Journal of Applied Statistics, Vol. 29, Nos. 1-4, 2002, 589-607

Routledge
Taylor & Francis Group

Estimating rates of population change for a neotropical parrot with ratio, mark-recapture and matrix methods

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ABSTRACT *Robust methods for estimating rates of population change (λ) are necessary for applied and theoretical goals in conservation and evolutionary biology. Traditionally, λ has been calculated from either ratios of population counts (observed λ or λ_{obs}), or population models based on projection matrices (asymptotic λ or λ_{asy},). New mark-recapture methods permit calculation of λ from mark-resighting information alone (realized λ or λ_{rea}), but empirical comparisons with other methods are rare. In this paper, rates of population change were calculated for a population of green-rumped parrotlets (*Forpus passerinus*) that have been studied for more than a decade in central Venezuela. First, a ratio method based on counts of detected birds was used to calculate $\hat{\lambda}_{obs}$. Next, a temporal symmetry method based on mark-recapture data (i.e. the λ-parameterization introduced by Pradel, 1996) was used to calculate $\hat{\lambda}_{rea}$. Finally, a stage-structured matrix model based on state-specific estimates of fecundity, immigration, local survival, and transition rates was used to calculate $\hat{\lambda}_{asy}$. Analyses were conducted separately for females and males. Overall values of $\hat{\lambda}$ from the three methods were consistent and all indicated that the finite rate of population change was not significantly different from 1. Annual values of $\hat{\lambda}$ from the three methods were also in general agreement for a majority of years. However, $\hat{\lambda}_{rea}$ from the temporal symmetry method had the greatest precision, and apparently better accuracy than $\hat{\lambda}_{asy}$. Unrealistic annual values of $\hat{\lambda}_{asy}$ could have been due to poor estimates of the transitional probability of becoming a breeder ($\hat{\psi}$) or to a mismatch between the actual and the asymptotic stable stage distribution. In this study, the trade-off between biological realism and accuracy was better met by the temporal symmetry than the matrix*

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ISSN 0266-4763 print; 1360-0532 online/02/010589-19
DOI: 10.1080/02664760120108818

method. Our results suggest that the temporal symmetry models can be applied with confidence to populations where less information may be available.

1 Introduction

Population growth is a biological process of great interest for population studies of plants and animals. Robust estimates of the finite rate of population change (λ) are essential for both applied and theoretical goals in ecology. In conservation biology, reliable estimates of λ are essential for identifying declining populations ($\lambda < 1$), and for evaluating management actions that could lead to stable or increasing population numbers ($\lambda \geqslant 1$; Beissinger & Westphal, 1998). In population biology, estimates of rates of population change are central to understanding the factors that regulate population numbers, and for investigating the dynamics of spatially structured populations, including models of source-sink interactions (Diffendorfer, 1998; Virgl & Messier, 2000). In evolutionary ecology, λ has been used as an index of fitness (Caswell, 2001). If variation in vital rates is due to genetic variance, then λ can be used to explore the adaptive function of life-history tactics, and the selective forces that shape them (McGraw & Caswell, 1996).

The intrinsic rate of population change is given by:

$$r = (B + I) - (D + E)$$

where population gains are determined by the per capita birth (B) and immigration rates (I), and population losses by death (D) and emigration rates (E). The finite rate of population change, or the rate of change per individual per unit time (λ), is related to r by:

$$\lambda = e^r$$

A number of methods can be used to estimate λ for open populations (Nichols, 1992; Nichols *et al.*, 2000; Nichols & Hines, 2002). The *ratio method* makes no attempt to determine B, I, D or E. Instead, if a complete census of a population is attainable, then the *observed* rate of population change (λ_{obs}) is simply the ratio of the population size (N) at two consecutive time periods (t):

$$\lambda_t = N_{t+1}/N_t$$

More often, only surveys are feasible, yielding counts that are related to the true population size by an unknown probability of detection (p) < 1:

$$C_t = N_t p_t$$

Use of a ratio of counts to estimate population change between two occasions:

$$\hat{\lambda}_{\text{obs}} = C_{t+1}/C_t = (N_{t+1}\, p_{t+1})/(N_t p_t)$$

requires that probabilities of detection do not vary across time (i.e. $p_{t+1} = p_t$), and $\hat{\lambda}$ is expected to be biased if this assumption is violated (Nichols, 1992).

The need to estimate p was one impetus that led to the development of early statistical models for analysis of mark-recapture data, such as the Cormack-Jolly-Seber (CJS) model (ϕ_t, p_t; Jolly, 1965; Seber, 1965). In the *temporal symmetry method*, Pradel (1996) presented a reparameterization of the CJS model that can be used to calculate direct estimates of the *realized* rate of population change ($\hat{\lambda}_{\text{rea}}$). In a conventional CJS model, capture-histories are analysed from the first capture forward, yielding estimates of local survival ($\hat{\phi}_t$) between consecutive occasions.

The complement of local survival is a measure of population losses, and no attempt is made to distinguish between D and E. Analysis of the same capture-histories from the last capture backwards yields a seniority probability ($\hat{\gamma}_t$), defined as the probability that the individual did not enter the population between $t-1$ and t. Thus, $1-\hat{\gamma}$ is a measure of population gains, although no attempt is made to determine whether the gains are due to B, I or to increases in banding effort or study area (Franklin, 2001). In the λ-parameterization of Pradel (1996), a ratio of these two probabilities yields a time-specific rate of population change:

$$\hat{\lambda}_{\text{rea}} = \hat{\phi}_t / \hat{\gamma}_{t+1}$$

In the *matrix method*, stage- or age-specific estimates of vital rates are synthesized into a projection matrix and used to calculate an *asymptotic* rate of population change ($\hat{\lambda}_{\text{asy}}$, Caswell, 2001). The matrix method differs from the ratio and temporal symmetry methods in that it requires detailed information on various demographic rates. Projection matrices are often developed for what are assumed to be closed populations, where changes in population size are due to births (B) and deaths (D), the latter measured as the complement of local survival (S):

$$\log_e(\lambda_t) = B_t - (1 - S_t)$$

In investigations of marked vertebrates on small study plots, however, it is difficult to distinguish between mortality and permanent emigration due to dispersal (Lambrechts *et al.*, 1999; Koenig *et al.*, 2000). Therefore, the complement of local survival is not deaths ($1 - S_t \neq D_t$), but deaths and emigration ($1 - S_t = D_t + E_t$). If $\hat{\lambda} < 1$, variation in either D_t or E_t may be responsible. To obtain reliable estimates of population change for an open population at a local site, it is important to incorporate immigration rates into the matrix model, although this is rarely done:

$$\log_e(\lambda_t) = (B_t + I_t) - (1 - S_t)$$

A potential drawback of the matrix method is that estimates of certain vital rates may be difficult to obtain or may require long-term study. Nonetheless, $\hat{\lambda}_{\text{asy}}$ may be a better characterization of population dynamics than $\hat{\lambda}_{\text{obs}}$ or $\hat{\lambda}_{\text{rea}}$ because $\hat{\lambda}_{\text{asy}}$ incorporates a more detailed, mechanistic understanding of underlying biological processes.

The metrics of population change from the three methods are subtly different in their properties. First, $\hat{\lambda}_{\text{obs}}$ and $\hat{\lambda}_{\text{rea}}$ are direct estimates of population change in past transitions, whereas $\hat{\lambda}_{\text{asy}}$ predicts what the future rate of population change would be for an observed set of vital rates. This distinction has been referred to as retrospective versus prospective analysis, respectively, although use of these terms is presently controversial (Caswell, 2000; Wisdom *et al.*, 2000). Second, unlike $\hat{\lambda}_{\text{obs}}$ and $\hat{\lambda}_{\text{rea}}$, $\hat{\lambda}_{\text{asy}}$ is asymptotic in nature. For a given projection matrix, $\hat{\lambda}_{\text{asy}}$ is the predicted rate of population change if the population is at a stable stage or age distribution. Population projections based on deterministic matrix models are sometimes criticized because such models do not incorporate the likely effects of stochasticity and negative density-dependence, but the effects of these processes may be of less concern if $\hat{\lambda}_{\text{asy}}$ is used for short-term projections of a few years.

In this paper, we use three methods to calculate $\hat{\lambda}$ for a small neotropical bird, the green-rumped parrotlet (*Forpus passerinus* L., hereafter 'parrotlet'). This species has been the focus of a long-term study since 1988 and has been used to investigate questions regarding the social behaviour (Beissinger *et al.*, 1998), hatching asynchrony (Stoleson & Beissinger, 1997, 1999) and demography of a tropical vertebrate (Beissinger & Waltman, 1991; Sandercock *et al*., 2000). Previously, we have shown that the adult population has a male-based sex ratio, and that the sexes have markedly different rates of survival, breeding propensity and natal dispersal (Sandercock *et al*., 2000). Most demographic models of birds are female-based or combine both sexes into one matrix model (Caswell, 2001). To control for heterogeneity due to sex and to facilitate comparisons with past work, all analyses and modelling were conducted separately for both sexes. The objective of this paper was to use field data collected over a decade of study to evaluate the relative performance of the ratio, temporal symmetry and matrix methods for calculating $\hat{\lambda}$.

2 Methods

2.1 Study species

Green-rumped parrotlets were studied at Hato Masaguaral, a cattle ranch 45 km south of Calabozo, in Guárico, Venezuela (8°34′N, 67°35′W). Field work was conducted over a 12-year period from 1988 to 1999. Analyses were restricted to data collected from 1990 to 1999 because samples of birds and nesting attempts were sometimes small in the first two years. Parrotlets are small parrots (25-34 g) that are monomorphic in body size and readily sexed by their dichromatic plumage. They are seasonal breeders, and nesting occurs during the wet season from May to November. Pairs raise 1-2 or rarely 3 broods per year (Waltman & Beissinger, 1992) and are unusual among tropical birds for laying a large clutch (mean = 7 eggs, range = 4-11, Beissinger & Waltman, 1991). This species is both socially and genetically monogamous (extra-pair paternity < 8%; Melland, 2000), and the number of young fledged is a good indicator of reproductive success for both parents. Dispersal is high among juvenile females, moderate among juvenile males, and negligible among adults (Sandercock *et al*., 2000; Beissinger, unpublished data). Parrotlets do not reproduce in their natal year, but both sexes breed as yearlings. The study population has a male-biased sex ratio, and a high proportion of parrotlets are non-breeders, especially among males (> 50%, Sandercock *et al*., 2000). Non-breeding parrotlets are often observed actively searching for nest sites and mating opportunities, sometimes harassing breeding pairs (Beissinger *et al*., 1998). During the dry season, parrotlets roost and forage in large flocks (Waltman & Beissinger, 1992).

2.2 Field methods

Fecundity information was derived from birds breeding in artificial nestboxes; the few nests that occurred in natural cavities were also monitored each year. The number of nestboxes in the study area was 40 in 1988 and 100 to 106 during 1989 to 1999. Nestboxes were checked daily throughout the breeding season. To calculate the number of attempts per pair, we included only nests where the identity of the female was known. Each year we observed a few small clutches (1-4 eggs) that were never incubated, and failed for unknown reasons. A small number of females also laid eggs in two nestboxes concurrently or consecutively, and then abandoned one or both attempts. We considered a nesting attempt to be a full clutch that was laid in a single nestbox.

Nests were considered successful if they fledged at least one chick. In several years, egg and chick numbers were experimentally manipulated as part of separate investigations (Stoleson & Beissinger, 1997, 1999). Nest manipulations did not lead to higher rates of depredation (Stoleson & Beissinger, 2001), so experimental nests were included in analyses of nest success. We used unadjusted rates of nest success instead of Mayfield estimators because clutches were found at the onset of laying. Manipulations of offspring number had some effect on number of fledglings produced, and analyses of number of fledglings per successful nest were restricted to unmanipulated nests.

We attempted to capture all nesting and prospecting parrotlets, and individual birds were banded with numbered metal rings and unique combinations of coloured leg-bands. Adult parrotlets were captured in mistnets at roosting sites and in the vicinity of nestboxes, or were trapped in the nestbox while feeding young. No parrotlet has been detected breeding during its natal year, and adults were assumed to have survived at least one dry season. Nestlings were captured by hand in the nestbox, 3 to 5 days prior to fledging. Parrotlets were resighted near nest boxes, at communal roosts and in feeding flocks. Band combinations and sometimes band numbers were read with binoculars (10 ×) and spotting scopes (40-60 ×) at distances of 10-75 m. Field effort consisted of daily surveys over a 7-month period and was similar in all years. From 1995 to 1999, however, we made a more concerted effort to resight and identify non-breeding birds in the study population.

A parrotlet was considered to be a breeder if it was associated with at least one nesting attempt during the study year, regardless of the fate of the nest. It is possible that a few breeders were overlooked each year. We think this is unlikely because nest boxes were monitored intensively and few nesting attempts were made in natural nest cavities (Beissinger & Bucher, 1992; Stoleson & Beissinger, 1997). Non-breeders were identified by their social interactions, and were never associated with a nesting attempt. Non-breeding males sometimes formed male-male pairs or remained in small flocks; non-breeders also included mated pairs that did not nest (Beissinger *et al.*, 1998). Non-breeders were frequently yearlings but also included older birds that failed to obtain a mate (Beissinger, unpublished data).

2.3 General approaches to statistical analyses

All analyses of mark-recapture data were implemented with Program MARK (version 1.9, White & Burnham, 1999) and model selection was based on the information theoretic approach described by Burnham & Anderson (1998). As a first step, we used a parametric bootstrap method to test the goodness-of-fit (GOF) of the global model to the data. A distribution of expected deviances was generated under the assumptions of no heterogeneity and full independence ($n = 1000$ simulations). A variance inflation or overdispersion factor ($\hat{c}$) was calculated by dividing the observed deviance of the global model by the mean expected deviance. GOF tests for multistrata models are not yet available in Program MARK, and were calculated with Program MSSURVIV instead (version 1; Brownie *et al.*, 1993).

Next, model structure was specified using parameter index matrices, and maximum likelihood models were constructed using the sine-link function. Model fit was described by the deviance ($\text{Dev} = -2\ln\mathscr{L}$) and the number of parameters in the model (K). Relative model fit was assessed with a modified version of Akaike's Information Criterion that included corrections for small sample size (AIC_c), and in most analyses, overdispersion as well (quasi-AIC_c or QAIC_c). Models were considered equally parsimonious if the difference in $\mathrm{AIC_c}$ or $\mathrm{QAIC_c}$ from the best-fit model was $\leqslant 2$.

Annual and overall estimates of demographic rates were calculated with two procedures. First, annual means and variances of population change ($\hat{\lambda}_{\mathrm{rea}}$), local survival ($\hat{\phi}$) and the transitional probability of becoming a breeder ($\hat{\psi}$) were derived from unconstrained global models, which included time-dependence. In analyses where $\hat{c} > 1$, the variances of parameter estimates were corrected by $\hat{c}$ and were taken from the estimate output of Program MARK. Second, overall means and variances for our 10-year time series were calculated by applying the variance components procedure of Program MARK to the annual parameters. Terminal and starting transitions that were non-identifiable were not included. The variance components procedure allowed us to remove the effects of sampling variation, leaving the process variation due to biological processes (Gould & Nichols, 1998).

Statistical analyses of other vital rates were performed with SAS procedures (version 8, SAS Institute Inc., Cary, NC 27513, USA). The effects of year on nesting success and the annual number of nesting attempts per pair were analysed with contingency tests (Proc FREQ). Few pairs produced more than two clutches per year so we avoided sparse cells by comparing the frequencies of birds that produced one versus two or more clutches. The effects of sex, social status and year on immigration rates were analysed with logistic analysis (Proc CATMOD). The number of fledglings per successful nest was normally distributed and year effects were analysed with single classification analysis of variance (Proc GLM). All tests were two-tailed and considered significant at probability levels < 0.05. For graphical clarity, means of vital rates are presented ± 1 SE, and means of rates of population change are presented $\pm 95\%$CI.

2.4 *Ratio method for estimating λ*

Annual rates of $\hat{\lambda}_{\mathrm{obs}}$ were estimated by using a ratio of the raw counts of marked individuals that were detected on the study area each year. Hence, an annual rate was:

$$\hat{\lambda}_t = (N_{\mathrm{non}} + N_{\mathrm{brd}})_{t+1} / (N_{\mathrm{non}} + N_{\mathrm{brd}})_t$$

where N_{non} and N_{brd} = the number of non-breeders and breeders detected in a given year (t).

2.5 *Temporal symmetry method for estimating λ*

Annual rates of $\hat{\lambda}_{\mathrm{rea}}$ were estimated using mark-recapture data only. Capture histories were coded for adult parrotlets using the following criteria for each occasion: 1 = banded, recaptured or resighted on the study area as either a breeder or a non-breeder, 0 = not detected. Handling records of juvenile parrotlets were discarded. Rates of population change were estimated using the λ-parameterization of Pradel's (1996) models. The global model contained time-dependence in population change, local survival and resighting rates (λ_t, ϕ_t, p_t). Goodness-of-fit (GOF) tests are not yet available for this model. Instead, we calculated GOF to the CJS model (ϕ_t, p_t) because the λ-parameterization model is derived from the CJS model and is based on the same set of assumptions (Pradel, 1996; Nichols & Hines, 2002). Our 10-year study period spanned nine transitions, and the global model yielded seven values of $\hat{\lambda}_{\mathrm{rea}}$ because the first and last transitions were non-identifiable (Franklin, 2001). In reduced models, ϕ and p were treated as nuisance parameters and were not constrained.

The $\hat{\lambda}_{\text{rea}}$-values from temporal symmetry models are determined by changes in the numbers of newly encountered individuals, whether they are due to local recruits, individuals immigrating onto to the study area or to changes in sampling effort or area. In this study, all newly captured birds were presumably true immigrants because the size of our study area and number of nestboxes monitored remained constant during 1991 to 1998. Moreover, the first annual value of $\hat{\lambda}_{\text{rea}}$ was preceded by three years of banding effort, and most breeder parrotlets are detected ($\hat{p} > 0.98$) although non-breeders may be overlooked ($\hat{p} = 0.31$ to 0.44, Sandercock *et al.*, 2000).

2.6 *Matrix method for estimating* λ

2.6.1 Estimation of vital rates. Annual rates of $\hat{\lambda}_{\text{asy}}$ were estimated using a stage-structured matrix model that synthesized information on births, immigrants, and losses due to mortality and permanent emigration.

Births were calculated in two steps. First, fecundity (F) or the expected number of fledglings per pair was calculated as the product of three components of reproductive output:

$$F = NA \ \ Succ \ \ FPN \ 0.5$$

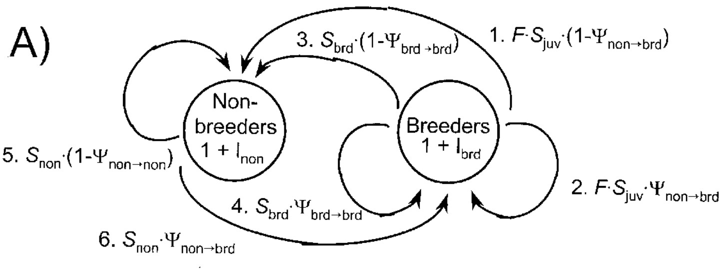
where NA = number of nesting attempts per female, $Succ$ = the percentage of nests fledging at least one young, FPN = the number of fledglings per successful nest and 0.5 is the correction factor for sex ratio at fledging (i.e. a 1:1 ratio, Beissinger, unpublished data). Secondly, the local survival of fledglings in their first year of life was estimated from mark-recapture data. Capture histories for nestling parrotlets that successfully fledged were coded using the following criteria: 1 = banded as nestling, or later recaptured or resighted on the study area as either a breeder or a non-breeder, 0 = not detected. Juvenile survival rates were then estimated using recapture-only models. Here, the global model was a two age-class model that separated local survival in the transition in the year after first banding (ϕ^{juv}) from local survival in all subsequent years (ϕ^{adt}). It contained time-dependence in both local survival and resighting rates (ϕ_t^{juv}, ϕ_t^{adt}, p_t). Local survival rates of adults (ϕ^{adt}) and resighting rates (p) were treated as nuisance parameters and were not constrained.

Per capita immigration rates can be estimated using the f-parameterization of the temporal symmetry models. Unfortunately, state information cannot yet be included in these models, and our matrix model required separate estimates of immigration rates for non-breeders and breeders. Per capita immigration rates were calculated for birds of each social state by dividing the number of newly marked birds by the number of returning birds. Newly marked birds were presumed to be immigrants whereas returning birds included philopatric young and adults showing breeding site-fidelity. This approach relies on the untested assumption that the detection rates of unbanded and marked birds are equal. However, it is not affected by known differences in resighting rates between birds of different social status (Sandercock *et al.*, 2000).

Local survival and transition rates of adults were calculated from mark-recapture data. The complement of local survival is comprised of losses due to mortality and permanent emigration, but no attempt was made to distinguish these processes here. Capture-histories were coded for adult parrotlets using the following criteria: B = detected on the study area as a breeder, N = detected on the study area as a non-breeder, or 0 = not detected. Handling records of juvenile parrotlets were discarded. State-specific estimates of local survival (S_{non}, S_{brd}) and the probabilities of becoming ($\psi_{\text{non-brd}}$) or remaining a breeder ($1 - \psi_{\text{brd-non}}$), and resighting rates (p_{non}, p_{brd}) were estimated using dynamic multistate models. Here, the global model included time-dependence within all parameters and strata ($S_{\text{status}*t}$, $\psi_{\text{status}*t}$, $p_{\text{status}*t}$). Previous analyses demonstrated large differences in S and ψ between non-breeders and breeders (Sandercock *et al.*, 2000). Thus, social status was retained in all models and no attempt was made to test for interactions between strata. Resighting rates (p) were treated as nuisance parameters and were not constrained.

2.6.2 Parameterization of the stage-structured matrix model. To synthesize the different components of parrotlet demography, we developed a stage-structured population model based on prebreeding surveys. A life-cycle diagram was constructed (Fig. 1(a)), and the vital rates were cast into a 2 × 2 projection matrix (Fig. 1(b)). This time-invariant model contained nodes for two stages: breeders and non-breeders. Age-structure was not included because differences in social status have a greater effect on parrotlet demography than absolute or relative age. Density-dependence was not included because the relationship between bird numbers and vital rates was unknown.

The two nodes of the life-cycle diagram were strongly connected by six arcs (Fig. 1(a)). Arcs 1 and 2 describe the fecundity of breeders, weighted by the subsequent survival of the fledglings produced and the probability that the juveniles become non-breeders or breeders by the next pre-breeding census. Arcs 3 and 4 parallel arcs 1 and 2, but are the transition rates of adult breeders, consisting of the survival rates of breeders and their subsequent social status. Finally, arcs 5 and



B)

$$\begin{array}{l|cc}
 & \text{Nonbreeders } (t_i) & \text{Breeders } (t_i) \\
\hline
\text{Nonbreeders } (t_{i+1}) & (1 + I_{\text{non}})\cdot[S_{\text{non}}\cdot(1-\Psi_{\text{non}\to\text{brd}})] & \begin{array}{c}(1 + I_{\text{brd}})\cdot[S_{\text{brd}}\cdot(1-\Psi_{\text{brd}\to\text{brd}}) \\ +\ F\cdot S_{\text{juv}}\cdot(1-\Psi_{\text{non}\to\text{brd}})]\end{array} \\
\text{Breeders } (t_{i+1}) & (1 + I_{\text{non}})\cdot[S_{\text{non}}\cdot\Psi_{\text{non}\to\text{brd}}] & \begin{array}{c}(1 + I_{\text{brd}})\cdot[S_{\text{brd}}\cdot\Psi_{\text{brd}\to\text{brd}} \\ +\ F\cdot S_{\text{juv}}\cdot\Psi_{\text{non}\to\text{brd}}]\end{array}
\end{array}$$

FIG. 1. The life-cycle diagram (a) and associated projection matrix (b) for a stage-structured population model of green-rumped parrotlets based on pre-breeding censuses. Notation includes: F = fecundity measured as fledglings per pair, I = per capita immigration rate, S = probability of local survival, ψ = probability of becoming or remaining a breeder. Subscripts include: juv = juvenile, non = non-breeder, brd = breeder. S_{juv} is equivalent to ϕ^{juv} of Table 3.

6 are the life-history pathways of non-breeders, and are composed of the survival of adult non-breeders and their breeding status in the following year. The non-breeder node did not have additional arcs for alternative life-history tactics because genetic analyses have shown that intraspecific nest parasitism does not occur and extrapair fertilizations by non-breeders are rare (Melland, 2000).

2.6.3 Calculation of matrix properties. Matrix properties were calculated using formulae and the general methods described by Caswell (2001). The stage-structured model was analysed as a time-invariant deterministic matrix:

$$\mathbf{n}(t+1) = \mathbf{A}\mathbf{n}(t)$$

where $\mathbf{n}(t)$ and $\mathbf{n}(t+1)$ are vectors giving the abundance of each stage in the population at times t and $t+1$, and $\mathbf{A}$ is the projection matrix (i.e. Fig. 1(b)). Asymptotic estimates of the finite rate of population change (λ or λ_1, the dominant eigenvalue) were derived with the power method (Caswell, 2001), and validated with algorithms of Program MATLAB (student version 11, Mathworks, Natick, MA 01760, USA). The sensitivity (s_{ij}) of λ to instantaneous changes in a given matrix element (a_{ij}) was calculated by:

$$s_{ij} = \partial\lambda/\partial a_{ij} = v_i\, w_j/\langle \mathbf{w}, \mathbf{v}\rangle$$

where $\mathbf{w}$ = the stable stage distribution, and $\mathbf{v}$ = the stage-specific reproductive value, and $\langle \mathbf{w}, \mathbf{v}\rangle$ = the scalar product of these two vectors. The sensitivity (s_x) of λ to instantaneous changes in individual vital rates (x), or 'lower-level' sensitivities was calculated by:

$$s_x = \partial\lambda/\partial x = \sum_{ij} [(\partial\lambda/\partial a_{ij})\ (\partial a_{ij}/\partial x)]$$

where $\partial\lambda/\partial a_{ij}$ is the sensitivity of a matrix element and $\partial a_{ij}/\partial x$ is the partial derivative of a matrix element with respect to x (i.e. the product of vital rates other than x in terms containing x, Caswell, 2001). Finally, the variance of the rate of population change was calculated by:

$$\mathrm{var}(\lambda) \approx \Sigma\, \mathrm{var}(x)\ (\partial\lambda/\partial x)^2$$

where var(x) is the variance of vital rate x and $\partial\lambda/\partial x$ is the lower-level sensitivity of the vital rate x (Alvarez-Buylla & Slatkin, 1994). The 95% confidence intervals of λ was then calculated by:

$$\lambda \pm 1.96\ \sqrt{\mathrm{var}(\lambda)}$$

3 Results

3.1 Ratio method

Annual values of $\hat{\lambda}_{\mathrm{obs}}$ based on raw counts of individuals ranged from 0.757 to 1.124 in females (in 1996-97 and 1995-96) and 0.707 to 1.360 in males (in 1996-97 and 1994-95, Fig. 2). The geometric mean of $\hat{\lambda}_{\mathrm{obs}}$ was 0.964 (0.833-1.095 95%CI) in females and 0.995 in males (0.809-1.181, Fig. 2).

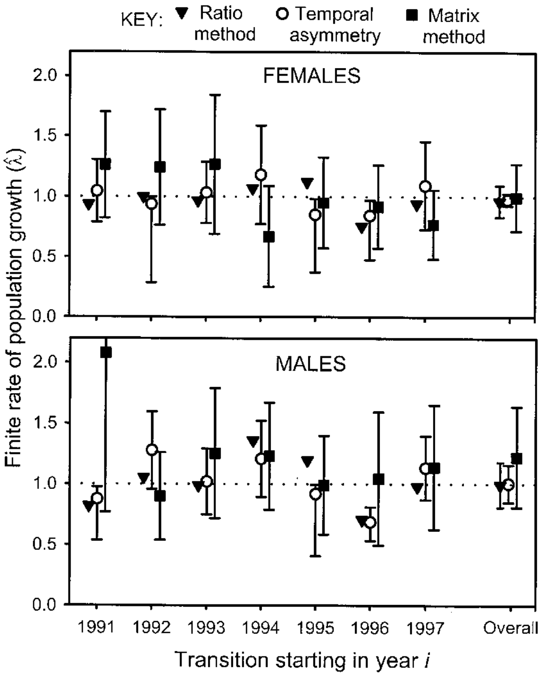


FIG. 2. Mean estimates of population growth rates (± 95%CI) for female and male green-rumped parrotlets calculated with the ratio method (observed $\hat{\lambda}$ or $\hat{\lambda}_{obs}$), the temporal symmetry method (realized $\hat{\lambda}$ or $\hat{\lambda}_{rea}$) and the matrix method (asymptotic $\hat{\lambda}$ or $\hat{\lambda}_{asy}$).

3.2 Temporal symmetry method

A total of 1624 adult parrotlets (females: $n = 602$, males: $n = 1022$) were marked during 1990 to 1998. The parametric bootstrap GOF test indicated that a conventional CJS model (ϕ_t, p_t) was a relatively poor fit to the capture histories of both females ($P < 0.001$) and males ($P < 0.004$). However, a poor fit was expected because breeders and non-breeders were pooled, and social status is a known source of heterogeneity in parrotlet capture-histories (Sandercock *et al.*, 2000). Nevertheless, we proceeded to use the λ-parameterization to estimate $\hat{\lambda}_{rea}$ because overdispersion factors were low (females: $\hat{c} = 1.304$, males: $\hat{c} = 1.310$). The $\hat{c}$-values were used to adjust the model selection with QAIC$_c$ and the 95%CI of $\hat{\lambda}_{rea}$. The global model λ_t, ϕ_t, p_t indicated that $\hat{\lambda}_{rea}$ varied from 0.844 to 1.181 in females and 0.688 to 1.277 in males (Fig. 2). Subsequent modelling revealed that the global model with annual variation in $\hat{\lambda}_{rea}$ was the best fit for males (Table 1). In females, the best fit model was one where $\hat{\lambda}$-values did not vary annually but collapsed to a constant. Overall, $\hat{\lambda}_{rea}$ calculated with the variance components procedure indicated that the long-term rate of population change was close to one for both females ($\hat{\lambda}_{rea} = 0.978$, 95%CI< ±0.001) and males ($\hat{\lambda}_{rea} = 1.004$, 0.849-1.159 95%CI, Fig. 2).

3.3 Matrix method

Nesting pairs of green-rumped parrotlets produced, on average, between 1 and 2 complete clutches per year (Table 2). The proportion of pairs producing more

TABLE 1. Temporal symmetry mark-recapture models used to estimate population growth rates of parrotlets

	Model structure[a]			Model statistics[b]			
Sex	λ	ϕ	p	Dev	K	ΔQAIC$_c$	w_i
Females	c	t	t	2875.9	20	0.0	0.989
	t	t	t	2871.3	26	9.1	0.011
Males	t	t	t	4935.4	26	0.0	0.995
	c	t	t	4965.0	20	10.3	0.005

[a] Population growth rates (λ) were estimated using the λ-parameterization model of Pradel (1996). Local survival (ϕ) and resighting rates (p) were treated as nuisance parameters and were not constrained. Model notation includes: t = time or annual variation, c = constancy.

[b] Model fit is described by the deviance (Dev), number of parameters in the model (K), and Akaike's Information Criterion corrected for both small sample sizes and overdispersion (QAIC$_c$). Models are presented in order of fit relative to the best fit model (ΔQAIC$_c$ = 0). Variance inflation factors were low in females ($\hat{c}$ = 1.304) and males ($\hat{c}$ = 1.310).

TABLE 2. Annual variation in components of reproductive performance of breeding parrotlets

Year	Nesting attempts per pair	n	Nest success[a]	n	Fledglings per successful nest	n[b]
1991	1.47 ± 0.06	87	0.846	130	4.65 ± 0.25	52
1992	1.34 ± 0.05	91	0.781	128	4.56 ± 0.50	16
1993	1.27 ± 0.06	81	0.660	100	—[c]	—
1994	1.60 ± 0.07	85	0.735	132	4.50 ± 0.52	10
1995	1.41 ± 0.07	71	0.613	106	3.86 ± 0.36	29
1996	1.56 ± 0.08	59	0.628	86	4.78 ± 0.47	23
1997	1.39 ± 0.06	69	0.758	95	4.57 ± 0.22	69

[a] Nest success = at least one chick was successfully fledged from the nest. Mayfield estimators were not used because all nests are found early in laying at 1-3 eggs.

[b] Samples based on unmanipulated nests only.

[c] No nests were left unmanipulated in 1993. An estimate of fledging success based on pooled years was used in the matrix model (FPN = 4.51 ± 0.13).

than one nesting attempt varied across years (contingency test, $\chi^2_6 = 19.7$, $P = 0.003$). Nesting success for this cavity-nesting species was generally high (Stoleson & Beissinger, 2001) and, in all years, more than 60% of nests produced at least one fledgling. Rates of nest success varied significantly among years (contingency test, $\chi^2_6 = 25.1$, $P < 0.001$), ranging from 61.3% in 1995 to 84.6% in 1991. Annual variation in number of fledglings produced per successful nest was not significant (ANOVA, $F_{5,193} = 0.84$, $P = 0.52$), and usually averaged about 4.5 young.

During the period 1990 to 1998, a total of 3569 juvenile parrotlets (females: $n = 1738$, males: $n = 1831$) were marked as nestlings and subsequently fledged. GOF tests based on bootstrap simulations indicated that an age-structured global model (ϕ_t^{juv}, ϕ_t^{adt}, p_t) provided a relatively poor fit to the capture histories of juveniles (females: $P = 0.011$, males: $P < 0.001$). Nonetheless, we retained this starting model because the overdispersion factors were low in both sexes (females: $\hat{c} = 1.344$, males: $\hat{c} = 1.373$). Most of the overdispersion was likely due to heterogeneity in the parameters of older age-classes. Such departures were unimportant because

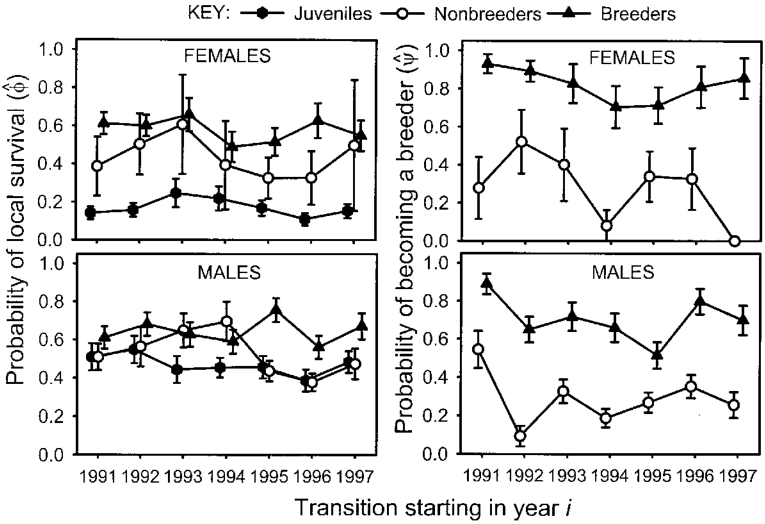


FIG. 3. Probability of local survival and the transitional probability of either becoming or remaining a breeder for green-rumped parrotlets of different ages and social status. Annual estimates were derived from the unconstrained global models presented in Tables 3 and 5. Means are presented ± 1 SE.

our estimates of adult survival were calculated with multistrata models and were based on a larger sample of parrotlets that included birds banded as adults.

The global model ϕ_t^{juv}, ϕ_t^{adt}, p_t indicated that local survival rates of juvenile parrotlets varied from 0.109 to 0.246 in females and 0.386 to 0.547 in males (Fig. 3). Natal dispersal movements suggest that juvenile males had greater local survival than juvenile females because males had stronger philopatry to their natal areas, but a possible sex difference in true survival cannot be discounted (see Sandercock *et al.*, 2000). In both sexes, the best fit model was one in which the local survival of juveniles (ϕ^{juv}) was constant across and did not vary annually (Table 3). Overall, $\hat{\phi}^{\text{juv}}$ from the variance components procedure was 0.141 in females (SE< 0.001) and 0.465 in males (SE< 0.001).

TABLE 3. Age-structured mark-recapture models used to estimate local survival of juvenile parrotlets (females $n = 1738$, males: $n = 1831$)

	Model structure[a]			Model statistics[b]			
Sex	ϕ^{juv}	ϕ^{adt}	p	Dev	K	ΔQAIC$_c$	w_i
Females	c	t	t	175.0	18	0.0	0.971
	t	t	t	165.2	25	7.0	0.030
Males	c	t	t	437.0	18	0.0	0.994
	t	t	t	431.6	25	10.3	0.006

[a] Local survival rate of juveniles (ϕ^{juv}) was estimated using a two age-class model that separated local survival in the transition in the year after first banding from all subsequent years (ϕ^{adt}). Local survival rates of adults (ϕ^{adt}) and resighting rates (p) were treated as nuisance parameters and were not constrained. Model notation includes: t = time or annual variation, c = constancy.

[b] See caption of Table 1 for definition of terms. Variance inflation factors were low in females ($\hat{c} = 1.344$) and males ($\hat{c} = 1.373$).

TABLE 4. Annual counts of birds and per capita immigration rates for adult parrotlets of different social status

		Nonbreeders			Breeders		
Sex	Year	Outside[a]	Local[b]	Immigration rate[c]	Outside	Local	Immigration rate
Females	1991	10	12	0.833	33	52	0.635
	1992	4	12	0.333	33	65	0.508
	1993	8	11	0.727	20	72	0.278
	1994	3	13	0.231	23	71	0.324
	1995	11	24	0.458	34	46	0.739
	1996	15	35	0.429	19	50	0.380
	1997	3	17	0.177	30	47	0.638
Males	1991	7	89	0.079	25	60	0.417
	1992	1	55	0.018	15	85	0.176
	1993	11	72	0.153	20	68	0.294
	1994	14	51	0.275	20	85	0.235
	1995	15	124	0.121	18	68	0.265
	1996	15	152	0.099	11	67	0.164
	1997	12	87	0.138	12	67	0.179

[a] Outside = birds that originated from outside the study area and were newly banded as immigrating adults.

[b] Local = birds of local origin that included philopatric young that originated on the study area and returning adults that were banded in a previous year.

[c] Immigration rate = outside/local.

As a consequence of sexual differences in local survival of juveniles, per capita immigration rates of adult parrotlets were generally higher in females (overall means, non-breeders: 0.455 ± 0.093 SE, breeders: 0.500 ± 0.067) than males (non-breeders: 0.126 ± 0.030, breeders: 0.247 ± 0.034, Table 4). The proportion of birds that were immigrants was significantly higher among females than males (main-effects logistic analysis, sex: $\chi^2_1 = 58.0$, $P < 0.001$), and among breeders than non-breeders (social status: $\chi^2_1 = 13.9$, $P < 0.001$), but annual variation was not significant (year: $\chi^2_6 = 9.9$, $P = 0.13$).

Local survival rates of adults were estimated from the same capture-histories that were used to calculate $\hat{\lambda}_{\text{rea}}$ in the temporal symmetry analyses above. In these analyses, however, information on social status of parrotlets was also included in the capture-histories. GOF tests calculated in Program MSSURVIV indicated that the global model $S_{\text{status}*t}$, $\psi_{\text{status}*t}$, $p_{\text{status}*t}$ was a good fit to the data in both sexes ($P > 0.99$). Annual estimates of local survival and transition rates from the global model varied among years (Fig. 3). Confidence intervals for female parameter estimates were generally wider than those of males (Fig. 3) because the male-biased sex-ratio among adults resulted in a smaller sample of females, among which non-breeders were less common (Table 4). Mark-recapture modelling revealed that the best-fit model in females was one where ϕ and ψ collapsed to constants, but a model that retained annual variation in the local survival of breeders was equally parsimonious (Table 5). In males, the best fit model was one without annual variation in the probability of becoming a breeder. The fit of this model was a twofold improvement over the global model where ϕ and ψ varied annually for both strata, but the global model was an equally parsimonious fit to the data.

TABLE 5. Multistate mark-recapture models used to estimate local survival and transition rates of adult parrotlets (females $n = 602$, males: $n = 1022$)

	Model structure[a]						Model statistics[b]			
Sex	ϕ_{non}	ϕ_{brd}	$\psi_{\text{non-brd}}$	$\psi_{\text{brd-non}}$	P_{non}	P_{brd}	Dev	K	ΔAIC_c	w_i
Females	c	c	c	c	t	t	307.7	22	0.0	0.630
	c	t	c	c	t	t	291.9	30	1.1	0.367
	t	t	t	t	t	t	262.6	52	19.8	0.000
Males	t	t	c	c	t	t	681.1	37	0.0	0.614
	t	t	t	t	t	t	650.8	52	1.4	0.303
	t	t	c	t	t	t	669.4	45	5.1	0.049

[a] Local survival rates of non-breeders (ϕ_{non}) and breeders (ϕ_{brd}) and the probability of changing social status ($\psi_{\text{non-brd}}$, $\psi_{\text{brd-non}}$) were estimated using multistate models that included information on parrotlet social status. Resighting rates of non-breeders (P_{non}) and breeders (P_{brd}) were treated as nuisance parameters and were not constrained. Model notation includes: t = time or annual variation, c = constancy.

[b] See caption of Table 1 for definition of terms. Of the models tested, only the global model and models with moderate support ($\Delta\text{AIC}_c < 6$) are presented.

Overall estimates from the variance components procedure indicated that local survival (S) of breeders was greater than that of non-breeders, and that males had higher local survival than females (female breeders: 0.594, SE< 0.001, female non-breeders: 0.393, SE< 0.001, male breeders: 0.659 ± 0.016 SE, male non-breeders: 0.512 ± 0.030). The transitional probability of becoming or remaining a breeder (ψ) was also higher among breeders but was higher in females than in males (female breeders: $\hat{\psi} = 0.875 \pm 0.020$ SE, female non-breeders: $\hat{\psi} = 0.212 \pm 0.046$, male breeders: $\hat{\psi} = 0.725 \pm 0.036$, male non-breeders: $\hat{\psi} = 0.287 \pm 0.040$). In both sexes, resighting rates (p) were generally at or close to unity for breeders, but were more variable for non-breeders.

Annual estimates of the mean and variance of the three components of reproductive output (*NA*, *Succ*, *FPN*), two immigration rates (I_{non}, I_{brd}), three survival rates (S_{juv}, S_{non}, S_{brd}) and two transition rates (ψ_{non}, ψ_{brd}) were then input into the matrix model (Fig. 1(b)). We used annual estimates to calculate $\hat{\lambda}_{\text{asy}}$ even if the annual variation in those vital rates was not significant. Annual $\hat{\lambda}_{\text{asy}}$-values ranged from 0.669 to 1.266 in females and 0.898 to 2.077 in males (Fig. 2). Overall, $\hat{\lambda}_{\text{asy}}$ from matrices based on mean annual parameters indicated the long-term rate of population change should be stable in females ($\hat{\lambda}_{\text{asy}} = 1.000$, 0.717-1.272 95%CI) and increasing in males ($\hat{\lambda}_{\text{asy}} = 1.223$, 0.8077-1.6381, Fig. 2).

3.4 *Comparison of methods*

The three analytical methods yielded overall values of $\hat{\lambda}$ that were not significantly different. In both sexes, the 95%CI of $\hat{\lambda}_{\text{obs}}$, $\hat{\lambda}_{\text{rea}}$ and $\hat{\lambda}_{\text{asy}}$ showed almost complete overlap. Furthermore, the three estimates of $\hat{\lambda}$ were close to, or not significantly different from, a value of 1 in both sexes (Fig. 2). This result supported our qualitative impression that population numbers of parrotlets were stable during the 10-year study period.

The precision and accuracy of annual estimates of $\hat{\lambda}$ were also fairly consistent. The ratio method performed quite well; $\hat{\lambda}_{\text{obs}}$ fell within the 95%CI of $\hat{\lambda}_{\text{rea}}$ and $\hat{\lambda}_{\text{asy}}$ in 5 of 7 years in females and 6 of 7 years in males (Fig. 2). The temporal symmetry method yielded $\hat{\lambda}$-values with the greatest precision. The 95% confidence intervals of $\hat{\lambda}_{\text{rea}}$ were narrower that the 95%CI of $\hat{\lambda}_{\text{asy}}$ in at least 6 of 7 years in both sexes. Extensive overlap of the 95%CI of $\hat{\lambda}_{\text{rea}}$ and $\hat{\lambda}_{\text{asy}}$ demonstrated that annual values of $\hat{\lambda}$ from the two methods were not statistically different in most years. However, annual values of $\hat{\lambda}_{\text{asy}} \geqslant \hat{\lambda}_{\text{rea}}$ in at least 5 of 7 years for both sexes (Fig. 2). Overall, the mean degree of relative bias (i.e. $(\hat{\lambda}_{\text{asy}} - \hat{\lambda}_{\text{rea}})\,((\hat{\lambda}_{\text{asy}} + \hat{\lambda}_{\text{rea}})/2)^{-1}$) was close to zero in females (-0.5%) but not males ($+16.8\%$). Years with a large discrepancy between $\hat{\lambda}_{\text{asy}}$ and $\hat{\lambda}_{\text{rea}}$ tended to be intervals where the transitional probabilities of becoming or remaining a breeder were particularly low or high. Thus, in females, the largest differences between $\hat{\lambda}_{\text{rea}}$ and $\hat{\lambda}_{\text{asy}}$ were observed in 1994-95 (-55%) and 1997-98 (-35%, other years $< \pm 28\%$, Fig. 2). These were intervals where the transitional probability of becoming a breeder was apparently low for non-breeding females (Fig. 3). In males, $\hat{\lambda}_{\text{asy}}$ was > 2 whereas $\hat{\lambda}_{\text{rea}}$ was < 1 in 1991-92, a percentage difference of $+81\%$ (Fig. 2). This was an interval where the transitional probabilities of becoming or remaining a breeder were particularly high for males (Fig. 3). Other years where differences between $\hat{\lambda}_{\text{rea}}$ and $\hat{\lambda}_{\text{asy}}$ were large (1992-93: -35%, 1996-97: $+41\%$, other years $< \pm 21\%$, Fig. 2) also coincided with outlying values of $\psi_{\text{non-brd}}$ and $\psi_{\text{brd-brd}}$ (Fig. 3).

4 Discussion

In this study, three analytical methods were used to calculate estimates of population change of green-rumped parrotlets from field data collected over a decade. The results were encouraging in that $\hat{\lambda}$-values calculated with ratios of counts of population numbers, mark-recapture models and projection matrices were in general agreement. To our knowledge, this study is one of the first attempts to compare simultaneously these three methods, and comparative data from other vertebrate taxa are not yet available. The temporal symmetry mark-recapture models introduced by Pradel (1996) are relatively new and have not received wide use. This study is an early empirical application of the λ-parameterization, although the γ-parameterization has been used to calculate recruitment rates for a few populations of birds (Pradel *et al.*, 1997; Schaub *et al.*, 1999; Oro & Pradel, 2000). This study also joins the small number of matrix models that have explicitly included population gains due to immigration (see also Wootton & Bell, 1992). Matrix models have been used to estimate rates of population change for a wide range of vertebrate taxa (e.g. Cunnington & Brooks, 1996; Hiraldo *et al.*, 1996; Crooks *et al.*, 1998; Woodworth, 1999), but populations are usually treated as closed and the problem of distinguishing mortality and emigration is overlooked (Haydon *et al.*, 1999). We first compare $\hat{\lambda}$ from the ratio, temporal symmetry and matrix methods and then make recommendations from our empirical results.

Evaluating the precision and accuracy of $\hat{\lambda}$ from the three different methods is difficult without benchmark values for comparison. A true λ can be set in a simulation study (e.g. Bart, 1995), but is usually impossible to measure for a wild population of free-living vertebrates. In the rare cases where a complete population census is possible, then use of mark-recapture and matrix methods becomes unnecessary because $p = 1$ and $\hat{\lambda}_{\text{obs}} = \text{true } \lambda$, respectively. Thus, a consideration for empirical comparison is that field projects will only offer alternative estimates of λ.

Despite the potential pitfalls of using the ratio method, $\hat{\lambda}_{\text{obs}}$ performed quite well and fell within the 95%CI of $\hat{\lambda}_{\text{rea}}$ and $\hat{\lambda}_{\text{asy}}$ in a majority of years. This may have been the case because resighting rates were close to unity for breeders and did not vary among years for non-breeders (this study, Sandercock *et al.*, 2000). Nonetheless, our analyses illustrate the inherent problems of using uncorrected counts to estimate $\hat{\lambda}$ because the lowest and the highest values of $\hat{\lambda}_{\mathrm{obs}}$ coincided with an increased effort to resight non-breeders in 1995 and 1996.

In our initial comparisons of $\hat{\lambda}$ from the three methods, we expected that $\hat{\lambda}_{\mathrm{asy}}$ would be best-suited as a benchmark for comparisons because the projection matrix incorporated all of our current understanding of the social system and demography of green-rumped parrotlets. However, the overall and annual estimates of $\hat{\lambda}_{\mathrm{rea}}$ from the temporal symmetry method were more precise than $\hat{\lambda}_{\mathrm{asy}}$ from the matrix method. The 95%CI of $\hat{\lambda}_{\mathrm{asy}}$ may have been wider than $\hat{\lambda}_{\mathrm{rea}}$ because the matrix model required estimates of 10 vital rates (or 13 including p) whereas the temporal symmetry models required estimates of only one parameter (or three including ϕ and p). The 95%CI of $\hat{\lambda}_{\mathrm{asy}}$ could also have been influenced by our methods for calculating the variance of $\hat{\lambda}_{\mathrm{asy}}$. We used analytical approach to calculate var($\hat{\lambda}_{\mathrm{asy}}$), but the variance could also have been estimated by bootstrapping annual estimates of the vital rates (Ebert, 1999). However, confidence intervals from analytical and bootstrapping approaches are generally in agreement if the coefficients of variation for vital rates are relatively small (Alvarez-Buylla & Slatkin, 1994), which was the case here.

In certain years, $\hat{\lambda}_{\mathrm{asy}}$ appeared to be an unrealistic prediction of population change (e.g. $\hat{\lambda}_{\mathrm{asy}} = 2.08$ in 1991 for males), and was markedly different from $\hat{\lambda}_{\mathrm{rea}}$ (percentage difference $> \pm 30\%$). While $\hat{\lambda}_{\mathrm{asy}}$ was based on a finer understanding of parrotlet demography, $\hat{\lambda}_{\mathrm{asy}}$ also appeared to be sensitive to poor parameter estimates for a handful of vital rates, particularly the transitional probabilities of becoming a breeder. Thus, the trade-off between biological realism and accuracy in $\hat{\lambda}$ was better met by the temporal symmetry than the matrix method.

Two caveats should be considered in evaluating our results. First, we applied the three methods to field data on females and males from the same study population. Some congruence in annual estimates of population change might have been expected because all analyses were based on the same dataset and because the dynamics of the two sexes could not be considered independent. Second, population numbers of parrotlets were apparently stable for the duration of our study. In conservation problems, however, it is in scenarios where populations are declining that these methods could have their greatest utility. While $\hat{\lambda}$ from the temporal symmetry and matrix methods were congruent for a stable population, this might not be the case if rates of population change were markedly different from 1.

With these cautions, some recommendations can be made regarding the relative merits of the ratio, temporal symmetry and matrix methods for estimating rates of population change. The ratio method required the least amount of information and was simple to calculate. Our observation that $\hat{\lambda}_{\mathrm{obs}}$ performed well should not be taken as an endorsement of this approach. Nevertheless, this method may be useful for certain conservation applications where limited resources preclude more rigorous analyses. If so, $\hat{\lambda}_{\mathrm{obs}}$ should only be presented if accompanied by appropriate caveats.

The matrix method required the most information but also allowed flexibility in specifying life-stages and their rates. An advantage of matrix methods is that they yield familiar metrics such as the stable stage distribution (**w**), the stage-specific reproductive value (**v**), and elasticities (*e*), which can be used to assess population status, and to predict the likely effects of changes in vital rates (Doak & Morris, 1999; de Kroon *et al.*, 2000). The poor performance of $\hat{\lambda}_{\mathrm{asy}}$ in a subset of years is not an indication that matrix methods are faulty, rather that our particular model of parrotlet demography may have been overparameterized. Better success might have been obtained if the matrix model had been parameterized differently: by pooling birds of different social status, or by using an age- instead of stage-structured model. Another consideration in using matrix methods is the asymptotic nature of the metrics derived from projection matrices. Differences between $\hat{\lambda}_{\text{rea}}$ and $\hat{\lambda}_{\text{asy}}$ are to be expected if there is a mismatch between the actual frequency of non-breeders and breeders in a given year and the asymptotic stable stage distribution. However, this bias is likely to be small for parrotlets because the damping ratio is high for this population model (Sandercock & Beissinger, unpublished manuscript).

The temporal symmetry method was easier to compute than the matrix method because only detections were used for direct estimation of λ. Like the CJS model from which it is derived, parameter estimates from the temporal symmetry model may be biased if ϕ or p contain heterogeneity due to age-structure or trap response (Nichols & Hines, 2002). Our results suggest that if the assumptions of the temporal symmetry model are met, $\hat{\lambda}_{\text{rea}}$ may be as good or superior to $\hat{\lambda}_{\text{asy}}$. A current advantage of matrix methods, however, is that they allow for a mechanistic analysis of the processes responsible for population change (Caswell, 2001). Empirical examples are scarce because temporal symmetry methods are relatively new, but mark-recapture methods can also be used to evaluate demographic contributions to λ. For example, the temporal symmetry models can be used to model $\hat{\lambda}_{\text{rea}}$ as a function of environmental covariates. Nichols *et al.* (2000) and Nichols & Hines (2002) have also shown that seniority probabilities (γ) are analogous to the elasticities derived from matrix methods. Unlike matrix methods, direct measures of $\hat{\lambda}$ and $\hat{\gamma}$ from mark-recapture data are not based on asymptotic assumptions, Thus, $\hat{\lambda}_{\text{rea}}$ may be more useful for characterizing populations over short periods of time or in variable environments (Nichols *et al.*, 2000). In conclusion, the greater biological realism offered by matrix methods has trade-offs, and temporal symmetry models are a useful shortcut for obtaining robust estimates of rates of population change.

Acknowledgements

We dedicate this paper with gratitude to Evan G. Cooch for his encouragement and mentorship, and for introducing B. K. Sandercock to mark-recapture methods in a graduate seminar in 1994. We thank Sr Tomás Blohm for encouraging us to study parrotlets on his private ranch in Venezuela, and the many field assistants and graduate students who worked hard to help us to collect the demographic information that is summarized here (listed in Sandercock *et al.*, 2000). A. B. Franklin and R. Green kindly invited us to participate in the session of direct estimation of λ at the EURING 2000 meeting. J. D. Nichols and J. E. Hines shared an unpublished manuscript, H. Caswell and L. S. Mills critiqued our matrix model, and E. G. Cooch, K. Martin and two anonymous reviewers made constructive comments on previous versions of this manuscript. B. K. Sandercock was supported by a Killam Postdoctoral Fellowship from the University of British Columbia, and field research was supported by grants to S. R. Beissinger from the National Geographic Society and the National Science Foundation (DEB-9503194, IBN-9407349).

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