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Bias in population growth rate estimation: sparse data, partial life cycle analysis and Jensen's inequality

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Demographic matrix models have become an integral part of population viability analysis for threatened and endangered species, but their use is often limited by data availability. A common solution to this problem is to assume constant annual rates within a multi-year stage. Partial life cycle analysis (PLC), which incorporates only juvenile and adult stages, is a noteworthy example of this approach because it has been described in the literature as a reliable approximation of age-structured populations. However, we predict from Jensen's Inequality that the required lumping of age classes leads to over- or underestimation of population fitness when survival rates are truly age-dependent. We illuminate this problem by comparing fitness estimates from Leslie matrix and PLC models for theoretical populations having different levels of age-dependence in their survival rates. We also propose a modification of the PLC approach to address this problem and demonstrate its applicability using data from a published long-term study of red deer *Cervus elephas*.

Demographic population models are widely applied in species conservation (Beissinger and Westphal 1998, Caswell 2001, Morris and Doak 2002), but their use and validity are often limited by difficulties in estimating stage- or age-specific vital rates for demographic classes (Ludwig 1999, Ellner et al. 2002, Doak et al. 2005). In the case of survival, a common solution is to estimate a single annual rate for a multi-year juvenile or adult stage, followed by repetition of this single estimate at multiple parameter locations (Powell et al. 1996, Gerber et al. 2004, Garshelis et al. 2005). However, because of Jensen's inequality (Ross 1994), the underlying assumption of constant survival can cause significant bias in population growth rate estimation.

Partial life cycle analysis (PLC; Oli and Zinner 2001a, 2001b, Oli 2003a, Oli and Armitage 2004) is one approach that makes the constant survival assumption explicit. Whereas most demographic models require age-specific estimates of survival and fecundity, partial life cycle models generally require such estimates for only two stages (juveniles and adults). In such a two-stage presentation, the simplicity of available data is immediately apparent. However, from analyses presented in this paper, we determine that partial life cycle models have a predictable bias when the constant survival assumption is violated.

Oli (2003b) recently reported strong agreement between estimates of population growth rate (λ) from Leslie matrix models (λ_L) and their partial life cycle model equivalents (λ_{PLC}) for 142 mammal populations. This result has important implications for conservation. Essentially, Oli

took the Leslie model as a 'full' model, reduced it to a PLC form, and then evaluated the reduced model's ability to retrieve the same growth rate estimate as the full model. However, we predict that concordance between the two models is limited to cases where constant survival is already present in the full model against which the PLC is compared. Based on Jensen's inequality, we predict less concordance in cases where the full model contains heterogeneous survival rates. We suspect these problems may be hard to detect in analyses involving single classes of animals such as in Oli's study of mammals. Since there is an expectation that life history strategies are conserved within phylogenies (Stearns 1992), and because mammalian survival schedules may differ from those of other classes (Caughley 1966), they may not be representative. Also, numerous mammalian species are relatively long-lived, meaning that untested assumptions of constant mortality in upper age classes are likely to be more commonly used given the practical limitations of long-term demographic studies. For reasons we will now describe, this presents challenges for generalizing from the mammal populations used in Oli's analysis (Oli 2003b).

The full Leslie matrix models in Oli's analysis were taken directly from the literature or derived from published and occasionally sparse life table data. The method of reducing these matrices to the PLC involves the use of weighted averages for both juvenile and adult stages (Oli and Zinner 2001a). For example, juvenile survival (P_j) in the PLC was taken as the mean of survival rates for all pre-reproductive

age classes, each of which being weighted by its corresponding contribution to the stable age distribution (i.e. the dominant right eigenvector of the Leslie matrix). Growth rate (λ) is then taken as the dominant right eigenvalue (λ_1) of the matrix.

In a Leslie matrix model with $\alpha - 1$ pre-reproductive stages (α = age at maturity), the probability that a stage one individual reaches reproductive age is a product of $\alpha - 1$ survival probabilities that may or may not differ from one another, depending on the life history strategy approximated by the model (e.g. type I, II or III survivorship; Deevey 1947). In a partial life cycle model, survivorship to reproductive age (l_α) is implicitly a product of $\alpha - 1$ identical probabilities. More formally, the following relationship is assumed:

$$l_\alpha = \prod_{i=1}^{\alpha-1} P_i \approx E(P_j)^{\alpha-1} \quad (1)$$

where l_i is survival to age i , P_i is survival of an individual of age i to age $i + 1$ and P_j is survival of any juvenile of age $< \alpha$ for one time step (hereafter we refer to P_x as survival and l_x as survivorship). Since the method of estimating P_j for the PLC is a weighted average, Eq. 1 implies equality between a geometric and arithmetic expectation (E ; the effect of weighting is discussed in a later section). Geometric and arithmetic means are equivalent only when there is zero variance. Thus, concordance between PLC and Leslie models should be greatest when the aggregate survival rates in the PLC (i.e. P_j and P_A) are estimated from a Leslie matrix with constant survival within each of the juvenile and adult classes. In other words, the manner in which PLC models are derived suggests they may be most appropriate when survivorship is well described by a type II survivorship function (i.e. with constant probability p_x of surviving from age x to $x + 1$). Similarly, agreement between λ_L and λ_{PLC} would exist when data gaps in the underlying life table are addressed by assuming constant survival, whether or not such an assumption is defensible. If survival is not constant, there may be considerable disagreement between the geometric and arithmetic mean, and thus between λ_L and λ_{PLC} . This disagreement is predicted by Jensen's inequality (Ross 1994) which, as discussed below, states that the inequality between the expectation of a function and the function of the expectation depends on the heterogeneity of the terms over which the function is taken (P_1, P_2 , etc.). We would expect effects of incorrect assumptions about adult survivorship on λ to be similarly complicated by the presence of age dependence in fecundity schedules. Here, we ignore this complexity by focusing on the shape of the overall survivorship schedule.

We sought to build upon Oli's analysis (Oli 2003b) by examining the influence of a range of survivorship functions on the performance of PLC models. Following Oli's approach, we assessed model agreement by comparing λ_{PLC} and λ_L . We first discuss expectations under a simple deterministic setting and then examine ways in which estimation of λ may be affected by interactions between parameter heterogeneity (e.g. $P_1 \neq P_2 \neq P_3$, etc.), stochastic parameter variation, and the parameter averaging steps implied by the PLC. Our analyses are based primarily on simulated matrix models constructed from theoretical life

histories, but we also use data for the red deer, *Cervus elephas*, (Benton et al. 1995) to obtain additional insights into the construction of partial life cycle models from real data.

Methods

Constructing the models

In order to explore effects of theoretical life history variation on partial life cycle analyses, we used the matrix form of the partial life cycle model (Oli and Zinner 2001a), denoted with the PLC subscript:

$$n_{t+1} = A_{PLC} \times n_t$$

$$A_{PLC} = \begin{bmatrix} & & F_A & \cdots & F_A \\ P_j & & & & \\ & \ddots & & & \\ & & P_j & & \\ & & & P_A & \\ & & & & \ddots \\ & & & & & P_A \end{bmatrix} \quad (2)$$

λ_{PLC} = dominant eigenvalue of A_{PLC}

where n_t is the population vector at time t . Construction of this model requires estimates of F_A , P_j , and P_A . Also required are age at maturity (α) and longevity (ω), which are implicit in the structure of the matrix model. Note that in the PLC, P_j is equivalent to the α th root of survival to age at maturity (l_α). The structurally equivalent Leslie matrix has identical dimensions and identical α and ω , but has age specific estimates of survival. Our analyses were limited to 5×5 matrices ($\omega = 5$) and do not incorporate age-structured fecundity. Thus,

$$n_{t+1} = A_L \times n_t$$

$$A_L = \begin{bmatrix} & & & & F_A & \cdots & F_A \\ & & & & & & \\ & & P_1 & & & & \\ & & & \ddots & & & \\ & & & & P_{\alpha-1} & & \\ & & & & & P_\alpha & \\ & & & & & & \ddots \\ & & & & & & & P_{\omega-1} \end{bmatrix} \quad (3)$$

λ_L = dominant eigenvalue of A_L

Our first analysis used a Weibull function (Johnson and Kotz 1970) to generate the survivorship curves for the survival parameters $P_1, \dots, P_{\omega-1}$ in Eq. 3. The Weibull function took the following form:

$$l_x = \exp[-(ax)^b] \quad (4)$$

where l_x is the probability of survival to age x and a and b are fixed parameters. b governs the sign and magnitude of the second derivative of the l_x survivorship curve. If $b > 1$, a decelerating (type I) curve is produced; if $b < 1$, an accelerating (type III) curve is produced. Constant survival (type II; linear l_x) is produced when $b = 1$.

To control for the known sensitivity of partial life cycle models to age at maturity (Cole 1954, Slade et al. 1998), we produced survivorship curves with identical l_α always equal to 0.35 but varying acceleration. This was done by solving

Eq. 4 for a using a fixed value of l_α and varying values of b:

$$a = \exp\left(\frac{\ln(-\ln l_\alpha)}{b}\right) / \alpha \quad 0.05 \leq b < 2 \quad (5)$$

The range of synthetic survival curve shapes used in our analysis was based in part on analysis of 55 haphazardly selected life histories (i.e. those most easily found in the open literature) from the 142 mammal populations used in Oli (2003b). In this subset, the shape parameter ranged from $b=0.3$ to $b>2$. We included smaller values in our analysis to accommodate populations with high mortality in the first life stage (e.g. for curves with $l_\alpha=0.35$, 60% mortality in the first age class and <7% thereafter, b was less than 0.1).

We converted the resulting survivorships to conditional survival rates ($P_x = l_x/l_{x-1}$). Thus, a unique set of P_x was generated for each b and inserted into Eq. 6 (below). In all models, we set l_α equal to 0.35, which would be roughly equivalent to two ($\alpha - 1$) pre-reproductive stage transitions with $P_x=0.6$. Next, we created partial life cycle approximations (Eq. 2) of these Leslie matrix models using the techniques of Oli and Zinner (2001a). We computed and compared λ_{PLC} and λ_L for each theoretical life history strategy as represented by b . All matrices had the following form with identical dimension and fecundity:

$$A = \begin{bmatrix} 0 & 0 & 2 & 2 & 2 \\ P_1 & 0 & 0 & 0 & 0 \\ 0 & P_2 & 0 & 0 & 0 \\ 0 & 0 & P_3 & 0 & 0 \\ 0 & 0 & 0 & P_4 & 0 \end{bmatrix} \quad (6)$$

Stochastic effects

We used computer-simulated time series to examine expected relationships between life history formulation (i.e. acceleration in the survivorship curve) and stochasticity on PLC and Leslie matrix estimation of population growth rate (λ).

Generation of pseudodata

We produced 20 time steps of computer-simulated demographic data (P_1, P_2, P_3 and P_4) for each of the different theoretical life histories described for the deterministic analyses (F_3, F_4 and F_5 were held constant at 2). We added variation to these life histories by replacing the P_x s with random variates drawn from beta distributions (Morris and Doak 2002) having P_x as their means and 95% confidence interval widths (upper+lower) equivalent to about 2% and 8% of the mean ('low' and 'high' variation). The upper bounds of the variance used in the generation of the pseudodata was dictated by the upper limit of the variance that could be simulated using a beta distribution given $l_\alpha = 0.35$. We conducted simulations with and without 40% correlation between age-specific survival rates within years (Morris and Doak 2002) but report only those without correlation due to similarity of the results. The simulations were initialized using the right eigenvector of the average projection matrix (i.e. the stable age distribution). After an initial 'burn-in' period of 30 time steps, the 20 time steps of

pseudodata were then separated into 'estimation' ($t=21-30$) and 'testing' periods ($t=31-40$).

Construction of new beta distribution functions

We used means and variances derived from the estimation period in the pseudodata to construct beta distributions for P_1, P_2, P_3 and P_4 . This step is intended to mimic the approach often seen in PVA, where multiple years of demographic data are used to inform prospective vital rate simulations. For the PLC projections, we first constructed Leslie matrices for each time step in the pseudodata, converted these to PLC matrices using the technique of Oli and Zinner (2001a), and then used the means and variances of the resulting survival parameters (P_J and P_A) to construct beta distributions.

Stochastic projections

To mimic the next step in PVA, we constructed stochastic population projections using matrices constructed from the estimation period. The initial population vectors were constructed in the same manner as the pseudodata and were projected forward 50 000 time steps. At each time step, we recorded total population size (N) and substituted new PLC or Leslie survival rates drawn from the beta distributions into the projection matrix.

Estimation of stochastic growth rates

We estimated stochastic population growth rate from population sizes using the following equation (Caswell 2001, sect. 14.3.6):

$$\log \hat{\lambda}_s = \frac{1}{T} \sum_{t=0}^{T-1} \log(N_{t+1}/N_t) \quad (7)$$

We repeated steps 1 through 4 one thousand times for each theoretical life history and compared the predicted growth rates of each of the two methods to the 'observed' change in population size in the pseudodata.

Red deer

We used data from a long-term pre-breeding study of the red deer (Benton et al. 1995) to analyze the difference in predicted population growth rates using the stochastic PLC and full-matrix approaches. As in the previous analyses, the fecundity for each of the age or stage-classes was set to the mean fecundity value for the red deer (Benton et al. 1995). For the full matrix approach, each survival rate was drawn from a beta distribution with the means and variances given in Benton et al. (1995). Variance for age class 18 was too high for proper construction of a beta distribution (Morris and Doak 2002) and was therefore taken as half the reported value. Mean juvenile and adult survival along with their variances for the PLC approach were calculated by bootstrapping 5000 values from the mean and variances of the known probability of surviving from age i to $i+1$ (Benton et al. 1995). For each bootstrap, a set of survival values was drawn and reweighted by the right eigenvector. The reweighted values were then averaged according to the age at first reproduction assuming a pre-breeding census

(Oli and Zinner 2001b). The stochastic simulation was initialized using the stable age distribution of the average projection matrix. We ran the simulation for 50 000 iterations and calculated the stochastic population growth rate using Eq. 7 and constructed 95% confidence intervals according to Caswell (2001, sect. 14.3.6).

Results

Deterministic comparisons supported our expectation that growth rates estimated using PLC (λ_{PLC}) would equal those for the Leslie matrix (λ_{L}) when $b=1$ (type II) and revealed greater differences between the two models for type III than for type I curves (Fig. 1). Differences in sensitivities, defined as the change in population growth due to changes in matrix elements (Caswell 1978, 2001), between the two models were weakly related to b (i.e.

$$\partial\lambda_{\text{PLC}}/\partial P_j - \sum_i^{\alpha-1} \partial\lambda_{\text{L}}/\partial P_i < 0.02 \text{ for all } b).$$

Results of the stochastic simulations followed a similar pattern (Fig. 2). Under the ‘low’ variance stochastic scenario, PLC analysis of type I life histories consistently overestimated the true population growth rate (defined here as λ_{L}), whereas for type III curves, PLC analysis consistently underestimated the true rate (Fig. 2a). For type II, all approaches predicted similar growth rates. The full-matrix approach was able to correctly predict true population growth rate.

When we increased the amount of variance, the differences between the PLC estimates and the true population growth rate decreased and were often within the confidence bands of the true estimates (Fig. 2b) for both type I and III life histories. For type III life-history curves, the PLC approach performed more poorly than under type I. This was due to the limitations of drawing survival values at the upper bounds of the variance from a beta distribu-

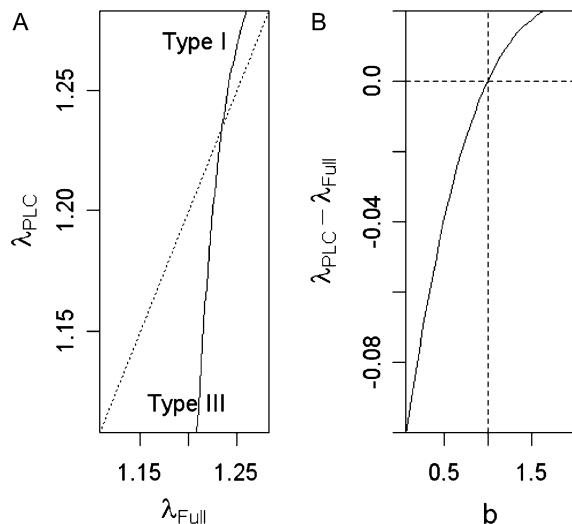


Figure 1. Comparison of population growth rate (λ) for the PLC and the full-matrix approach (A) and the impact of the shape parameter (b) of the Weibull function on the difference between PLC estimates and full matrix estimates. The diagonal line in (A) is the one to one line. The dashed vertical line in (B) corresponds to a type-II life history.

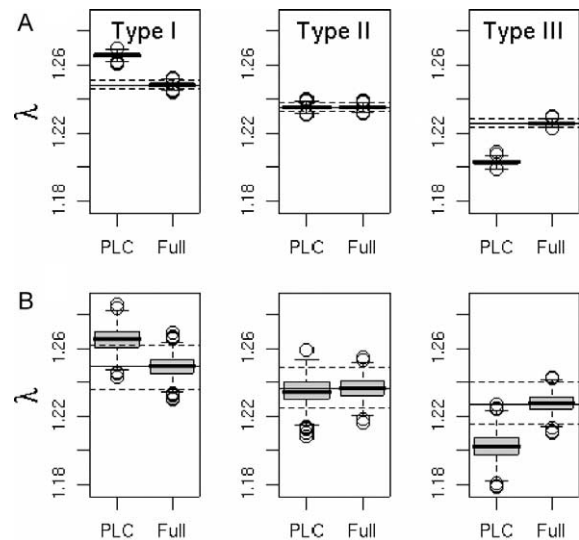


Figure 2. Box-plot comparisons of the partial-life cycle (PLC) approach and a full-matrix approach by calculating the stochastic population growth rate for both the low (A) and high (B) variance scenarios. The solid line represents the ‘true’ median population growth rate and the dashed lines represent the 95% CI.

tion, which led to a number of the survival rates having to be redrawn. With increased stochasticity, the full-matrix approach routinely estimated true population growth rates across all life histories.

For the Scottish Isles red deer data of Benton et al. (1995), we obtained growth rate estimates of $\lambda = 1.068 \pm 0.05$ (95% confidence interval) with the full matrix and $\lambda = 1.048 \pm 0.05$ using the PLC method.

Discussion

One of the strengths of PLC is that the form of the characteristic equation allows exploration of model sensitivity to parameters not appearing in Leslie models (i.e. age at maturity and lifespan; Oli and Zinner 2001a). In fact, partial life cycle models are rooted in life history analysis of effects of age at maturity on individual fitness (Cole 1954, Stearns and Crandall 1984). This may explain the slow uptake by conservation biologists since maturation rate is not perceived as a flexible trait that is sensitive to human activity (but see Olsen et al. 2004). Nonetheless, partial life cycle models require less data than demographic population viability analysis (PVA) and may allow fuller use of available data than do non-structured population models (Dennis et al. 1991, Brook et al. 2006).

Overall, the PLC method performed just as well as the full matrix approach when a type II life history was used to generate the simulated populations. If there was little or no stochasticity in the system, the method consistently overestimated population growth rates for type I life histories and underestimated for type III life histories. As might be expected, the wider confidence intervals for the true growth rate under higher stochasticity made the two methods less distinguishable in terms of estimation accuracy.

As anticipated due to Jensen's inequality (Ross 1994), for the deterministic and stochastic computations, the PLC approach, in general, consistently overestimated type I life-history and underestimated type III life-history population growth rates. For a type I life-history, the survivorship curve (l_x) is concave down ($b > 1$ in Eq. 4). Therefore, the curve associated with the probability of surviving from age class i to $i + 1$ is concave up. The opposite is true for a type III life-history curve ($b < 1$). Due to Jensen's inequality, the greater the concavity of the curve over which the average is taken, the greater the overestimation or underestimation of population growth. For a type I life-history, Jensen's inequality takes the form of:

$$f(E[X]) \geq E[f(X)] \quad (8)$$

which states that the function of the expectation is greater than the expectation of the function. Thus, growth rate will be consistently overestimated by the PLC model for type I life histories since the product of the probability of survival used in constructing the PLC matrix model will be greater than the product of probability of survival used in constructing a matrix with varying survival probabilities for each age class. The juvenile survival rate (P_j) used in constructing the PLC matrix for type I is always larger than the corresponding average of the age-based matrix parameters (P_x), so that $P_j^n > \prod_{x=1}^n P_x$. The opposite is true for a type III life history, whereas for type II life histories, the expectation is equal to the function of the expectation because the curve associated with the probability of surviving from age class to age class is constant. In our stochastic simulations, this curvature was blurred by variability, so the effects of Jensen's inequality were less obvious.

The relationships between P_j^n and $\prod_{x=1}^n P_x$ are not as simple as Eq. 1 and 8 would suggest because the P_x s used to compute P_j (and P_A) are weighted by the elements of the stable age distribution (w_x). However, from Eq. 4.66 in Caswell (2001) we can derive the relationship $w_x \propto \frac{l_x}{\lambda^{x-1}}$,

the denominator of which increases with age (x) when $\lambda > 1$. This results in higher weights for rates in the early life stages and therefore worsens the survival (and growth rate) overestimation for type I and the underestimation for type III. When $\lambda < 1$, the sign of the inequality in Eq. 8 is unchanged but the magnitude of bias is reduced rather than worsened because λ^{x-1} decreases with x (Fig. 4).

The PLC approach presents a useful method for taking advantage of limited data. The sizes of bias we report will in some cases be insignificant given the stochastic processes and observation errors inherent to contemporary applications of PVA, especially for data-poor analyses (Fieberg and Ellner 2000). One solution to this uncertainty, at least for count-based models, has been to estimate relative risk among multiple species or populations (Elder et al. 2003). However, in PLC applications, relative risk will still be sensitive to bias if, as we show, the direction and magnitude of that bias differs across life histories or between declining vs increasing populations (Fig. 4).

Although we highlight limitations of the PLC approach, further analysis of our simulated populations based on Jensen's inequality show that slight modifications of the

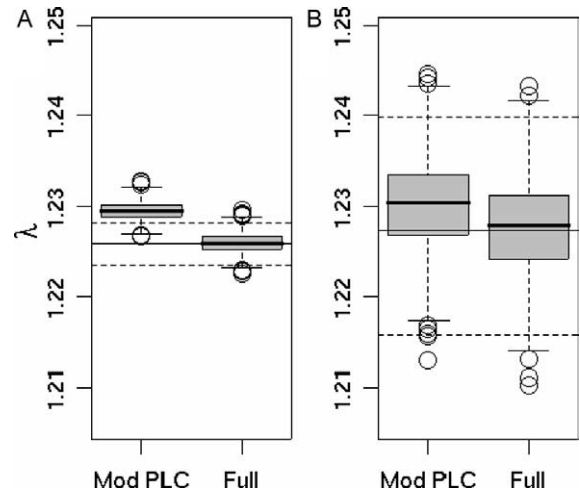


Figure 3. Box-plot comparisons of the modified estimates of a partial-life cycle (PLC) approach for a type-III life history and a full-matrix analysis using stochastic approaches for both the low (A) and high (B) variance scenarios. The solid line represents the 'true' median population growth rate and the dashed lines represent the 95% CI.

PLC approach can provide reasonable estimates of population growth rate (λ) for type I and type III life histories. For instance, for type III life histories, it may be useful to estimate survival for the first age class and average across all other age classes even though the subsequent age classes may be pre-breeding (i.e. age less than α). This avoids averaging over the steep part of the survivorship curve and thereby should reduce effects of Jensen's inequality. When we did this with our type III simulated populations, averaging across all but the first age class, the PLC method was

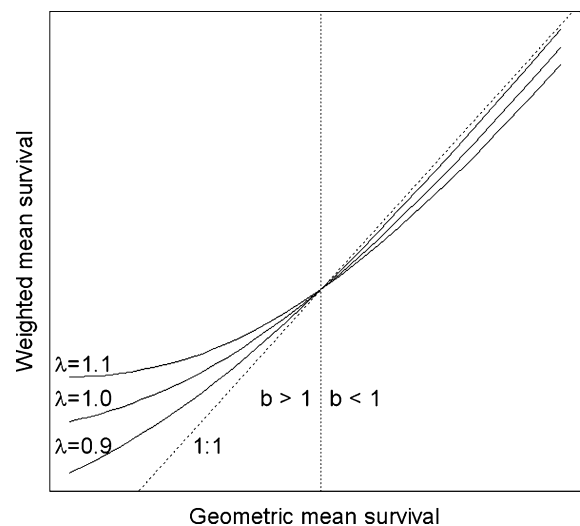


Figure 4. Relationship between the geometric mean of age-specific survival rates and the aggregated survival rates for the partial life cycle model under varying acceleration (b) in the survival curve. Three growth rate scenarios are shown. The magnitude but not the sign of the bias is affected by growth rate (λ) because the weights (w_x) used in aggregation are proportional to l_x/λ^{x-1} .

improved (Fig. 3; note, however, this eliminates α , and sensitivity thereto, as an index of age at maturity). Similarly, averaging across the first three classes and separately estimating survival for the final class may be appropriate for type I life histories.

For the red deer, the data suggest that a priori knowledge about life-history may also allow construction of a more realistic PLC model. We used the modified approach outlined above to reanalyze the red deer pre-breeding census data (Benton et al. 1995) and obtained growth rate estimates ($\lambda = 1.052 \pm 0.04$ 95% CI) much closer to those of the full matrix ($\lambda = 1.068 \pm 0.05$; 95% CI) than with the PLC method ($\lambda = 1.048 \pm 0.05$; 95% CI). In this analysis, we used the point on the curve where the slope changed signs. This was calculated by a non-linear regression on the probability of survival, to break the red deer's life-history into two classes.

Our modification of the PLC for the red deer was enabled by an ample supply of survivorship data. In an analogous approach, DelGiudice et al. (2006) used hazard functions to identify breaks for pooling survival data and showed reduced bias when these informed breaks were incorporated into population growth rate estimation. When age-specific survival data are scarce, finding appropriate change points will be more difficult. However, change points based solely on a reasonable set of a priori life history assumptions such as those used in the modified theoretical approach above should still provide improvements over the current practice of dividing the survivorship curve at α .

In conclusion, we note that conversion of Leslie models into the PLC is not likely to be a common practice in population modeling simply because it is unnecessary if the Leslie matrix is complete. However, we scrutinized conversion methods using weighted averaging of survival rates because they form the basis for confidence in the PLC approach when data are too scarce for Leslie models (Oli 2003b). We found that for type-II survivorship curves, the PLC approach works well. However, the PLC can drastically over- or under-estimate population growth rates for species that exhibit either type-I or type-III life histories, respectively. By incorporating a priori information concerning a species' life-history and thereby choosing a more realistic division between the two classes in the PLC model, the modified PLC approach agrees more closely with the full Leslie model. While the ability to examine the sensitivity to age at first reproduction (α) and longevity (ω) in the standard PLC is lost, better estimation of population growth rate is gained. The latter seems to be of more immediate concern when working with endangered and threatened species. Thus, when faced with a paucity of data for species exhibiting type-I or type-III life histories, the modified PLC is a promising approach for population viability analysis.

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