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LETTER

Demographic origins of skewed operational and adult sex ratios: perturbation analyses of two-sex models

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Abstract

Skewed sex ratios – operational (OSR) and Adult (ASR) - arise from sexual differences in reproductive behaviours and adult survival rates due to the cost of reproduction. However, skewed sex-ratio at birth, sex-biased dispersal and immigration, and sexual differences in juvenile mortality may also contribute. We present a framework to decompose the roles of demographic traits on sex ratios using perturbation analyses of two-sex matrix population models. Metrics of sensitivity are derived from analyses of sensitivity, elasticity, life-table response experiments and life stage simulation analyses, and applied to the stable stage distribution instead of lambda. We use these approaches to examine causes of male-biased sex ratios in two populations of green-rumped parrotlets (*Forpus passerinus*) in Venezuela. Female local juvenile survival contributed the most to the unbalanced OSR and ASR due to a female-biased dispersal rate, suggesting sexual differences in philopatry can influence sex ratios more strongly than the cost of reproduction.

Keywords

Elasticity, *Forpus passerinus*, life stage simulation analysis, life table response experiment, mating competition, sensitivity, sex ratio, stable stage distribution, two sex population model.

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INTRODUCTION

The operational sex ratio – the number of adult males to adult females available to mate in a population – is thought to be an important driver of intra-sexual competition, sexual selection and the evolution of sex differences (Emlen & Oring 1977; Kvarnemo & Ahnesjö 1996; Kokko & Monaghan 2001; Clutton-Brock 2007). While the mechanisms underlying sex differences in reproductive competition may be more diverse and complex than initially realized (Roughgarden *et al.* 2006; Clutton-Brock 2007; Fitze & Le Galliard 2008), the operational sex ratio (OSR) has remained a central tool in understanding and predicting the direction of sexual selection.

Skewed OSRs may arise from sexual differences in parental investment and behaviours that reduce the availability of individuals to mate (i.e., 'time in' and 'time out' from mating) and from sexual differences in adult survival rates due to the cost of reproduction that affect the adult sex ratio (ASR) (Emlen & Oring 1977; Clutton-Brock & Parker 1992; Kvarnemo & Ahnesjö 1996; Ahnesjö *et al.* 2001; Simmons & Kvarnemo 2006). However, a skewed OSR may arise from an unbalanced ASR caused by skewed sex-ratio at birth, sex-biased dispersal (Clarke *et al.* 1997) and immigration, and sexual differences in juvenile mortality (Clutton-Brock 2007; Donald 2007). In other words, any processes that lead to an unbalanced population sex ratio could skew the OSR. Measuring the influence of these processes on generating the OSR may be key to understanding different life histories driven by a skewed or variable OSR, such as mating systems, sexual selection, or migratory strategies (Kokko & Monaghan 2001; Donald 2007; Kokko & Jennions 2008).

Four issues complicate estimating OSR in natural populations and determining the relative importance of the factors affecting it. First, defining which males and females are available to mate is challenging and debate exists on how to correctly measure OSR (Houston *et al.* 2005; Kokko & Jennions 2008). Individuals already committed to parental activities or to reproducing together (e.g., established pairs) could be removed from the total counts of each sex to estimate the sex ratio of individuals available to mate (Clutton-Brock & Parker 1992; Kvarnemo & Ahnesjö 1996). However, ASR has often been used as a proxy of OSR, especially in experimental studies where conditions are manipulated so that all adults contribute to the OSR (Kokko & Jennions 2008). Second, the time period for estimating OSR is important to define carefully (Kvarnemo & Ahnesjö 1996). Third, a straightforward analytical method is required to jointly analyse the impact of all demographic components affecting the ASR and OSR (Donald 2007; Caswell 2008). Fourth, obtaining an unbiased estimate of OSR or ASR in natural populations is often difficult because the behaviour of males and females differs (Vanderkist *et al.* 1999; Donald 2007; Townsend & Anderson 2007). This necessitates estimating sex-specific probabilities of detection to produce unbiased estimates of survival rates and population counts (Lebreton *et al.* 1992; Nichols *et al.* 1994; Townsend & Anderson 2007).

We present a framework using discrete-time population models to decompose the roles of the cost of reproduction expressed as a sex-specific cost on survival and/or the future chance of breeding (Reznick 1992), sex ratio at fledging, immigration and other demographic rates on OSR, as measured by both ASR and estimators that qualify mate availability. Whereas previous attempts have evaluated the impact of a skewed OSR on population growth rate (Rankin & Kokko 2007; Becker *et al.* 2008), we present sensitivity, elasticity and life-table response experiments for matrix population models that evaluate the contribution of each demographic parameter to the OSR, and examine the effect of their variation on the OSR by adapting life-stage simulation analyses (Wisdom & Mills 1997). A complementary approach was recently developed by Caswell (2008). We then examine the processes that cause male-biased sex ratios (SR) in two populations of green-rumped parrotlets (*Forpus passerines*, Linnaeus) in Venezuela using 15 years of demographic data to parameterize a matrix model and examine the influence of its parameters on the SR. We use multi-state capture-recapture methods to estimate the SR, adult and juvenile survival, and breeding probability to account for heterogeneity in detectability between males and females (Nichols *et al.* 1994; Lebreton & Pradel 2002).

Green-rumped parrotlets represent a good model for evaluating the OSR. Both adults and nestlings are plumage dimorphic (Waltman & Beissinger 1992), providing sex-specific demographic data through the entire lifespan. This species is both socially and genetically monogamous (extra-pair paternity < 8%; Melland, 2000), with both parents providing care until fledging (Waltman & Beissinger 1992). Parrotlets do not reproduce in their natal year, but both sexes breed as yearlings. There is a high proportion of non-breeding parrotlets, especially among males, and a male-biased ASR (Sandercock *et al.* 2000; Beissinger 2008). Parrotlets nest in boxes that are distributed in two populations (upland and lowland) separated by ~600 m of forest that differ in elevation and soil type, which results in different flooding regimes and vegetation. The upland site is drier and supports more parrotlets, whereas the lowland population is wetter and tends to support fewer birds (Beissinger 2008).

PERTURBATION ANALYSES OF THE SEX RATIO

Age or stage-structured matrices are classical, discrete-time, population models (Caswell 2001). They are commonly used in ecology or evolutionary biology to: (i) estimate the sensitivity and elasticity of the asymptotic growth rate (λ) of a population to an absolute or proportional change, respectively, in a vital rate (e.g., survival, growth or reproduction)(Caswell 1978; Benton & Grant 1999); (ii) analyse how differences between vital rates in two matrices contribute to differences in λ using a fixed-effect life table response experiment (LTRE) (Caswell 2001; chap. 10); and (iii) examine how temporal variation in vital rates affects variation in λ through life stage simulation analysis (LSA) (Wisdom & Mills 1997; Wisdom *et al.* 2000) or random design LTRE analysis (Caswell 2001). Analyses of the sensitivity of the stable-stage distribution have less commonly been used, but have been applied to test theories about maximizing fitness (Caswell 1980), and to study the impact of variation of the stable-age distribution on λ (Caswell 2001; p. 247) or on the population momentum (Koons *et al.* 2007).

We can apply similar approaches to analyse the sensitivity of the SR by first developing a two-sex matrix model (Caswell 2001; chap. 17). Two sex models are useful when demographic rates vary by sex. Demographic estimates are used to construct matrix elements separately for each sex, and they are linked by a marriage and birth function that incorporates the demographic interactions between the sexes. Two-sex models are non-linear when they are constructed so that reproduction depends on the relative abundances of the sexes (Caswell 2008). Reproduction becomes limited by the scarcer sex and this is termed the 'marriage squeeze' (Schoen 1983). Human demographers have examined a variety of ways of constructing marriage functions (Pollak 1986). Because of the non-linearity of two sex-models, analyses of sensitivity of the stable-stage distribution are treated as analysis of the equilibrium of a non-linear model (Caswell 2001, 2008).

Reproduction events do not depend solely on the availability of partners, and environmental factors, such as climatic variation and the availability of food or nest sites, may play a major role. Because disentangling different sources of variation can be complex, an alternative approach is to formulate a linear two-sex model that includes breeder and non-breeder nodes, and a transition parameter that reflects the likelihood of becoming a breeder. While the probability of becoming a breeder does not explicitly incorporate mating as a function of the abundance of the opposite sex, mate availability implicitly affects our measure of the probability of breeding as well as other factors that delay breeding. Then, analyses of sensitivity of the stable-stage distribution can be approached more classically as an eigenvector perturbation problem (Caswell 2001 p. 247; Caswell 2008). A single-sex model with a similar structure provided an accurate description of the demography and population dynamics of green-rumped parrotlets (Sandercock *et al.* 2000; Sandercock & Beissinger 2002). The two-sex, pre-breeding model (Fig. 1a) is expressed as a matrix $\boldsymbol{M}$ that provides the parameters for projecting a vector of population size $\boldsymbol{n}$ of four stages (non-breeding females, breeding females, non-breeding males and breeding males) from time t to $t + 1$ as

$$n_{t+1} = \boldsymbol{M} \times n_t, \tag{1}$$

where non-breeding individuals are potentially are available to reproduce but do not mate.

We have chosen to estimate OSR on an annual basis coinciding with the onset of breeding, which matches the annual time-step and events encapsulated in our pre-breeding matrix model. The onset of breeding is arguably the most appropriate time to estimate OSR because it quantifies all potential individuals competing to reproduce at the time when competition for mates is likely to be the most intense. Modelling within-breeding season changes in OSR might be possible by constructing multiple seasonal or submatrices using smaller time steps if such data were available (Lima *et al.* 2003).

Matrix models are flexible in their structure and can account for behavioural differences and mating systems through the design of different nodes. In the case where all mature adults of both sexes are considered available and ready to mate at the beginning of the breeding season, such as polygynous species or monogamous species where pairs are capable of changing partners, OSR = ASR. A model with two nodes for each sex (breeder and non-breeder), as discussed above for parrotlets, accommodates this situation (Fig. 1a). Alternatively, adults in pair bonds that persist for consecutive mating seasons may be unavailable to breed. The pool of available mates can be formulated by providing a separate node for individuals previously paired with the same partner (OP for 'Old pairs'), who would not be considered operational, from individuals who competed with other non-breeders (NB) and successfully formed new pair bonds (NP)(Fig. 1b). In this case, OP individuals would be excluded from the estimate of OSR, which would be the ratio of NP to NB individuals. We called this index the qualified sex ratio (QSR) following Ahnesjö *et al.* (2001). We can also apply the QSR to green-rumped parrotlets. Their pair bond fidelity is very high, as only 1–2% of pairs divorce within and between years, but 75% of the pairs nested together for only 1 year due to mortality of a pair member (Beissinger 2008). Other ways to qualify OSR can be derived from this general approach through the delineation of nodes that represent behavioral or demographic categories of individuals.

Regardless of how they are defined, SR can be deduced from the stable stage-distribution of the two-sex population model, which in turn is the right eigenvectors $\boldsymbol{w^1}$ associated with the dominant eigenvalue (λ_1) of the stage-structured matrix $\boldsymbol{M}$ as:

$$\mathrm{SR} = \sum w^1_{\mathrm{males}} / \sum w^1_{\mathrm{females}} \tag{2}$$

with subindices referring to the vector elements corresponding to each sex. In the parrotlet example of OSR = ASR, the right eigenvector $\boldsymbol{w^1}$ has four components reflecting the four stages of the life cycle (Fig. 1a): $w^1{}_1$ the proportion of non-breeding females, $w^1{}_2$ the proportion of breeding females, $w^1{}_3$ the proportion of non-breeding males, and $w^1{}_4$ the proportion of breeding males and

$$\mathrm{ASR} = (w^1_3 + w^1_4)/(w^1_1 + w^1_2) \tag{3a}$$

For the formulation where OSR = QSR, there are six different stages in the life cycle (Fig 1b): $w^1{}_1$ the proportion of non-breeding females, $w^1{}_2$ the proportion of breeding females in new pairs, $w^1{}_3$ the proportion of breeding females in OP, $w^1{}_4$ the proportion of non-breeding males, $w^1{}_5$ the proportion of breeding males in new pairs and $w^1{}_6$ the proportion of breeding males in OP, and

$$\mathrm{QSR} = (w^1_4 + w^1_5)/(w^1_1 + w^1_2) \tag{3b}$$

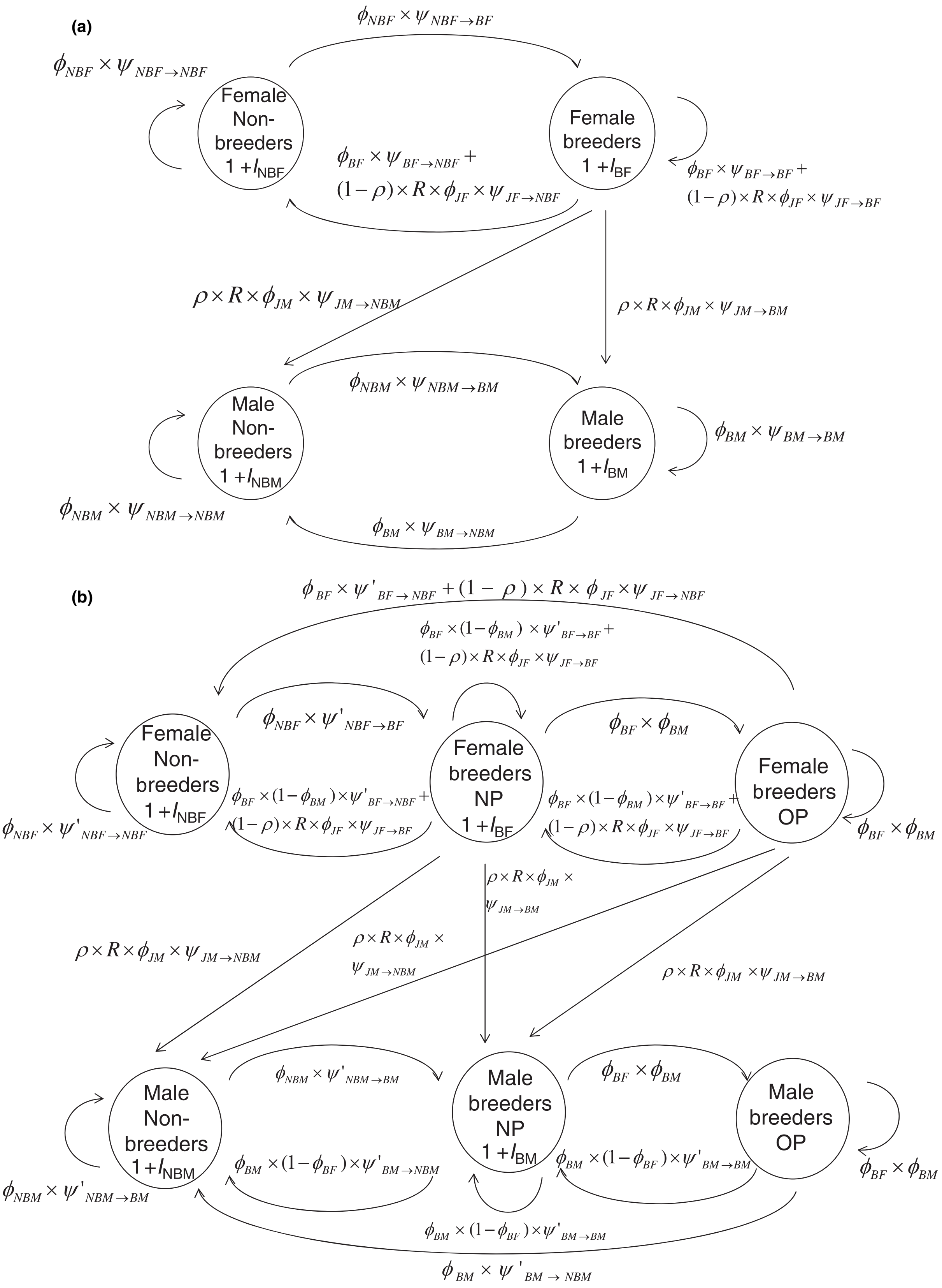
From the stable structure of the population and the asymptotic SR, one can examine the sensitivity of SR to changes in a demographic parameter θ:

$$\frac{d\mathrm{SR}}{d\theta} = \sum_{k=1}^{n} \frac{\partial \mathrm{SR}}{\partial w^1_k} \frac{\partial w^1_k}{\partial \theta} \tag{4}$$

$$\text{with}\, \frac{\partial w^1_k}{\partial \theta} = \sum^{j} \sum^{i} \frac{\partial w^1_k}{\partial a_{i,j}} \frac{\partial a_{i,j}}{\partial \theta}, \tag{5}$$

where $a_{i,j}$ is the matrix entry of row i, and column j. Finally, $\frac{\partial w^1_k}{\partial a_{i,j}}$ are the sensitivities of the right eigenvectors, which in the case of a ratio gives the same result whether or not the values are scaled, and are equal to:

$$\frac{\partial w^1_k}{\partial a_{i,j}} = w^1_j \sum_{m \neq 1}^{n} \frac{\bar{v}^m_i}{\lambda_1 - \lambda_m} w^m_k \tag{6}$$


(a)
$\phi_{NBF} \times \psi_{NBF\to BF}$
$\phi_{NBF} \times \psi_{NBF\to NBF}$
Female Non-breeders $1+l_{NBF}$
Female breeders $1+l_{BF}$
$\phi_{BF}\times\psi_{BF\to NBF} + (1-\rho)\times R\times\phi_{JF}\times\psi_{JF\to NBF}$
$\phi_{BF}\times\psi_{BF\to BF} + (1-\rho)\times R\times\phi_{JF}\times\psi_{JF\to BF}$
$\rho\times R\times\phi_{JM}\times\psi_{JM\to NBM}$
$\rho\times R\times\phi_{JM}\times\psi_{JM\to BM}$
$\phi_{NBM}\times\psi_{NBM\to BM}$
Male Non-breeders $1+l_{NBM}$
Male breeders $1+l_{BM}$
$\phi_{BM}\times\psi_{BM\to BM}$
$\phi_{NBM}\times\psi_{NBM\to NBM}$
$\phi_{BM}\times\psi_{BM\to NBM}$
(b)
$\phi_{BF}\times\psi'_{BF\to NBF} + (1-\rho)\times R\times\phi_{JF}\times\psi_{JF\to NBF}$
$\phi_{BF}\times(1-\phi_{BM})\times\psi'_{BF\to BF} + (1-\rho)\times R\times\phi_{JF}\times\psi_{JF\to BF}$
$\phi_{NBF}\times\psi'_{NBF\to BF}$
$\phi_{BF}\times\phi_{BM}$
Female Non-breeders $1+l_{NBF}$
Female breeders NP $1+l_{BF}$
Female breeders OP
$\phi_{NBF}\times\psi'_{NBF\to NBF}$
$\phi_{BF}\times(1-\phi_{BM})\times\psi'_{BF\to NBF} + (1-\rho)\times R\times\phi_{JF}\times\psi_{JF\to BF}$
$\phi_{BF}\times(1-\phi_{BM})\times\psi'_{BF\to BF} + (1-\rho)\times R\times\phi_{JF}\times\psi_{JF\to BF}$
$\phi_{BF}\times\phi_{BM}$
$\rho\times R\times\phi_{JM}\times\psi_{JM\to BM}$
$\rho\times R\times\phi_{JM}\times\psi_{JM\to NBM}$
$\rho\times R\times\phi_{JM}\times\psi_{JM\to NBM}$
$\rho\times R\times\phi_{JM}\times\psi_{JM\to BM}$
$\phi_{NBM}\times\psi'_{NBM\to BM}$
$\phi_{BF}\times\phi_{BM}$
Male Non-breeders $1+l_{NBM}$
Male breeders NP $1+l_{BM}$
Male breeders OP
$\phi_{BM}\times(1-\phi_{BF})\times\psi'_{BM\to NBM}$
$\phi_{BM}\times(1-\phi_{BF})\times\psi'_{BM\to BM}$
$\phi_{BF}\times\phi_{BM}$
$\phi_{NBM}\times\psi'_{NBM\to BM}$
$\phi_{BM}\times(1-\phi_{BF})\times\psi'_{BM\to BM}$
$\phi_{BM}\times\psi'_{BM\to NBM}$

where λ_m is the m$^{\text{th}}$ eigenvalue associated with the right eigenvector w^m and the conjugate left eigenvector $\bar{v}^m$ (Caswell 1980, 2001 p.250). In the same way, the elasticity can be estimated as the proportional response of the OSR to a proportional perturbation of a demographic parameter θ (Caswell 2001 p. 226) as:

$$e(\theta) = \frac{\theta}{SR}\frac{dSR}{d\theta}. \quad (7)$$

The demographic parameters that contribute most to skew the SR can be determined using LTRE (Caswell 2001 p. 267). The 'experiment' compares the effect of differences between male and female vital rates on the SR; whereas the 'control' gives the value of the SR if demographic parameters did not differ between the sexes. Modifying the LTRE, we can define the contribution C(θ) of each demographic parameter to the observed SR as:

$$C(\theta) = (\theta^{\text{males}} - \theta^{\text{females}})\frac{\partial SR}{\partial \theta} \quad (8)$$

where $\frac{\partial SR}{\partial \theta}$ is the sensitivity of SR to changes in a demographic parameter θ of a matrix $\boldsymbol{M'}$ where $\boldsymbol{M'} = (\mathbf{M} + \mathbf{M}_0)/2$, $\boldsymbol{M}$ is the stage-structured matrix with male and female rates as defined above, and $\boldsymbol{M_0}$ is the matrix of a theoretical population which is obtained by assigning male demographic estimates to female as well as male parameters.

Sensitivity, elasticity and fixed effect LTREs are usually calculated from one set of mean, invariant vital rates, but the vital rates that often vary the most are the ones with the smallest elasticities (Pfister 1998; Wisdom *et al.* 2000). Life-stage simulation analysis represents a complementary approach to the matrix sensitivity/elasticity analyses because it evaluates the relative importance of each rate on the variation in annual SR, taking into account variation among rates (Wisdom *et al.* 2000; Cross & Beissinger 2001). Using estimates of vital rates and their annual variation, a probability distribution is specified from which vital rates are randomly and independently drawn to create a set of 1000 matrices. Sex ratios are then calculated for each matrix, and the coefficient of determination (r^2) is calculated between the value of each vital rate and the SR, or their log-transformed value if they are lognormally distributed. The r^2 indicates the variation in SR explained by each vital rate (Wisdom *et al.* 2000).

METHODS

Life cycle and matrix model structure

We constructed two two-sex, pre-breeding models (Fig. 1) described above with a female dominant birth function (i.e., birth rates depended on the number of females). Juveniles (i.e., hatch-year birds) were not explicitly represented in the model and nodes were only composed of adult stages (i.e., after hatch-year birds). For each sex, we distinguished between two adult stages – non-breeding adults and breeding adults, which in the QSR model were separated (Fig. 1b) between newly paired adults (NP) and adults paired to the same individual that they had mated with the previous year (OP). Transitioning from one breeding status to another depends on survival (ϕ) and transition probabilities (ψ). Both breeding and survival rates differ greatly between breeding and non-breeding stages for each sex, but were assumed to be equal for NP and OP breeding individuals (Sandercock *et al.* 2000; Sandercock & Beissinger 2002). New individuals in the population can be either immigrants or juveniles. Immigrants were incorporated by multiplying each stage class, except OP Breeders, by 1+ I, a stage-specific immigration rate (Appendix S1). Each breeding female produced R fledgings with a ρ proportion of males. Even though the SR at fledging was near unity, it varied slightly among years (Budden & Beissinger 2004). To explore the sensitivity of SR to variation in SR at fledging, we incorporated it explicitly in the model. Male and female fledglings can breed the following year ($\psi_{J \to B}$) or delay their first reproduction ($\psi_{J \to NB}$). For the sake of consistency and to maintain the same population trajectories for the two models (Fig. 1), we did not estimate different sets of parameters for each model. Instead, we reparameterized the ASR model transition probabilities (Fig. 1a) to accommodate the model structure required to quantify QSR (Fig 1b); as the divorce rate is negligible in parrotlets (Beissinger 2008), the transition from NP to OP was estimated by the probability that each member of the pair survives (see details in Appendix S1).

We parameterized separate matrix models for the two parrotlet populations. Transitions between the two populations were incorporated through immigration rates of new individuals originating from the other population. The rate of emigration was implicitly incorporated; transition probabilities within a population from one status to any other do

Figure 1 Life-cycle diagram composed of (a) four stages (non-breeding females, breeding females, non-breeding males, and breeding males) and (b) six stages (non-breeding females, newly-paired breeding females, previously-paired breeding females, non-breeding males, newly-paired breeding males and previously- paired breeding males) for green-rumped parrotlets based on pre-breeding censuses. Notation includes: ϕ = probability of local survival, ψ = probability of becoming or remaining a breeder, R = fecundity, ρ = primary sex-ratio, and I = immigration rate. Subscripts include: J = juveniles, NB = non-breeders, B = breeders, NP = new pair and OP = previous (old) pair, M = males, and F = females.

not sum to 1 and this difference represents the emigration rate to the other population. Models were parameterized using means and variances over the 16-year period of study.

Estimation of demographic parameters and observed sex ratios

We used capture-recapture data during the breeding season (May to November) for 1656 male and 939 female green-rumped parrotlets banded as chicks or adults between 1990 and 2006 in Hato Masaguaral, Guarico, Venezuela (8°34′ N, 67°35′ W). See Beissinger (2008) for details of the study site. Capture-recapture effort was focused on both breeding and non-breeding birds. A parrotlet was considered to be a breeder if it was associated with a nesting attempt during the year, regardless of the fate of the nest. Few breeders were overlooked each year because nest boxes were monitored daily 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 (Sandercock *et al.* 2000).

We used multistate capture-recapture models to account for variation in detection and survival probabilities associated with breeding status and location (Lebreton & Pradel 2002). These models included three kinds of parameters: recapture probability p, survival rate ϕ, and conditional transition probability ψ (Lebreton *et al.* 1992; Nichols *et al.* 1994). Males and females were classified for each in six categories or states: three states accounting for status (juveniles, breeders and NB) nested within two states accounting for location (upland and lowland). Juveniles were birds in their natal year, whereas NB were individuals that were not associated with a nesting attempt but older than 1 year (Sandercock *et al.* 2000). Multistate models were parameterized by a transition matrix and vectors of survival and resighting probabilities (See Appendix S2 for details of the model structure).

For all models, we began by testing whether our starting global model (survival, transition and capture probabilities being state-, time- or gender-dependent) provided an adequate description of our data, using the Goodness-of-fit test for multistate models implemented in program U-Care (Choquet *et al.* 2005). We then proceeded by modelling the capture probability first, in order to retain as much power as possible for tests on transition and survival probabilities (Lebreton *et al.* 1992), using program M-Surge (Choquet *et al.* 2004). Model selection procedure was performed based on the Akaike information criterion (AIC), where the model with lowest AIC was selected (Burnham & Anderson 2002).

The population model also incorporated immigration rates for both males and females. A straightforward method to estimate immigration rate, which is the number of new recruits not produced locally, is the reverse-time model (Pradel 1996). But in the case of age and stage structure, where samples include individuals marked as young and as adults, there is no approach for handling these models in a statistical framework at present (Sandercock 2006). Following the concept of the reverse-time modeling (Pradel 1996), immigration rates were estimated by reversing the capture-histories and, at each time step, dividing the number of birds captured for the first time by the number of birds recaptured at least once previously in the same population. However, newly banded birds might have been in the population for one or more years before first capture, which would result in a biased time-varying immigration estimate; years with lower capture effort might underestimate immigration if immigrants were missed, whereas years with greater capture effort might overestimate immigration if some birds captured for the first time had immigrated in previous years.

For each site, annual reproductive success (R) was estimated as the total number of offspring fledging from all nesting attempts divided by the number of recaptured breeding birds. Sex ratio at fledging was estimated for each site from the sex of birds banded at 24–27 days of age just prior to fledging (Stoleson & Beissinger 1997).

Finally, we developed an estimate of the SR by dividing the number of individuals of each sex detected in each stage class annually by the detection probabilities estimated by capture-recapture models. For each year i and each stage class or state r, the number of individuals is $\widehat{N}_i^r = n_i^r/\hat{p}_i^r$ (Nichols *et al.* 1994). Thus, the annual estimate of SR are given by the ASR:

$$\mathrm{ASR}_i = \frac{\widehat{N}_i^{\mathrm{NBmales}} + \widehat{N}_i^{\mathrm{Bmales}}}{\widehat{N}_i^{\mathrm{NBfemales}} + \widehat{N}_i^{\mathrm{Bfemales}}} = \frac{n_i^{\mathrm{NBmales}}/\hat{p}_i^{\mathrm{NBmales}} + n_i^{\mathrm{Bmales}}/\hat{p}_i^{\mathrm{Bmales}}}{n_i^{\mathrm{NBfemales}}/\hat{p}_i^{\mathrm{NBfemales}} + n_i^{\mathrm{Bfemales}}/\hat{p}_i^{\mathrm{Bfemales}}} \tag{9}$$

and the QSR:

$$\mathrm{QSR}_i = \frac{\widehat{N}_i^{\mathrm{NBmales}} + \widehat{N}_i^{\mathrm{NPmales}}}{\widehat{N}_i^{\mathrm{NBfemales}} + \widehat{N}_i^{\mathrm{NPfemales}}} = \frac{n_i^{\mathrm{NBmales}}/\hat{p}_i^{\mathrm{NBmales}} + f_{NP} \times n_i^{\mathrm{Bmales}}/\hat{p}_i^{\mathrm{Bmales}}}{n_i^{\mathrm{NBfemales}}/\hat{p}_i^{\mathrm{NBfemales}} + f_{NP} \times n_i^{\mathrm{Bfemales}}/\hat{p}_i^{\mathrm{Bfemales}}} \tag{10}$$

where f_{NP} is the proportion of newly paired birds among breeding individuals.

RESULTS

Unbiased estimate of sex ratios

We found evidence of several sources of heterogeneity in detecting parrotlets of different stages that would bias estimates of SR based only on counts of males and females.

Goodness of fit tests using Program U-CARE (Choquet *et al.* 2005) found that a global model differentiating birds from the two sites (upland and lowland), while pooling breeding and non-breeding birds, did not fit the data (females:$\chi^2 = 405$, $P < 0.001$, d.f. = 113; males: $\chi^2 = 474$, $P < 0.001$, d.f. = 208). Tests for transience (3G in Program U-CARE) and trap-dependence (M in Program U-CARE) were significant for both sexes, indicating strong heterogeneity in capture probabilities (females: $\chi^2 = 324$, $P < 0.001$, d.f. = 91 for Test 3G and $\chi^2 = 81$, $P < 0.001$, d.f. = 22 for Test M; males: $\chi^2 = 324$, $P < 0.001$, d.f. = 155for Test 3G and $\chi^2 = 150$, $P < 0.001$, d.f. = 53 for Test M). Once site and breeding status were taken into account, our general model met the assumptions of homogeneity (males: $\chi^2 = 273$, $P = 0.80$, d.f. = 294; females: $\chi^2 = 111$, $P = 0.99$, d.f. = 162). The best model had capture probabilities that differed between breeding and non-breeding birds for both males and females (see Appendix S3 for model selection results). All breeding females on both sites and upland breeding males were nearly always recaptured ($P = 1 \pm 0.001$), while the capture probability of lowland breeding males was slightly lower ($P = 0.979 \pm 0.018$). However, the average capture probability of NB was much lower and differed between the sexes (females: $P = 0.394 \pm 0.006$; males: $P = 0.482 \pm 0.001$).

Estimates of both ASR and QSR indicated a strongly male-biased SR based on both capture probabilities and numbers of recaptured birds (Fig. 2), and were strongly correlated (upland $r = 0.97$, $P < 0.01$; lowland $r = 0.96$, $P < 0.01$). ASR based on capture probabilities ranged over time from 0.56 to 3.02, QSR ranged from 0.55 to 3.33, and both were biased toward males in all but two of the 15 years. Over all years ASR averaged 2.09 ± 0.16 in the upland and 1.68 ± 0.13 in the lowland, and QSR averaged 2.29 ± 0.19 in the upland and 1.85 ± 0.18 in the lowland. These unbiased estimates were slightly greater than SR estimated without correcting for resighting probabilities (ASR upland: 1.90 ± 0.09; lowland: 1.56 ± 0.08, QSR upland: 2.06 ± 0.10; lowland: 1.56 ± 0.08).

Demographic rates: general pattern and differences between the two populations

Survival and breeding probability estimates differed greatly between the sexes and by breeding status (Table 1). The overall survival of breeding birds was 16% higher for males than for females. For both sexes, the annual probability of survival averaged 30 and 91% higher for breeding than for non-breeding males and females, respectively (Fig. 3), and breeding males and females had about twice as high a chance of breeding in the following year as non-breeding birds. The survival of juvenile males was only slightly lower than survival of non-breeding males, whereas juvenile females had the lowest survival; their values were ~60% less than survival of breeding females in both sites. The opposite was found for transition rates; juvenile females that

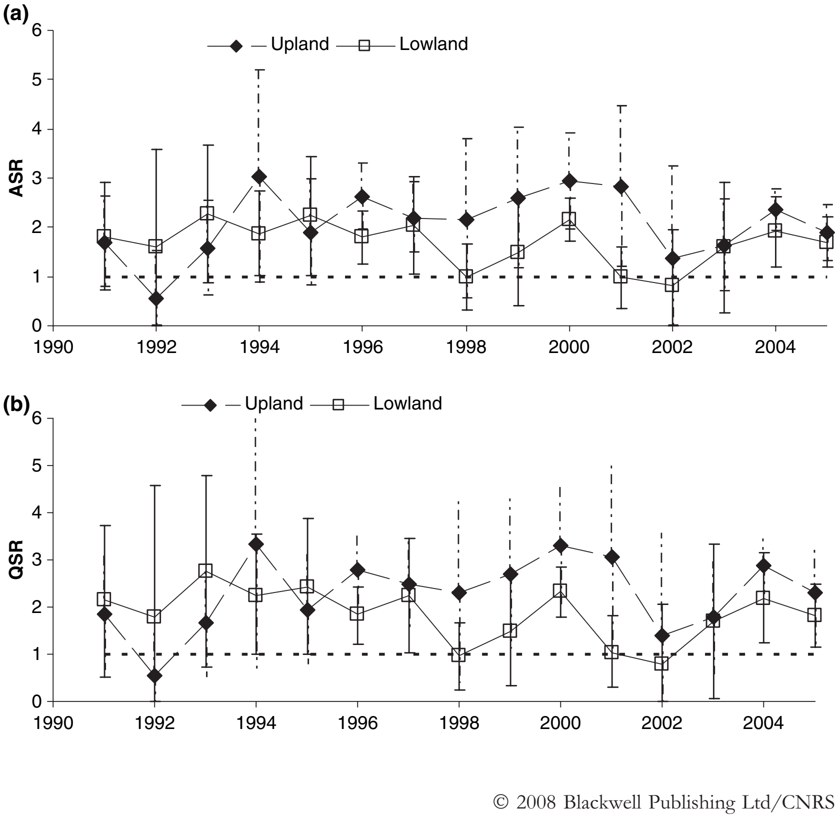


Figure 2 Annual sex ratios as (a) adult males/adult females (ASR), and (b) non-breeding and newly paired males/non-breeding and newly paired females (QSR) in the lowland and upland population of green-rumped parrotlets. Values above 1 indicate a male-biased sex ratio.

Table 1 Estimates of demographic parameters (mean and standard errors) for green-rumped parrotlets in the upland and lowland populations used in matrix population models

		Upland		Lowland	
Vital rate	Stage	Male	Female	Male	Female
Survival	Breeder	0.679 ± 0.026	0.618 ± 0.024	0.679 ± 0.026	0.536 ± 0.034
	Non-breeder	0.520 ± 0.016	0.352 ± 0.038	0.520 ± 0.016	0.248 ± 0.055
	Juvenile	0.506 ± 0.031	0.220 ± 0.026	0.505 ± 0.031	0.220 ± 0.026
Transition to breeding status	Breeder	0.616 ± 0.023	0.767 ± 0.027	0.678 ± 0.032	0.806 ± 0.033
	Non-breeder	0.295 ± 0.019	0.281 ± 0.045	0.278 ± 0.030	0.425 ± 0.093
	Juvenile	0.078 ± 0.009	0.249 ± 0.028	0.029 ± 0.007	0.124 ± 0.025
Transition to non-breeding status	Breeder	0.363 ± 0.026	0.211 ± 0.027	0.248 ± 0.031	0.161 ± 0.032
	Non-breeder	0.645 ± 0.021	0.626 ± 0.051	0.566 ± 0.038	0.446 ± 0.104
	Juvenile	0.840 ± 0.017	0.512 ± 0.042	0.750 ± 0.027	0.415 ± 0.070
Immigration	Breeder	0.247 ± 0.028	0.586 ± 0.076	0.330 ± 0.038	0.894 ± 0.167
	Non-breeder	0.379 ± 0.052	1.217 ± 0.129	0.444 ± 0.110	1.960 ± 0.201
Fecundity*		4.350 ± 0.418		4.281 ± 0.437	
Sex ratio at fledging*		0.484 ± 0.008		0.512 ± 0.014	

See (Appendix S1) for calculation of rates of transition to breeding status for breeders and non-breeders, and of immigration for the six-stage model adapted from estimates given here.
*Rates are same for males and females.

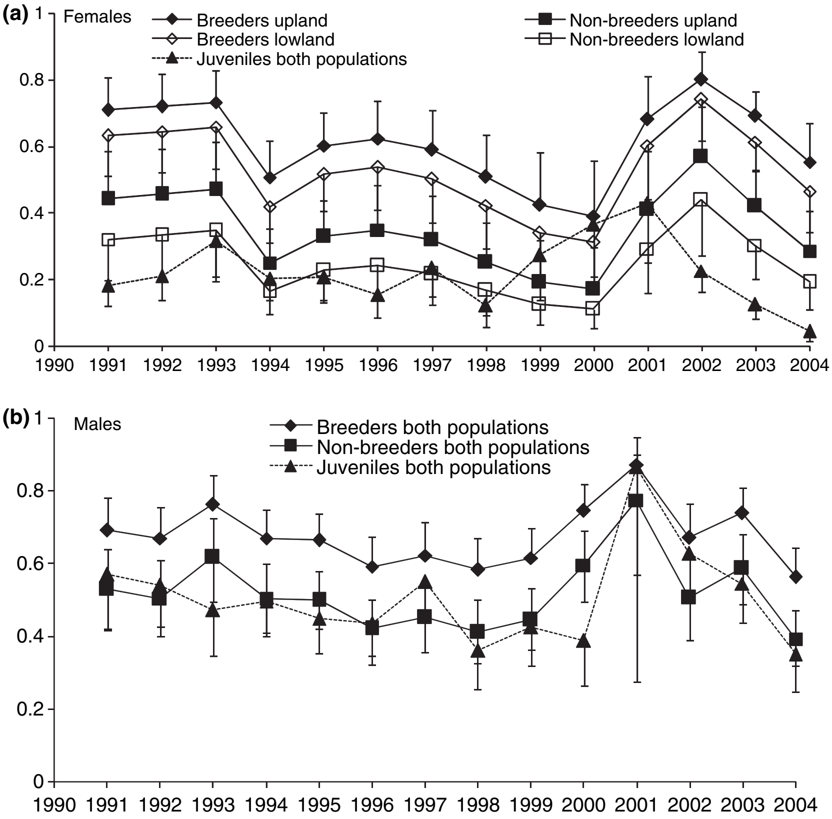


Figure 3 Estimates of juvenile and adult survival for green-rumped parrotlet by population and for each stage for (a) females and (b) males.

remained in their natal site or moved to the other site had a probability of breeding in their second year that was four times and nine times higher, respectively, than juvenile males. Although most juvenile males delayed their first reproduction, only 14% (± 2%) of these individuals moved to the other population, representing half as much emigration as occurred for juvenile females. This pattern was also reflected in adults, where per capita immigration rates were on average three times higher for females than for males, and between 35% and 120% higher for non-breeders than for breeders in both genders (Table 1).

Demographic rates also differed between parrotlet populations. Breeding and non-breeding females survived 15 and 42% better, respectively, in the upland than in the lowland (Fig. 3). Juveniles of both sexes were two times more likely to move from lowland to upland than vice-versa. Lowland immigration rates were more than 50% higher for females and 17% higher for males compared to the upland. Lastly, the average SR at fledging was slightly female-biased in the upland and slightly male-biased in the lowland (Table 1).

Origins of the skewed sex ratios from perturbation analyses

Asymptotic SR from the demographic model (Fig. 1) were all strongly male-biased. ASR was 1.92 for the upland and 2.27 for the lowland, and QSR was 2.38 for the upland and 3.13 for the lowland. These values fell well within the 95% confidence intervals of the long-term average OSRs for the upland (1.77–2.42 for ASR and 1.80–2.68 for QSR), but above lowland values (1.34–2.02 for ASR and 1.50–2.15 for QSR). Nevertheless, estimates based both on resightings of marked birds and from our demographic model indicate a strongly male-biased OSR.

Sensitivity and elasticity analyses yielded similar patterns for the potential influence of demographic rates on both estimators of QSR and ASR at both sites (Fig. 4). Given that SR are typically expressed as males : females, female parameters have a negative impact on QSR and ASR because an increase in a female vital rate decreases the asymptotic ratio. Sensitivity analysis identified SR at fledging, and juvenile, breeder and non-breeder survival for both sexes as the four most important vital rates potentially influencing SR (Fig. 4a). On the other hand, immigration rates and fecundity had a low impact on the SR. The influence of transition rates was intermediate. When rescaled to elasticity (Fig. 4b), SR at fledging again had the highest potential effect on both ASR and QSR, followed by breeding female survival, female probability of remaining breeder, and by non-breeding and juvenile male survival.

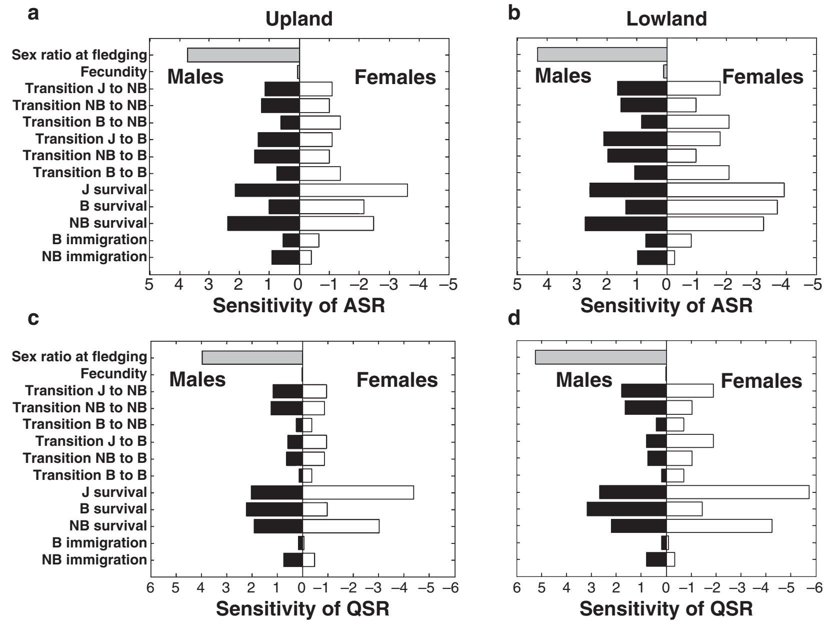
Both LTRE analysis (Fig. 5a) and LSA (Fig. 5b) clearly show that juvenile survival made the key contribution to the skewed SR observed. LTRE analysis indicated that differences between the sexes in the average rate of juvenile survival (0.506 for males vs. 0.220 for females) had 2.9 and 1.6 times the impact on the ASR and 3.8 and 2.0 times the impact on the QSR in the upland and lowland, respectively. The second most important parameter was the transition rate from juvenile to non-breeder. Although immigration rates contributed toward re-equilibrating the SR, rates of females entering the population were not nearly large enough to compensate for the difference in SR caused by sex differences in juvenile survival (Fig. 5a). Immigration rates of non-breeding females would need to be increased 2.3 times and 3.7 times for the upland and lowland, respectively, to compensate for the skewed ASR, and 3.3 times and 5.1 times to compensate for the skewed QSR. Sex ratio at fledging did not significantly contribute to the biased SR as its average value was close to 1 : 1 for both sites (Table 1). Results from the LSA (Fig. 5b) also found that the annual variation in female juvenile survival had the strongest influence on annual variation in SR (ASR upland: $r^2 = 0.24$; ASR lowland $r^2 = 0.15$; QSR upland: $r^2 = 0.20$; QSR lowland $r^2 = 0.18$). Survival of breeding females had the second strongest influence on ASR in the lowland followed by immigration of breeding females, whereas in the upland survival of non-breeding females was the second-most important parameter followed by survival of breeding females. Sex-ratio at fledging had little influence on annual variation in SR in the upland but had a higher impact in the lowland, where its annual variation explained 5.4% of the ASR variation and 11.7% of the QSR variation.

DISCUSSION

Most studies of the origin of SR variation are either empirical works based on comparative analyses using variation in SR and life histories among different taxa (Mayhew & Pen 2002), or are theoretical studies based on mathematical models of 'expected-future- fitness' or 'evolutionary stable strategy' (Seger & Stubblefield 2002). Linking these two approaches are demographic studies that use empirical data to test mathematical predictions, but such studies are rare (Kokko & Lopez-Sepulcre 2007). Our work provides an illustration of how demographic studies and models can provide insights to the origin and variation over time of skewed SR in natural populations. We modified classical, discrete-time, stage-structured matrices to examine SR at the onset of breeding in monogamous species with strong pair bond fidelity. Matrix models provide great flexibility to model complex behaviour, especially mating systems, through the design of life cycle nodes and by changing the mating function (Caswell 2001).

Quantifying OSR in natural populations remains a challenge for many reasons, among them is determining which individuals are available to mate (Houston *et al.* 2005; Kokko & Jennions 2008). We evaluated and compared two measures of OSR; one measure considered all individuals

(a) Sensitivity analyses



(b) Elasticity analyses

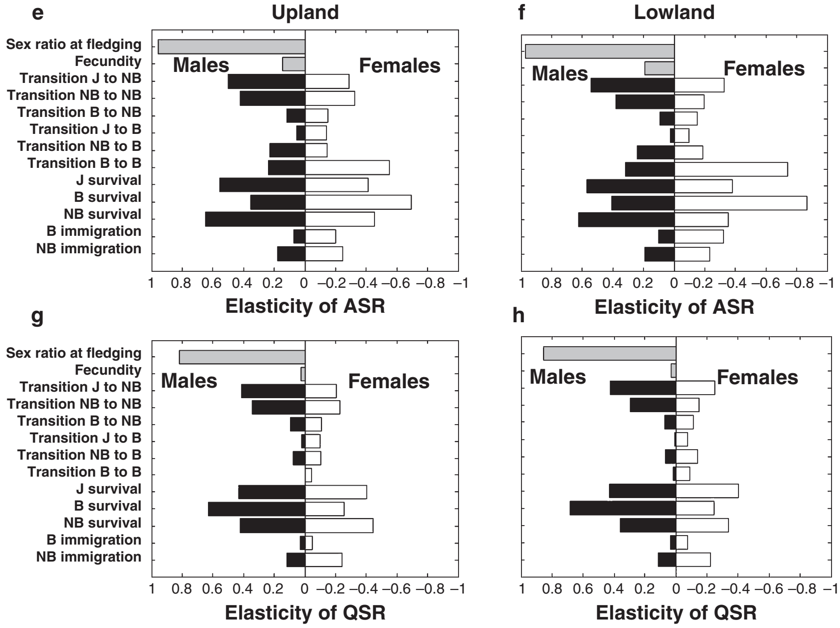
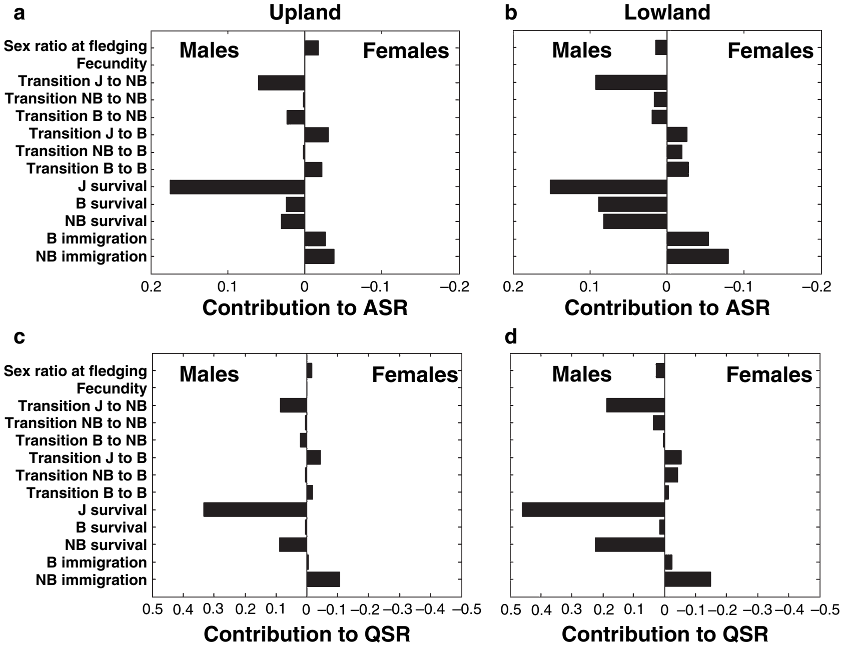


Figure 4 Sensitivity analysis (a) and elasticity analysis (b) of sex ratio of green-rumped parrotlets measured as the adult sex ratio (ASR) and the Qualified Ratio (QSR) in relation to demographic parameters (male parameters in black with positive values, female in white with negative values, and fecundity and primary sex ratio in grey) for upland and lowland populations. Notation includes J for juveniles, NB for non-breeders and B for breeders.

available to mate at the beginning of the breeding cycle, which was equivalent to the ASR, while a second measure excluded individuals previously paired from the pool of available or qualified mates QSR. Whether ASR is a useful index of OSR depends upon the mating system; in strictly monogamous species with biparental care, the 'time in' when an individual is ready to mate should be equal for males and females. Moreover, these ratios covary when sex roles are fixed (Kokko & Jennions 2008). In our study, both ASR and QSR were strongly correlated, were male-biased, and were affected by demography in similar ways (Figs. 2,4,5).

We present a straightforward analytical method to jointly analyse the impact of all demographic components affecting SR based on classical analyses of eigenvector perturbation (Caswell 2001, 2008). Although its use is limited to linear two-sex models, this method could probably be adapted for many species; when one sex is rare, which occurs with a

(a) LTRE analyses



(b) LSA analyses

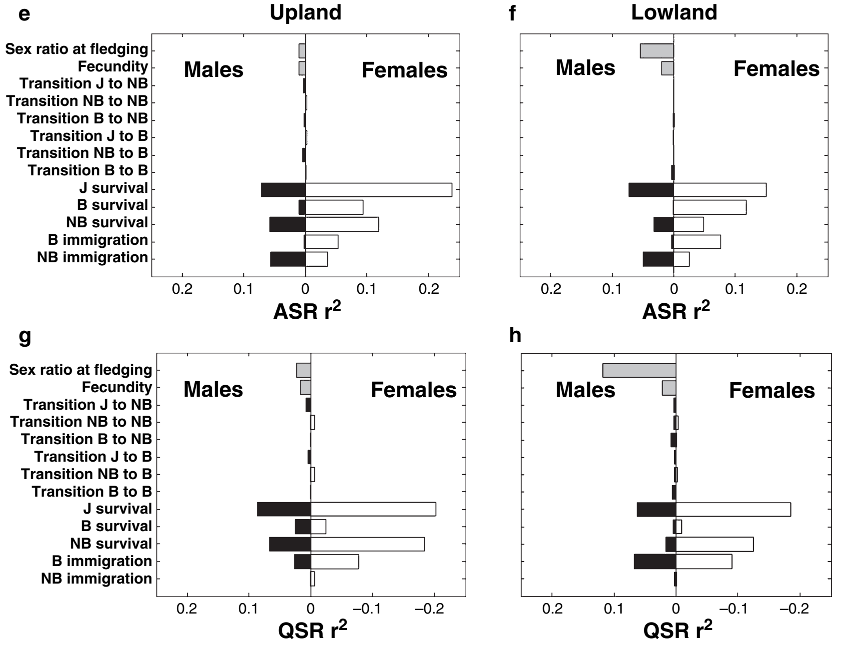


Figure 5 Contributions of different demographic parameters of green-rumped parrotlets in upland and lowland populations to sex ratio, measured as the adult sex ratio (ASR) and the qualified sex ratio (QSR), analysed by a (a) life table response experiment and (b) life-stage simulation analysis. In (a) the contribution represents differences in values of vital rates between males and females times the sex ratio sensitivity of each parameter (see eqn 8). In (b) plots represent the coefficient of determination (r^2) between the value of each vital rate and the ASR and the QSR respectively indicating the variance explained by each vital rate (male parameters in black, female in white, fecundity and primary sex ratio in grey). Notation includes J for juveniles, NB for non-breeders and B for breeders.

biased ASR, the one-sex dominant birth function used in this study and the minimum birth function lead to similar results (Caswell 2008). For more complex non-linear models, sensitivity of the stable-stage distribution can be approached as analysis of the equilibrium of a non-linear model (Caswell 2008).

We adapted four different measures of perturbation to analyse the impact on SR of demographic parameters: sensitivity, elasticity, LTRE and LSA. Although the distinctions among them can be subtle, each measure requires a different interpretation and each contributes to the overall understanding of how demographic components affect SR.

In the classical context of a perturbation analysis of population growth rate, sensitivity and elasticity can be categorized as 'prospective' analyses and LTRE and LSA as 'retrospective' analyses (Caswell 2000). Prospective analyses explore the functional dependence between a parameter (in our case SR) and one or more the vital rates, independent of any actual variation in those rates. They help to identify the factors that have the most *potential* to affect life history (Saether & Bakke 2000; van Tienderen 2000), or in our case the SR. In contrast, retrospective analyses are not concerned with the functional dependence of SR on the vital rates. They express variation in SR as a function of variation in the vital rates (Caswell 2000). In our study, they helped to identify the origin of the skewed SR through a fixed effect LTRE and which parameters best explained the variation of SR over time through LSA.

Both retrospective and prospective analyses emphasized the key contribution of male-biased juvenile survival to the highly skewed ASR and OSR in green-rumped parrotlets, whereas a cost of reproduction, expressed in this case as a higher male breeder survival, only played an intermediate role. Similar patterns occurred in both populations despite a strong disparity of habitat quality (Beissinger 2008), which is reflected in demographic differences of many traits between populations, such as female survival and breeding probabilities (Table 1). Sex- and population-differences in survival were not caused by differences in emigration, as the site fidelity of breeders of both sexes is very high and distances moved by breeders between years were small relative to the size of the study area (Sandercock *et al.* 2000). Moreover, the difference in survival between breeding males and females was 0.094 (Table 1), which represents a large effect compared to the average difference in avian mortality rates between the sexes (Liker & Szekely 2005). Despite the large difference in survival between parrotlet sexes, it contributed much less to the skewed OSR and ASR than the low rate of female juvenile survival (Figs. 4,5). Sex differences in the rates of immigration and survival of NB also contributed more to the skewed OSR and ASR than the cost of reproduction. Cost of reproduction can also affect an individual's probability of future reproduction. In such a case, one would expect to find a lower probability of breeding the following year for a breeding bird than for a non-breeding bird (Reznick 1992; Cam *et al.* 1998), which in turn would affect the OSR. In our study, we did not find such a pattern, indicating a cost of reproduction affected on survival, but not on future reproduction.

Our findings confirm recent studies contradicting classical sexual theory ~ the factors contributing to a skewed OSR. Theoretical models showed that OSR is not solely an index of differential parental investment and that the potential reproductive rates are not a good proxy of either OSR or of mating competition (Kokko & Monaghan 2001). The cost of reproduction could not explain a male-biased SR in monogamous Nazca boobies (*Sula granti*) because survival estimates differed little among breeding males and females (Townsend & Anderson 2007).

Sex differences in juvenile survival that drive the skewed OSR and ASR in parrotlets are probably due to two factors. First, it is very likely that the low survival rate of juvenile females compared to juvenile males was partly due to sex-biased dispersal and emigration in this species (Sandercock *et al.* 2000), a pattern that is typical in birds (Clarke *et al.* 1997; Becker *et al.* 2008). Our estimate of juvenile survival only reflects local survival and does not account for females that emigrate to other populations and survive. Sex differences in philopatry have a variety of potential causes, including inbreeding avoidance, intra-sexual competition, defense of territories by males prior to mating, and factors that may differentially affect the availability of mates and local resources to the sexes (Greenwood 1980; Ludwig & Becker 2006; Arlt & Part 2008). Second, juvenile females that remained in the study area dispersed farther than males and sex differences in juvenile survival may partly reflect dispersal-related mortality.

Although females, both non breeders and breeders, immigrated into both populations at much greater rates than their male counterparts (Table 1), female immigration rates were not large enough to compensate for the low female juvenile local survival in either parrotlet population. The difference between the flow of immigrants into the population and the rate of local juvenile survival, which accounts for losses from the population due to both emigration and mortality, may represent a cost of dispersal, where dispersing juvenile females experience higher mortality than philopatric juvenile males (Yolder *et al.* 2004). Alternatively, the abundance of nest sites that we have added may have created a source population (Pulliam, 1988) that exports juvenile females at a higher rate than nearby populations can produce potential female immigrants. Estimates of population growth from several methods indicate these two populations were stable or increasing populations in most years of study (Sandercock & Beissingere 2002).

Variation in SR at fledging did not explain much of the variation of SR observed in green-rumped parrotlets (Fig. 5), mainly because on average it was balanced between the sexes and varied little among years (Budden & Beissinger 2004). Nevertheless, sex ratios were extremely sensitive to changes in the SR of fledglings (Fig. 4). This suggests that adjustment of offspring SR has perhaps the greatest potential to impact the SR in birds.

Our findings generally support conclusions of recent analyses of the evolution of sex role divergence and mating systems (Kokko & Jennions 2008), which contradict the classical theory that anisogamy and male-male competition explain sexual differences in parental care patterns (Trivers

1972), and predict precisely our results: a monogamous mating system with both parents providing parental care in a strong male-biased ASR and OSR population. Our perturbation analyses (Figs. 4,5) confirmed that the higher cost of reproduction to females has little influence on the male-biased OSR, which instead is driven by sex differences in dispersal. Our results are also consistent with the consequences of the Fisher condition (Houston *et al.* 2005; Kokko & Jennions 2008): in both populations with a male-biased ASR, female juveniles have a higher probability of breeding than male juveniles. Furthermore, in the lowland population where our model yielded the strongest skew for OSR, non-breeding females also had a higher probability of becoming breeders than non-breeding males. The rarer sex in parrotlet populations had higher per capita reproductive success, whereas the most abundant sex had a lower probability of transitioning to become a breeder and required more time to find a mate. Given the choice to care or compete for males, the Fisher condition predicts selection for egalitarian parental investment (Kokko & Jennions 2008), which typifies the shared equal parental investments exhibited by parrotlets (Waltman & Beissinger 1992; Curlee & Beissinger 1995; Stoleson & Beissinger 1997).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Relationship between the four-stage and six-stage matrix models depicted with their life cycle diagrams in Fig. 1.

Appendix S2 Transition matrix and vectors of survival and resighting probabilities of the multistate capture-recapture model.

Appendix S3 Modelling capture (p), survival (ϕ) and transition (ψ) probabilities for adult green-rumped parrotlets for six states with two status (breeders and non-breeders) and two sites (upland and lowland), and two groups (males and females).

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