (Fig. 2a). In this case, p_i^{1-k} is 1, and the first observed cohort has already survived the first time interval. In our 4 cohort example there are 3 observable cohorts (newborns are not observed), the first of which is indexed as $i = 1$, and survival of newborns is indexed with $i = 0$.

b. *Census just after the birth-pulse.* -- If k approaches 0, animals have just reproduced, and all mortality in the interval occurs after the census. In this case, all 4 cohorts are observed, and survival of newborns is again indexed with i = 0 (Fig. 2b).

Note that age classes are defined in relationship to survival: if the survival over the interval has not occurred, the animal is in the same age class as at the start of the interval. Only when the census occurs just before the birth-pulse (Fig. 2a), where animals have survived the entire interval, are the animals indexed into the higher age class. Otherwise (when k is not close to 1), the age class is indexed by the lower bound of the age, as is p.

The values for F_i are restricted to the top row of the Leslie matrix. For post-breeding censuses (Table 2), the first element of the top row, F_0, represents projected recruitment to t+1 from age-class 0 at time t, the second element, F_1, from age-class 1, and so on. In contrast, for a pre-breeding census (Table 2), the first element of the projection matrix is F_1, representing projected recruitment to t+1 from age-class 1. Comparison of the difference equations at the two times of census (Table 2) indicates that when the population is censused after the birth-pulse the members of age-class 0 are in their first year of life; for a population censused just before the birth-pulse, members of age-class 1 are about to begin their second year of life. The age-class distributions also differ: it is the set $\{N_{0,t}, N_{1,t}, \ldots, N_{w-1,t}\}$ if sampled after the birth pulse, and $\{N_{1,t}, N_{2,t}, \ldots, N_{w-1,t}\}$ if sampled before the birth pulse.

THE CHARACTERISTIC EQUATION

It is valuable to estimate the finite rate of increase for the population (λ) for the Leslie model or a life table model. The number λ indicates whether the population is growing (λ >1), is stationary (λ=1), or is declining (λ<1). The basic equation of the Leslie model for post-breeding censuses is:

$$N_{0,t+1} = \sum_{i=0}^{w-1} F_i N_{i,t} \quad . \tag{1}$$

TABLE 2. Difference equations and matrices for Figs. 2a,b, and 3.

Census before the birth-pulse (Fig. 2a)

Age Class	Difference Equations
1	$n_{1,t+1} = n_{1,t}\,(p_0 m_1) + n_{2,t}\,(p_0 m_2) + n_{3,t}\,(p_0 m_3)$
2	$n_{2,t+1} = n_{1,t}\,p_1$
3	$n_{3,t+1} = n_{2,t}\,p_2$

Leslie Matrix (A)

$$\begin{bmatrix} p_0 m_1 & p_0 m_2 & p_0 m_3 \\ p_1 & 0 & 0 \\ 0 & p_2 & 0 \end{bmatrix}$$

Census after the birth-pulse (Fig. 2b)

Age Class	Difference Equations
0	$n_{0,t+1} = n_{0,t}\,(p_0 m_1) + n_{1,t}\,(p_1 m_2) + n_{2,t}\,(p_2 m_3)$
1	$n_{1,t+1} = n_{0,t}\,p_0$
2	$n_{2,t+1} = n_{1,t}\,p_1$
3	$n_{3,t+1} = n_{2,t}\,p_2$

Leslie Matrix (A)

$$\begin{bmatrix} p_0 m_1 & p_1 m_2 & p_2 m_3 & 0 \\ p_0 & 0 & 0 & 0 \\ 0 & p_1 & 0 & 0 \\ 0 & 0 & p_2 & 0 \end{bmatrix}$$

Census after the birth-pulse, stage-class matrix (Fig. 3)

Stage Class	Difference Equations
0	$n_{0,t+1} = n_{0,t}\,(p_0 m_1) + n_{1,t}\,(p_1 m_2) + n_{2,t}\,(p_2 m_3) + n_{3,t}\,(p m_3)$
1	$n_{1,t+1} = n_{0,t}\,p_0$
2	$n_{2,t+1} = n_{1,t}\,p_1$
3	$n_{3,t+1} = n_{2,t}\,p_2 + n_{3,t}\,p$

Stage Matrix (A)

$$\begin{bmatrix} p_0 m_1 & p_1 m_2 & p_2 m_3 & p m_3 \\ p_0 & 0 & 0 & 0 \\ 0 & p_1 & 0 & 0 \\ 0 & 0 & p_2 & p \end{bmatrix}$$

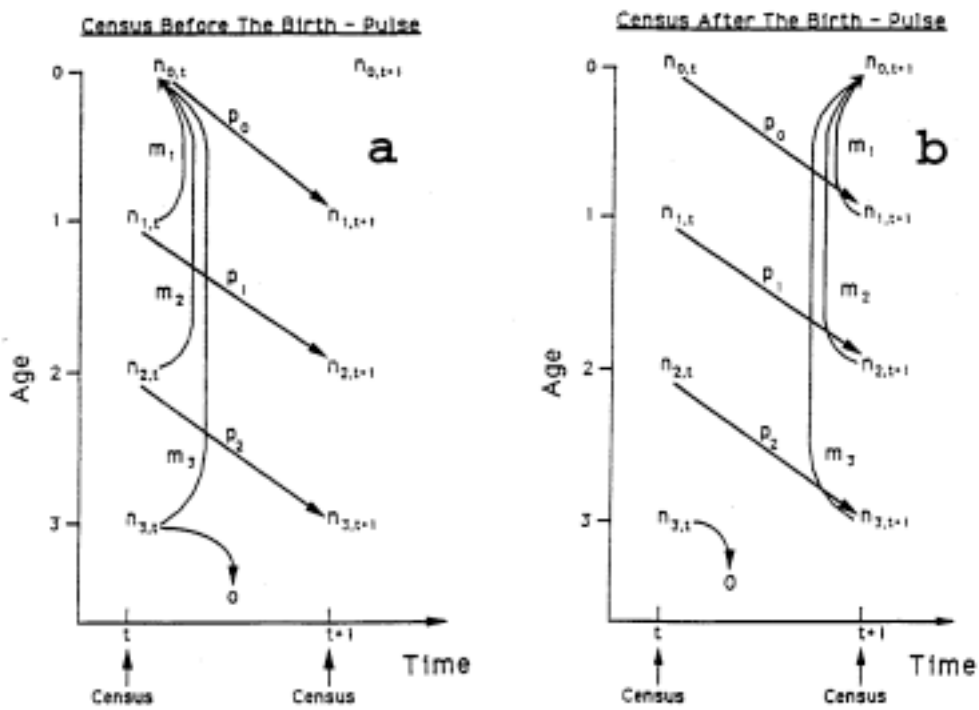


Fig. 2. a. A time-by-age biplot, for a census occurring just before the birth-pulse, illustrating cohort transitions between census periods. Symbols are: $n_{i,t}$, the number of age-class i individuals observed at census period t; p_i, the survival rate from age-class i to i+l; and m_i, the reproductive output of individuals of age-class a at the birth-pulse. Note that members of age-class 0 (n_0) are not observed at the time of census. b. A time-by-age biplots, for a census occurring just after the birth-pulse, illustrating cohort transitions between census periods. The corresponding difference equations and the Leslie projection matrix, which summarizes the dynamics shown in the biplots, are given in Table 2.

Algebraic manipulation of equation (1) leads to:

$$\lambda^{w} - F_0\lambda^{w-1} - \sum_{i=0}^{w-1} l_i F_i \lambda^{w-i-1} = 0 \quad , \tag{2}$$

where $l_i = p_0 p_1 \ldots p_{i-1}$, which is the familiar characteristic equation of the Leslie matrix of which λ is the principal root.

The basic equation of the life table model is:

$$N_{0,t} = \sum_{i=0}^{w-1} m_i N_{i,t} \quad , \tag{3}$$

which follows from the fact that the set of age classes for a given census at a fixed time in interval t partitions $N_{0,t}$, into the component contributions from each reproductive age class at t-1. By algebraic manipulation of equation (3) (Noon and Biles 1990: appendix), one obtains:

$$1 = \sum_{i=0}^{w-1} l_i m_i \lambda^{-i} \quad , \tag{4}$$

which is the familiar Lotka equation. Again, λ is the principal root. Either model can be constructed for a given population to determine λ, which will be the same for a fixed timeline but arbitrary time of census.

CHOOSING AMONG MODELS

Population projections and analyses based on either a life table or Leslie matrix approach are fundamentally identical. On the basis of how survival and fecundity parameters can be estimated from field data, however, it is possible to chose among model representations. Empirical estimates of F_i are usually not possible (see Caughley 1977:111) and direct estimate of m_i are usually required. Further, projection models based on censuses taken just before the birth-pulse confound estimates of fecundity (m_i) with first year survival rate (p_0). As a consequence, estimates of these two parameters are not separable. For species whose rates of population change (λ) are highly sensitive to fecundity and/or first year survival rate, such as most passerine birds (see below), we recommend censusing just after the birth-pulse.

The models we have outlined so far all require age-specific estimates of the vital rates. For example, to estimate Leslie's F_i we would need to know the number of age-class zero individuals observed at the census at time t+1 whose mother was in age-class i at the census at time t. In the majority of field studies the ages of reproductive females are unknown. Even data from long-term banding studies often fail to provide this information. A further problem is the large number of parameters to be estimated in age-specific models which, because of small sample sizes, are often estimated imprecisely. One can develop simpler projection models if it is possible to assume constant vital rates across two or more age-classes. In passerine birds, for example, it may be legitimate to assume that beyond the age at first reproduction fecundity and survival rates become constant (Deevey 1947, but see Loery et al. 1987). This assumption greatly simplifies model structure and affords more degrees of freedom for estimates of the remaining parameters.

The reduced, age-specific Leslie matrix is referred to as a stage projection matrix (Lefkovitch 1965). Structurally, the dynamics of the two models are equivalent to the

degree the assumption of constant vital rates within a stage is justified, and the same methods can be used for analysis. We illustrate a hypothetical stage projection model assuming four distinct stages -- stages 0-2 are each identical to age classes 0-2 and stage 3 includes all birds ≥ 3 years old (Fig. 3). The model assumes constant survival beyond age 3 ($p_i = p$, $i \geq 3$), constant fecundity for birds ≥ 3 years old (m_{i+1}, $= m_i$, $i \geq 3$), and the possibility for infinite life span. Note the difference equations and the resulting projection matrix (Table 2).

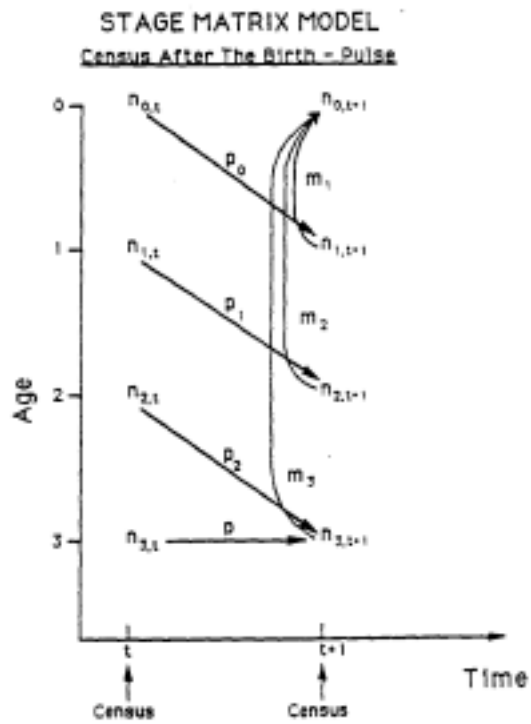


Fig. 3. A time-by-age biplot, for a census occurring just after the birth-pulse, illustrating cohort transitions between census periods. No obligate mortality (or reproductive senescence) is assumed at age 4; therefore, the plot represents a stage model with stage n_3 including individuals ≥ age 3. Symbols are: $n_{i,t}$, the number of age-class i individuals observed at census period t; p_i, the survival rate from age-class i to i+l; and m_i, the reproductive output of individuals of age-class i at the birth-pulse. The corresponding difference equations and the Leslie projection matrix, which summarizes the dynamics shown in the biplot, are given in Table 2.

THE STAGE PROJECTION MODEL

In subsequent analyses we start with age-specific life table parameters and assume that the population is censused immediately after the birth pulse. Starting with the basic

life table equation,

$$1 = \sum_{x=0}^{w-1} l_x m_x \lambda^{-x} \quad , \tag{5}$$

expressing l_x as $l_x = \prod_{i=0}^{x-1} p_i$, equation (5) can be rewritten as

$$1 = \sum_{x=0}^{w-1} \lambda^{-x} \prod_{i=0}^{x-1} (p_i) m_x \quad . \tag{6}$$

Invoking the assumption that reproduction and survival are independent of age upon reaching the age of first reproduction (α), equation (6) can be rewritten as:

$$1 = \sum_{x=\alpha}^{w-1} \lambda^{-x} \prod_{i=0}^{\alpha-1} (p_i) p^{x-\alpha} m \tag{7}$$

where $p_i = p$ and $m_x = m$ for all age classes ≥ α, and $m = 0$ for all age classes < α. If we further assume no reproductive senescence and that birds can live forever (w--> ∞), equation (7) can be rewritten as:

$$1 = m \left[\prod_{i=0}^{\alpha-1} \frac{(p_i)}{p^{\alpha}} \right] \left(\frac{p}{\lambda} \right)^{\alpha} \sum_{x=0}^{\infty} \left(\frac{p}{\lambda} \right)^{x} = m \left[\prod_{i=0}^{\alpha-1} \frac{(p_i)}{\lambda^{\alpha}} \right] \left[\frac{1}{1-(p/\lambda)} \right] \tag{8}$$

Equation (8) can be rewritten to provide the general characteristic equation for the completely stage-structured model as:

$$\lambda^{\alpha} - p\lambda^{\alpha-1} - m \prod_{i=0}^{\alpha-1} (p_i) = 0 \quad . \tag{9}$$

If we assume that the age at first reproduction (α) is one year, as it is for most passerine birds, we have a 2-stage model and equation (9) reduces to:

$$\lambda - p - p_0 m = 0 \quad . \tag{10}$$

For species which first breed at age 2 years (α = 2; 3 stages), equation (9) reduces to

$$\lambda^2 - p\lambda - p_0 p_1 m = 0 \quad , \tag{11}$$

If distinct, age-specific estimates of the vital rates are available, equation (2) can be as explicit as the data allows. As a result, the model structure will deviate, to varying degrees, from the simple two-stage model (equation 9) to models that have more stage-specific information. There are a large number of possible model structures (6)

when more age-specific information is incorporated. However, three scenarios cover most of the information available from field studies of passerine birds: (1) a distinct fecundity value for the first breeding season, (2) reproductive senescence or finite longevity, and (3) the combination of (1) and (2).

It is not uncommon for many passerine species to have lower expected reproductive rates during their first year of breeding (e.g., Clutton-Brock 1988, Saether 1990). Thus, assuming $\alpha = 1$, we have reproductive parameters m_1 and m. If we further assume no reproductive senescence ($w = \infty$), the characteristic equation for the stage model with a distinct first year reproduction becomes:

$$\lambda^2 - \lambda(p+p_0m_1) + p_0p(m_1-m) = 0 \quad . \tag{12}$$

Additionally, data on the expected life span of individuals may be available for some species. If we assume reproductive senescence at w years, age at first reproduction α, and constant survivorship beyond age α, then we rewrite equation (7) as:

$$1 = \left[\prod_{i=0}^{\alpha-1} (p_i)m/p^{\alpha}\right](p/\lambda)^{\alpha}\left[\frac{1-(p/\lambda)^{(w-1-\alpha)+1}}{1-(p/\lambda)}\right], \ \lambda > p \quad . \tag{13}$$

If we assume $\alpha = 1$, the characteristic equation is:

$$\lambda - p - p_0m\,[(1-(p/\lambda)^{w-1})] = 0 \quad . \tag{14}$$

A final elaboration of equations (6) and (7) allow us to explore the case of a distinct first year fecundity value and reproductive senescence. We assume $\alpha = 1$ year, reproductive parameters m_1 and m, and reproductive senescence at age w years. The characteristic equation is:

$$\lambda^2 - \lambda(p+p_0m_1) + p_0p\left[m_1 - m[1-(p/\lambda)^{w-1}]\right] = 0 \quad . \tag{15}$$

Equations (9), (12), (14), and (15) provide the characteristic equations needed for most life history studies of passerine birds.

ANALYSIS OF POPULATION PROJECTION MODELS

The basic projection equation for either the age- or stage-specific model is $n(t+1) = An(t)$, where n is a time-specific age (stage) distribution vector and A is the projection matrix (Table 2). In general, assuming constant parameter values, $n(t+k) = A^kn(t)$. If a projection matrix is an appropriate description of a population's dynamics and certain structural criteria are met (e.g., Beddington 1974), the eigenvalues and eigenvectors of A provide information on the long-term trajectory of the population. The dominant eigenvalue (λ_1) equivalent to λ from the characteristic equation (above), is the finite rate of change, and the right and left eigenvectors corresponding to λ_1 are the stable

(age) stage distribution and reproductive value vectors, respectively. Because λ is both the quantity maximized by natural selection (Fisher 1958), and an apparent measure of population persistence (Goodman 1980), there has been a great deal of interest in how changes in the elements of the projection matrix (denoted as a_{ij}'s) affect λ.

Point estimates of λ

Estimates of the finite rate of population change (λ) provide insights into the dynamics of a population assuming (1) constant parameter values, and (2) a stable age distribution. For a typical passerine bird, λ can be directly estimated from equation (9) as $\lambda = p+p_0m$, and for birds first breeding at age 2 from equation (11) by use of the quadratic equation. For example, the solution for λ from equation (11) is

$$\lambda = \frac{p+(p^2+4p_0pm)^{1/2}}{2} \quad . \tag{16}$$

Estimates of λ from equations invoking senescence (equations (14) and (15)) must be solved iteratively. Alternatively, once the appropriate projection matrix has been constructed, λ and its associated eigenvectors can be calculated numerically from A using any of a number of available software packages.

Sensitivity analyses

If simplifying assumptions are made about adult survival and fecundity (e.g., time invariance), implicit differentiation of the characteristic equation can be used to evaluate the effects of changes in the vital rates on λ. In addition, the values of the partial derivatives:

$$\frac{\partial \lambda}{\partial a_{ij}}$$

where a_{ij} represents the estimate of the ij^{th} parameter of matrix A can be ranked according to their magnitude and used to infer which parameters, when changed in value, most affect the value of λ. Survival and fecundity rates are measured on different scales, however, which may make direct comparison of their sensitivities difficult. Fortunately, a measure of the sensitivity of λ to proportional change in the vital rates, or elasticity, has been developed by de Kroon et al. (1986). The elasticity of λ with respect to a_{ij} is defined as:

$$e_{ij} = \frac{a_{ij}}{\lambda}\frac{\partial\lambda}{\partial a_{ij}} = \frac{\partial \ln\lambda}{\partial \ln a_{ij}} \quad .$$

Information on sensitivities and elasticities can be very important in the allocation of effort in field studies and in the design of management plans for threatened and endangered species (see Mertz 1971, Nichols et al. 1980, and Noon and Biles 1990 for examples).

Interval estimates of λ

Estimates of the sampling error of λ are needed for assessing the confidence of growth projections and for tests of hypotheses. For example, test of the H_0: $\lambda \geq 1.0$ is relevant to species whose populations are believed to be declining. The sampling variance of λ can be approximated by (Laude 1988:206):

$$\sigma_\lambda^2 = \sum_i (\partial\lambda/\partial a_{ij})^2 \sigma_{ij}^2 \qquad (17)$$

where σ_{ij}^2 = Var(a_{ij}). Variance of the survival rates can be made by assuming a binomial sampling distribution $\sigma_i^2 = p_i(1- p_i)$) or, if estimated from banding data, by the methods of Jolly (1965) and Seber (1965, 1982). The variance in the m_x values can be based, for example, on the variance in clutch size among known-age females.

Equation (17) neglects possible covariances among the demographic parameters and fails to account for between-year changes in the vital rates. Between-year changes, estimated by factoring out the temporal component of variation from the total variance estimates of the vital rates and λ, can be estimated by a components of variance analysis (Burnham et al. 1987:22-25; 260-275).

ESTIMATION OF MODEL PARAMETERS

The crucial link between model structure and the actual population is the estimation of transition elements (a_{ij}'s). Estimates of survival and productivity provide information on the structure of a population model. Assessing age-specificity of estimates allows evaluation of the need for distinct age classes. Time specificity of estimates indicates a need for higher-level structure in the model such as density dependence. Finally, environmental effects on survival and fecundity can be modelled. Previous perspectives on model structures and demographic parameters have been muddled by use of inappropriate estimators. Development of innovative new statistical methods for both estimating parameters and assessing environmental effects on parameters should allow us to implement appropriate models for passerine birds. Because several recent reviews on estimating demographic parameters (Lebreton et al. 1990) have provided more detail on specific examples than space permits here, we will only briefly summarize the status of knowledge on estimating parameters.

Local or large scale estimates?

Demographic studies can be based upon estimates from either local populations or from results of large-scale surveys. Large scale data sets such as surveys or banding data often provide data too diffuse for site specific analysis. Investigators have only the option of fitting simple models to composite data sets. There are many potential flaws associated with this approach, because spatial and temporal heterogeneity can not be

appropriately assessed and incorporated using sparse data sets.

Estimating survival rates in passerines

All reliable methods of estimating survival rates involve the use of marked birds. Nichols et al. (1981) reviewed many of the existing passerine studies as of 1980, and presented original analyses of several data sets. Although surprisingly few additional studies have been published since Nichols et al. (1981), several recent works (e.g., Lebreton and Clobert 1991, Pollock et al. 1990, Lebreton et al. *in press*), are leading to a unified theory of estimating survival rates in time and space, and evaluating associations between survival rates and environmental covariables. Here we discuss some of the problems in survival estimation and recent applications relevant to passerines. See Clobert and Lebreton (1991) for a detailed review of estimation of bird demographic parameters.

Estimation of survival from recoveries of banded birds.-- A series of simple models (e.g., Hickey 1952, Haldane 1955) have been used to estimate survival rates for passerines (e.g., Henny 1972, Dobson 1990). Building on a model developed by Seber (1982), Brownie et al. (1985) and others (White 1983, Conroy and Williams 1986) have developed a sophisticated series of models for band-recovery analyses, which are commonly used for analysis of waterfowl and other harvested species (e.g., Chu and Hestbeck 1986). The basic assumption of no time-specificity of the simple models has been convincingly rejected for waterfowl (Burnham and Anderson 1979). Unfortunately for passerine banding studies, the very low recovery rates inherent in nongame birds make it impractical to fit all except the simplest of the Brownie et al. (1985) models, which is similar to the Haldane (1955) model. Fitting this model has risks, as it is unlikely that passerines have constant survival rates and many banded samples must be combined for analysis, which likely causes heterogeneity (e.g., Clobert and Lebreton 1991). Because of these potential difficulties, band recovery data have not recently been used to estimate survival rates of North American passerine birds.

Estimation of survival from mark-recapture and mark-resighting.-- Use of recapture or resighting data from marked birds provides the only reasonable framework for estimating time and age-specific survival in passerine birds. Burnham et al. (1987), Clobert et al. (1987b), Pollock et al. (1990), and Lebreton et al. (1991) discuss the appropriate modelling structure for mark-recapture models, and how to incorporate environmental covariates into those analyses. Although few studies have as yet made use of procedures for evaluating time and age-specificity in the Jolly-Seber models, analyses have been conducted for great tits (*Parus major,* Clobert et al. 1988), black-capped chickadees (*Parus atricapillus,* Loery and Nichols 1985, Loery et al. 1987), and European starling (*Sturnus vulgarus,* Clobert et al. 1987a, Stromborg et al. 1988, Krementz et al. 1989).

Estimation of seasonal or period-specific survival.-- It is possible to use mark-recapture methods to estimate survival of young birds from fledging to periods later in the summer, although most such studies have been experimental manipulations of cavity-nesting birds (e.g., Krementz et al. 1989, Fauth et al. 1991). Because of the interest in Neotropical migrant birds, there has been increased interest in experimental designs that evaluate seasonal survival on breeding and wintering grounds, although only

a few investigators have actually applied the analysis to wintering areas (e.g., Karr et al. 1990).

Estimation of survival from telemetry studies.-- Radio-tagging can be used to estimate interval survival rates of local populations. Although telemetry has been used extensively to estimate survival rates of larger birds (Bunck 1987), the technology has only recently advanced to the extent that passerines can be reliably radio-tagged. One crucial assumption in analysis of radio-tagged animals is that tagging does not affect animal behavior or survival. Transmitter-related mortality has caused the premature termination of at least one passerine study (D. G. Krementz, *personal communication*). White and Garrott (1990) review statistical methodologies for survival estimation from radio-tagged birds, and discuss experimental designs for evaluating the effects of transmitters on bird survival.

Estimates of first year survival.-- For many bird species, estimation of first year survival rate (p_0) by any of the above methods is difficult or impossible because many species are not philopatric to their natal area. As a consequence, first year survival estimates from banded nestlings, for example, are confounded with permanent emigration from the study area. Estimates based on a subsequent year recovery or recapture of birds banded before dispersal from their natal area, but which show limited philopatry, will be negatively biased. Even the use of telemetry methods for annual estimates is limited for many species because of long-distance migration sometime during the annual cycle. Given these problems, we suggest that indirect estimates may be appropriate in some cases. For example, given an independent estimate of λ (i.e., from census or survey data) in combination with estimates of the other vital rates, p_0 can be computed directly from the characteristic equation (e.g., equations 10 and 11). Unfortunately, no estimate of the precision of p_0 is possible.

Estimation of fecundity elements

Estimation of proportion of females breeding.-- The estimate of fecundity combines two important components: the number of females fledged per nest and the proportion of breeding aged females that breed. The latter parameter is generally assumed to equal 1.0 for adult birds, although that is clearly not true for at least some species (e.g., scrub jays *Aphelocoma coerulescens,* Woolfenden and Fitzpatrick 1984). Although not yet applied to passerine birds, Lebreton et al. (1990) have described a method of estimating age-specific breeding probabilities in which the proportions of individuals in each age class are estimated and compared to observed age proportions of breeding birds to determine proportion of breeding females. In any case, determining the proportion of females breeding requires intensive studies of local populations.

Estimation of clutch size.-- An enormous amount of data exist in the Cornell University Nest Record Card Program on average sizes of clutches, and similar programs exist in other countries (Temple and Wiens 1989). Consequently, information on average clutch sizes are readily available for many species. Unfortunately, extensive data sets provide no information on variation in clutch size in association with population density or other demographic characteristics.

Estimating nest success in passerines.-- The Mayfield method (Mayfield 1961, 1975) is a well known procedure for estimating nest success in passerines, and models

which provide statistically reliable estimates have been developed (Johnson 1979, Hensler and Nichols 1982, Hensler 1986, Bart and Robson 1982). Although there have not yet been sufficient applications to allow a true comparative study of regional variation in nest success, nest survival rates are presently the subject of extensive studies as a consequence of hypothesized predation and parasitism risks in relation to habitats selected for nests (e.g., Martin and Roper 1988). At this time, however, relatively few applications of the Mayfield method have been published for passerines.

Higher-level relationships among parameters

Given the crucial importance of density dependence in life history theory and demography, it is astonishing that no compelling demonstrations of the phenomena have ever been published for passerines. Most of the literature on density dependence of primary demographic characteristics involves key factor analysis (e.g., Stenning et al. 1988, Moller 1989), which has been questioned on statistical grounds (Kuno 1974). An alternative approach, that of detecting density dependence from a series of sequential surveys, is also of questionable validity (Barker and Sauer, *this volume).* Consequently, little guidance exists from experimental literature on proper incorporation of density dependence into population models. It is a challenge for passerine biologists to design experiments to detect density dependence.

A BRIEF EXAMPLE

In the following we illustrate a sensitivity analysis of the life histories of two species based on quantitative information (Table 3). Estimates of adult ($x \geq 1$ yr) survival rate and ages at first and last reproduction were available for both the red-eyed vireo (*Vireo olivaceous*) and the wood thrush (*Hylocichla mustelina*) from a 13-year (1959-71) capture-recapture study conducted in Maryland (C. Robbins, *unpublished data).* Survival rate estimates were based on the methods of Jolly (1965) and Seber (1982:200) using program JOLLY (Pollock et al. 1990). Estimates of mean clutch size, number of broods, length of the incubation and fledging periods, and daily nest survival rates were provided from the Cornell University Nest Record Program. Estimates of the daily nest survival rate were based on the methods of Bart and Robson (1982). Because neither species is philopatric to its natal area, survival from fledging to age 1 yr (p_0) could not be estimated from empirical data. Rather, we assumed a stable population ($\lambda = 1.0$) based on census data, and estimated p_0 indirectly based on the other parameter estimates (Table 3) and equation (6). Fecundity (m) was estimated by $m = (c)(n_c)(r)(dsr)^{l_i + l_f}$.

Both for the design of field studies and to gain insights into effective species management, it is important to know how variation in individual aspects of a species' life history affect its rate of population change (λ). These insights are provided by the elasticities of λ, the dominant eigenvalue of the species' projection matrix (Table 3). Often, a better understanding of eigenvalue sensitivities is gained from a graphical representation. For both age- and stage-structured models for the red-eyed vireo and the

TABLE 3. Parameter values used in the demographic analysis of red-eyed vireo (REVI) and wood thrush (WOTH) life histories. History data from C. Robbins (*unpublished data*) and the Cornell University Nest Record Program.

Parameter	VALUE REVI	VALUE WOTH	Label
Age at first breeding	1 yr	1 yr	α
Reproductive senescence	6 yr	6 yr	w
Adult survival	0.575	0.422	p
Post-fledging survival	0.281	0.324	p_0
Fecundity	1.52	1.79	m
mean clutch size	4.0	4.0	c
mean no. clutches	2	2	n_c
sex ratio	1:1	1:1	r
daily nest survival	0.96029	0.96686	dsr
incubation period	13 days	12 days	l_i
fledging period	11 days	12 days	l_f

Stage projection matrix

$$\begin{bmatrix} p_0 m & pm \\ p_0 & p \end{bmatrix} \quad \begin{bmatrix} 0.427 & 0.874 \\ 0.281 & 0.575 \end{bmatrix}_{\text{REVI}} \quad \begin{bmatrix} 0.580 & 0.755 \\ 0.324 & 0.422 \end{bmatrix}_{\text{WOTH}}$$

wood thrush, and based on solutions to equation (7), we computed the decline in λ given proportional declines in the vital rates considered individually (Figs. 4 and 5). For the age-structured models, we introduced reproductive senescence at age w and relaxed the assumption that $\lambda > p$ (see Meyer and Boyce *in press*). The slope of the curves in Figs. 4 and 5 indicate the sensitivity of λ. to a proportional decline in the given parameter.

The red-eyed vireo showed greater sensitivity to declines in adult survival (p) than to fecundity (m) or first-year survival (p_0) for the stage-structured model (Fig. 4a). In contrast, the species showed almost identical sensitivities to parameter reduction for the age-structured model (Fig. 4b). The wood thrush consistently showed greater sensitivity to variation in first-year survivorship (p_0) or fecundity (m) (Figs. 5a and 5b). The wood thrush result is consistent with the general principle that short-lived, small-bodied bird species show greater sensitivity to variation in fecundity and pre-reproductive survival than long-lived birds species which are more sensitive to variation in adult survival (Emlen and Pikitch 1989). Using the wood thrush as an example, these results suggest that management actions which affect first year survival (p_0) or fecundity (m) are of more

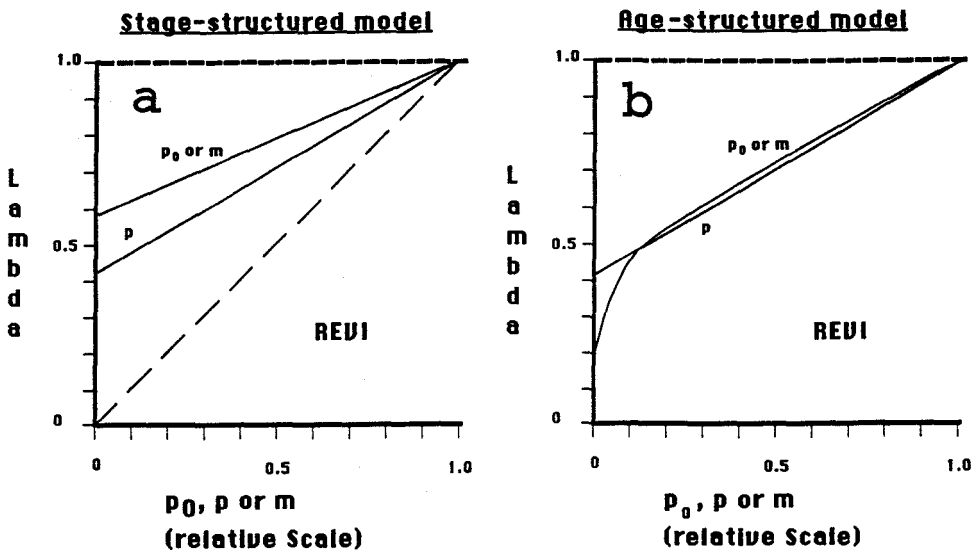


Fig. 4. Population growth rate (λ) for a stage-structured model (a) and (b) an age-structured model of the red-eyed vireo (*Vireo olivaceous*). 1.0 on the abscissa represents the empirical mean of survivorship or fecundity.

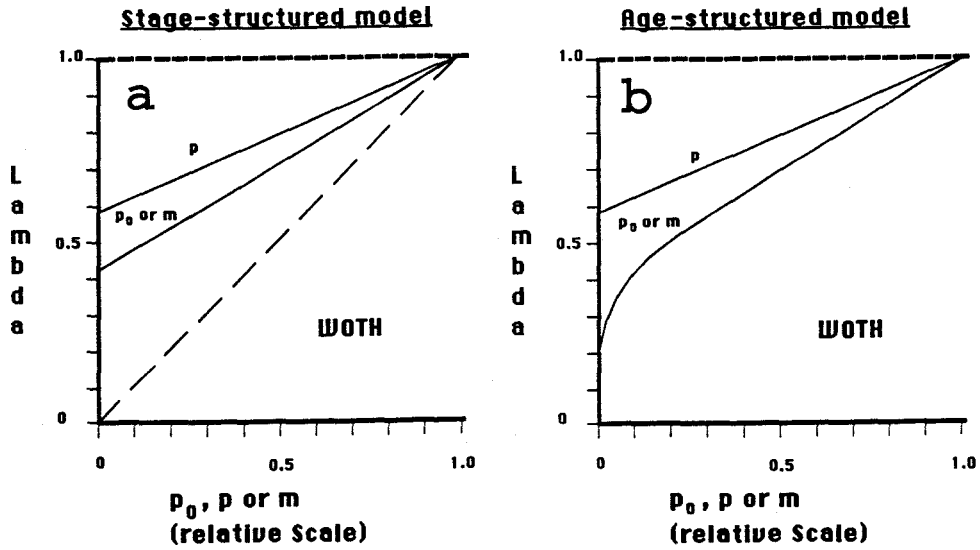


Fig. 5. Population growth rate (λ) for a stage-structured model (a) and (b) an ages-tructured model of the wood thrush (*Hylocichla mustelina*). 1.0 on the abscissa represents the empirical mean of survivorship or fecundity.

immediate concern than those which affect adult survival (*p*). Further, when designing field studies, perhaps greater effort should be allocated to achieving precise estimates of m and of sources of variability in *m*. There are, however, important limits to inferences from these analyses. They incorporate no information on the annual variability in parameter values and it may be that variation in λ is more closely associated with the vital rate(s) that shows the most natural variation.

CONCLUSIONS

Despite the useful insights provided by quantitative analyses of the life histories of passerine and other small-bodied birds, such analyses are seldom conducted. This is unfortunate since the life history structures of these species are amenable to analysis using simple mathematical models. Model parameterization, that is, estimating the birth and death rates, requires a formidable field effort, but information on appropriate study design, data to be collected, and statistical models to provide reliable parameter estimates are widely available. Analyses of the resulting mathematical models provide useful insights to guide management decisions and to aid conservation planning efforts.

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