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Demographic sensitivity and persistence of the threatened white- and orange-bellied frogs of Western Australia

Abstract Anurans have been the subject of numerous experimental and monitoring studies, yet their autecology under natural conditions remains poorly understood. Previous work has focussed on the pre-metamorphic life stages, with data suitable for estimating demographic parameters for all life stages collected in few species. This deficiency has almost certainly confounded current views of amphibian autecology and understanding of which mechanisms of decline represent the greatest threats to the persistence of amphibian species. We used a stage-structured metapopulation model, parameterised with comprehensive field data, to explore the sensitivity of two species of myobatrachid frogs from the southwest of Australia, *Geocrinia alba* and *G. vitellina*, to changes in demographic parameters at all life stages. The simulation modelling indicated that the population dynamics of both species were consistently most sensitive to changes in juvenile survival, then to fecundity, and third to both adult survival and standard deviation of survival to about equal extent. In practical terms, this indicates that management interventions which attempt to mitigate reductions in juvenile survival are likely to be most successful in arresting anuran metapopulation declines.

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Introduction

Amphibian declines are now recognised as a global phenomena above and beyond the general biodiversity crisis, yet ecological theory has been able to provide little predictive insight into these problems (Alford and Richards 1999). Numerous experimental studies have been used to develop a mechanistic understanding of the impacts of various biotic or abiotic factors on one or two life stages of amphibians, often independent of previous or subsequent stages (e.g. Ovaska et al. 1997; Berger et al. 1998; Kiesecker and Blaustein 1998). Alternately, monitoring studies have focussed on measuring fluctuations in amphibian populations in relation to associated environmental factors (e.g. Fellers and Drost 1993; Sherman and Morton 1993; Stewart 1995; Gillespie and Hollis 1996; Meyer et al. 1998; Magnusson et al. 1999). Yet, as noted by Biek et al. (2002), although these approaches enable the detection of declines and the identification of potential causes, they are not sufficient to explain the dynamics of declines, nor for predicting which perturbations in vital rates are most likely to drive future declines. Further, many amphibian species occur as metapopulations, so the dynamics of local populations may be poor indicators of the species' overall dynamics (Alford and Richards 1999). A more comprehensive understanding of the problems of amphibian declines therefore requires a robust metapopulation dynamics context.

The dynamics of metapopulations can be conveniently explored via computer simulation models, providing a critical link to experimental and monitoring approaches (Boyce 1992). Although data inadequacies and simplifying assumptions can limit confidence in the absolute predictions of quantitative models (Ludwig

1999), their primary value lies in the identification of crucial life stages or processes. This is useful not only in aiding our understanding of ecological theory and species' autecology, but also in enabling conservation efforts to be concentrated appropriately (Reed et al. 1998; Coulson et al. 2001). Quantitative models can be used to identify key population parameters and the threats faced by a species or population, as well as to evaluate the likelihood that it will persist for a given time in the future (Brook et al. 2000). Because the most sensitive parameters require the most precise data, sensitivity analyses can also be used to focus researchers' efforts on improving estimates of the most important variables.

In this study we investigate the metapopulation dynamics of two threatened Australian myobatrachid frog species, *Geocrinia alba* and *G. vitellina* (Roberts et al. 1999), using a detailed stage-structured simulation model. *G. alba* and *G. vitellina* are restricted to corridors of riparian vegetation within extremely localised distributions in the lower southwest of Australia. *G. alba* occupies a range of 130 km^2 (Roberts et al. 1999), with an area of suitable habitat of less than 1.9 km^2 (Wardell-Johnson and Roberts 1993), and populations have been found in 88 localities (K. Williams, Conservation and Land Management W.A., unpublished data). Twenty three of these populations have apparently gone extinct since 1983 (Roberts et al. 1999) and have not been recolonised (Wardell-Johnson et al. 1995; Roberts et al. 1999). *G. vitellina* occupies a range of only 6.3 km^2 (Roberts et al. 1999) and has an area of suitable habitat of only 8 ha comprised of 11 known populations (K. Williams, unpublished data).

Conroy (2001) argued that the juvenile phase may be critical in the population dynamics of these species, because (1) it has an extended duration, (2) juveniles are more vulnerable than adults to the vagaries of the environment, and (3) most adults live to breed only once, so recruitment to the breeding population must be reliable. Using extensive life history and spatial data assembled as part of a broader study on the reproductive ecology and population biology of these species (Conroy 2001), we test the hypothesis that juvenile survival is a key parameter in the population dynamics of these species by exploring the sensitivity of their respective metapopulation models to changes in both demographic parameters and environmental factors.

Materials and methods

Model structure and parameterisation

We used a stage-structured, transition matrix modelling approach, based on the demographic parameters estimated in Conroy (2001), to explore the short- and long-term population dynamics of *G. alba* and *G. vitellina* metapopulations. Matrix projection methods simulate the changes in a population with a given age- or stage-structure through time (Caswell 2001). We built separate but similar models for *G. alba* and *G. vitellina* using RAMAS Metapop

v3 (Akçakaya 1998), a program designed for building spatially explicit metapopulation models with density-dependent, stochastic, stage-structured dynamics within each sub-population.

Stage structure

The models consist of only two stages and assume that all individuals of both species first reproduce in the second breeding season after metamorphosis. Stage one is the second year as a juvenile (i.e. the second year after metamorphosis), with the first year incorporated in the fecundity rate (see below). Stage two is a composite class consisting of all reproductive individuals. Each reproductive individual has a fecundity rate, f, derived as a product of mean clutch size (M), sex ratio (SR), proportion of females breeding each year (P_x), rate of survival to metamorphosis (φ_0), and rate of survival post-metamorphosis to become a 1-year-old (φ_1). The proportion of 1-year-old juveniles surviving to become 2-year-olds (and hence to reproduce) is φ_2, and φ_3 is the proportion of reproductive individuals (2+ years old) who survive to reproduce in the next breeding season. This results in the following transition matrix:

$$
\begin{array}{c}
 \\
\text{Time } t+1 \\
\text{Juveniles} \\
\\
\text{Breeding adults}
\end{array}
\begin{array}{cc}
\multicolumn{2}{c}{\text{Time } t} \\
\text{Juveniles} & \text{Breeding adults} \\
\left[\begin{array}{cc}
0 & M \cdot SR \cdot P_x \cdot \varphi_0 \cdot \varphi_1 \\
\\
\varphi_2 & \varphi_3
\end{array}\right]
\end{array}
$$

M and φ_0 were estimated during a 2-year study of the reproductive ecology of these species (Conroy 2001), while φ_1 and φ_2 were estimated during a 3-year mark recapture study on metamorphosing *G. alba* and *G. vitellina* recaptured as calling males at six *G. alba* populations and three *G. vitellina* populations (Conroy 2001). φ_3 was estimated during a 7-year mark recapture study of adult male *G. alba* and *G. vitellina* at three *G. alba* populations and two *G. vitellina* populations (Conroy 2001). We assumed a sex ratio of 1:1 and that all reproductive females (2+ years old) attempt to breed each year (Conroy 2001).

Population-specific transition matrices were derived for three *G. alba* and two *G. vitellina* populations for which long-term mark-recapture data was available. Fecundities were adjusted to match the finite rate of increase (λ) predicted by these population-specific matrices to the geometric mean λ derived from the mark-recapture studies, the rationale being that estimates of adult survival were deemed to be robust due to the long-term and intensive nature of the effort to quantify this parameter, but fecundities were more uncertain. A mean matrix for each species was used for all other populations. The population-specific and mean transition matrices for *G. alba* and *G. vitellina* are provided in Table 1.

Populations of *G. alba* occupy sites with varying levels of disturbance. To differentiate between populations on relatively undisturbed sites and those on disturbed sites, we imposed a "disturbance multiplier" on each element of the mean transition matrices at three levels: 1.0 (public estate), 0.98 (private tenure, uncleared), and 0.94 (private tenure, cleared).

Stochasticity

Environmental stochasticity

Environmental stochasticity was modelled by sampling the matrix elements from a lognormal distribution using the means and estimated standard deviations given in Table 1. Estimates of standard deviations for survival rates for reproductive animals, s_3, were derived from the mark-recapture analysis of calling males, after removing the effects of sampling error (Conroy 2001). Equivalent

Table 1 Population-specific and mean transition and standard deviation matrices for *Geocrinia alba* and *G. vitellina*

Species	Transition matrix	Standard deviation matrix
Site		
G. alba		
Boathaugh B	$\begin{bmatrix} 0 & 1.703 \\ 0.507 & 0.390 \end{bmatrix}$	$\begin{bmatrix} 0 & 0.978 \\ 0.224 & 0.224 \end{bmatrix}$
Bruce Road	$\begin{bmatrix} 0 & 0.624 \\ 0.528 & 0.390 \end{bmatrix}$	$\begin{bmatrix} 0 & 0.359 \\ 0.224 & 0.224 \end{bmatrix}$
Forest Grove South	$\begin{bmatrix} 0 & 1.633 \\ 0.486 & 0.293 \end{bmatrix}$	$\begin{bmatrix} 0 & 0.585 \\ 0.105 & 0.105 \end{bmatrix}$
Mean matrix	$\begin{bmatrix} 0 & 1.633 \\ 0.486 & 0.358 \end{bmatrix}$	$\begin{bmatrix} 0 & 0.841 \\ 0.184 & 0.184 \end{bmatrix}$
G. vitellina		
Spearwood North	$\begin{bmatrix} 0 & 1.713 \\ 0.445 & 0.334 \end{bmatrix}$	$\begin{bmatrix} 0 & 0.672 \\ 0.131 & 0.131 \end{bmatrix}$
Spearwood South	$\begin{bmatrix} 0 & 1.813 \\ 0.442 & 0.315 \end{bmatrix}$	$\begin{bmatrix} 0 & 0.996 \\ 0.173 & 0.173 \end{bmatrix}$
Mean matrix	$\begin{bmatrix} 0 & 1.763 \\ 0.444 & 0.325 \end{bmatrix}$	$\begin{bmatrix} 0 & 0.826 \\ 0.152 & 0.152 \end{bmatrix}$

estimates were unavailable for juveniles (i.e. φ_1, φ_2), so we used the estimate for reproductive animals (i.e. $s_1 = s_2 = s_3$) based on the assumption that environmental conditions would affect survival rates for both stages in a similar way. Applying the same logic, we multiplied the coefficient of variation of survival rates of reproductive animals:

$$CV = \frac{s_3}{\phi_3}$$

by the fecundity rate to derive the standard deviation for that parameter (s_f). This results in the following standard deviation matrix:

	Time t	
Time $t+1$	Juveniles	Breeding adults
Juveniles	$\begin{bmatrix} 0 \\ \\ s_3 \end{bmatrix}$	$\begin{matrix} f \cdot CV \\ \\ s_3 \end{matrix}$
Breeding adults		

The population-specific and mean standard deviation matrices for *G. alba* and *G. vitellina* are provided in Table 1.

Environmental correlation among patches

We arbitrarily assumed a 50% correlation in environmental stochasticity among populations. This is probably a reasonable assumption, given that all the populations are restricted to a geographically small area, and therefore experience similar temperature and rainfall regimes.

Catastrophes

We modelled two types of fire as rare "catastrophic" events affecting these metapopulations. Most fires are low intensity (cool) fuel-reduction burns, with occasional wildfires or changing conditions during a fuel-reduction burn resulting in a hot fire. We estimated the frequency of these two types of fire based on average fire rotation lengths, planned rotation lengths, and from our knowledge of local land management practices. For *G. alba* we imposed

different fire regimes on the basis of land tenure (public vs private estate). For *G. vitellina* we imposed separate fire regimes for populations inside and outside a fire exclusion zone within that species' range. We assumed that fire caused an immediate reduction in population size by 20% for cool fires and 50% for hot fires. Fire regimes are detailed in Table 2.

Density dependence

We used ceiling-type density dependence, which assumes density-independent growth below a maximum size (K) and a proportional truncation across stage classes when above K. Estimates for carrying capacity were not available for any *G. alba* or *G. vitellina* populations. We therefore assumed $K = 1.25N_{max}$, where N_{max} was the largest historical estimate of population size (N) at each population, except when $1.25N_{max} < 40$, in which case we assumed a minimum $K = 40$. There were only two *G. alba* populations for which no historical estimates of N were available. For these populations we also assumed $K = 40$. Initial N was derived from the most recent estimates of N at each population.

Dispersal

We estimated the number of effective migrants per generation, N_m, following Wright (1951),

$$N_m = \frac{1 - F_{st}}{4F_{st}}$$

where F_{st} is a measure of the allelic variation between, relative to within, populations. Driscoll (1998) calculated weighted mean F_{st} values of 0.444 for *G. alba* populations ($N_m = 0.31$) and 0.302 for *G. vitellina* populations ($N_m = 0.51$) sampled throughout their respective ranges, equating to a very low average patch-to-patch dispersal rate of less than 1 effective migrant per generation (actual rate would be higher, assuming some migrants failed to survive to breed). We used the average values of N_m as a basis for calculating distance-related dispersal rates as follows: (1) using the average K of all patches, we estimated the average proportional dispersal rate (APDR) that would result in the average N_m observed from the genetic data, (2) we calculated the average pairwise distance between all patches, and assumed the APDR was applied specifically at this average distance, (3) we then modified the average APDR for each pair of patches in the metapopulation, using the four-point categorical scale described in Table 3. This scale, which accounts for the distance between patches (following streams) and the quality of the intervening matrix, approximates the APDR when averaged across all patch pairs.

Analysis

Sensitivity of the model predictions to variation in input parameter values were evaluated to: (1) assess the effect of potential inaccuracies in parameter input values on model results and (2) indicate which parameters may be of particular significance for a species' dynamics. Our sensitivity analysis design incorporated both a classic one-way sensitivity analysis and a Latin Hypercube sensitivity analysis (see Iman et al. 1980). The latter approach permits the model parameters to be varied concurrently, thereby allowing for potential interactions. We considered three output or "state" variables: mean patch occupancy (MPO), mean final N (MFN), and the probability of extinction (PE), and we recorded values for each state variable at projection lengths of 10, 20, and 100 years, based on 1,000 stochastic replications for each scenario.

In the classic sensitivity analysis the model was first run with the best estimates of each of 11 key input parameters, then re-run with all parameters but one set at their best estimates, and one set at its upper or lower plausible bound (Table 2), repeated for all

Table 2 Input parameter values used for estimating the sensitivity of the *G. alba* metapopulation model to variation in a single parameter (*SE* = standard error, *BE* = best estimate)

Parameter	Lower	Best	Upper
Juvenile survival (φ_1,φ_2)	−1 SE	BE	+1 SE
Adult survival (φ_3)	−1 SE	BE	+1 SE
SD of survival (s_1,s_2,s_3)	0.5 BE	BE	1.5 BE
Fecundity (*f*)	0.75 BE	BE	1.25 BE
SD of fecundity (s_f)	0.5 BE	BE	1.5 BE
K-N multiplier factor	1	1.25	2
Cool fire impact (proportional reduction in *N*)	0.9	0.8	0.7
Hot fire impact	0.7	0.5	0.3
Fire frequency—*G. alba* [a]			
Public estate	0.10	0.14	0.33
Private estate	0.07	0.10	0.20
Fire mix—*G. alba* (cool fires, hot fires)[b]			
Public estate	0.13, 0.01	0.11, 0.03	0.09, 0.05
Private estate	0.07, 0.03	0.05, 0.05	0.03, 0.07
Fire frequency—*G. vitellina* [a]			
Fire exclusion zone	0.05	0.07	0.165
Outside fire exclusion zone	0.10	0.14	0.33
Fire mix—*G. vitellina* (cool fires, hot fires)[b]			
Fire exclusion zone	0.06, 0.01	0.03, 0.04	0.02, 0.05
Outside fire exclusion zone	0.13, 0.01	0.11, 0.03	0.09, 0.05
Patch correlation	0%	50%	100%
No fires	Zero frequency: cool and hot fires		
No *K*	Exponential growth model		
No dispersal	All patches entirely isolated		
EV for fecundity and survival normal	Not lognormal distribution (standard)		

[a] Ratio of cool fires to hot fires fixed, frequency of all fires varies

[b] Frequency of all fires fixed, ratio of cool fires to hot fires varies. Frequencies are listed as CF, HF. Low and high plausible bounds refer to bounds for hot fires

Table 3 Criteria used to estimate rates of dispersal between populations of *G. alba* and *G. vitellina*, based on distance between patches and the level of disturbance of the intervening matrix

Scale	Disturbed	Undisturbed	Estimated dispersal rate
0 No dispersal	> 500 m	> 1000 m	0
1 Highly improbable	401–500 m	601–1000 m	0.001
2 Improbable	301–400 m	401–600 m	0.005
3 Occasional	151–300 m	201–400 m	0.01
4 Frequent	1–150 m	1–200 m	0.03

parameters for a total of 23 simulations for each species. A sensitivity coefficient, C_p, was used to quantify the influence of a parameter, p, on a particular state variable, V (Drechsler et al. 1998), calculated for each relevant parameter as:

$$C_p = \left| \frac{\Delta V}{V_{BE}} \right|$$

where V_{BE} is the value of the state variable derived from the "best estimates" simulation, and ΔV is the difference between that value and the value derived from the simulation with p varied from its best estimate. We calculated sensitivity coefficients for each relevant parameter at 10, 20, and 100 years for each of the three state variables, and for each group of pairs (increasing persistence, decreasing persistence), for a total of 18 separate rankings for each species. Within each group we ranked the input parameters according to their sensitivity parameters, and used Kendall's *W* (Siegel and Castellan 1988) to test for concordance among the rankings.

Additional simulations with the following characteristics were also run (Table 2): (1) no dispersal, (2) lognormal sampling of survival and fecundity, (3) no fires, (4) exponential growth, (5) *K* reduced by 50% over 100 years for all populations or (6) for populations on private tenure only or (7) for a random 30% of populations on private tenure and to 0 over 100 years for another random 30% of populations on private tenure.

Classic sensitivity analysis ignores interactions between parameters (which may lead to misleading conclusions if these are important), yet a full examination of all interactions between 11

Table 4 Input parameter ranges and stratification increments (uniform across range) used in the Latin Hypercube sampling sensitivity analysis, based on 25 parameter combinations

Parameter	Plausible range		
	Min	Max	Increment
Juvenile survival (φ_1,φ_2)	0.5 BE	1.5 BE	0.04
Adult survival (φ_3)	0.5 BE	1.5 BE	0.04
SD of survival (s_1,s_2,s_3)	0.5 BE	1.5 BE	0.04
Fecundity (*f*)	0.5 BE	1.5 BE	0.04
SD of fecundity (s_f)	0.5 BE	1.5 BE	0.04
K-N multiplier factor	0.75	1.75	0.04
Cool fire frequency	0	0.28	0.0112
Cool fire multiplier	1	0.6	0.016
Hot fire frequency	0	0.16	0.0064
Hot fire multiplier	0.8	0.2	0.224
Patch correlation	0%	100%	0.04

parameters adjusted from best estimates to upper and lower plausible bounds (i.e. three levels) would require $3^{11} = 177{,}147$ separate simulations. We therefore used a Latin Hypercube random sampling procedure (Iman and Conover 1980) to generate a stratified random subset of parameter input values for simulation, by assigning a plausible range to each of 11 relevant parameters (Table 4), and (arbitrarily) dividing the parameter space into 25 consecutive strata between the lower and upper bounds of the

relevant parameter range, with each stratum representing equal sized increments of the parameter space. For each of 25 simulations, we then randomly sampled a stratum, without replacement, for each parameter. The Latin Hypercube sampling procedure we have used is superior to classical Monte Carlo approaches because the whole parameter space gets covered in far fewer iterations (McKay et al. 1979).

We used multiple regression response-surface analysis to approximate the complex function that relates the model input parameters to the state variables, and to investigate the importance of interactions among parameters (McCarthy et al. 1995). We used multiple linear regression when mean patch occupancy or mean final N was the dependent variable, and transformed mean final N using a Box–Cox function (Box and Cox 1964) to normalise the data. Multiple logistic regression was used to model extinction probability because the dependent variable in this case is a binary outcome (extinct or not extinct).

For the multiple linear regressions, we used a backwards stepwise elimination procedure using the statistical package MINITAB v12.2 (Ryan et al. 1994) to eliminate unimportant parameters. For the multiple logistic regression procedures, Akaike's Information Criterion (AIC) was used as an objective means of model selection based on considerations of both predictive power and parsimony (see Burnham and Anderson 1998). The magnitude of the coefficient of the linear (MPO, MFN) and logistic (PE) regressions for a given input parameter reflects the effect of this parameter on the state variable and, when scaled by the level of uncertainty, can be interpreted as a sensitivity value (McCarthy et al. 1996).

Results and discussion

Best estimate model

The baseline (best estimate) models indicated that both species are in decline. Over a 20-year time frame about one third of the 65 extant *G. alba* populations are predicted to decline to local extinction. For *G. vitellina* the MPO after 20 years is 10.3, down from the current 11 extant populations. Over 100 years, the best estimates models predict MPO of just 12.1 for *G. alba* and 4.6 for *G. vitellina*. Current and predicted metapopulation structures for *G. alba* and *G. vitellina* are shown in Fig. 1 and 2, respectively.

The predicted rates of metapopulation decline over 20 years are supported by observational data. Twenty-three populations of *G. alba* have now been declared extinct in the 20 years since the species were discovered (Roberts et al. 1999). Many of these extinctions have been in relatively undisturbed sites. All of the 11 *G. vitellina* populations remain extant, although several have apparently declined in size. This rate of loss of populations is very similar to that observed in our simulations over a 20-year time frame, indicating that the models are robust.

Sensitivity analysis

The results of the classic and Latin Hypercube sensitivity analyses were in broad agreement. Juvenile survival rate (φ_1, φ_2) was consistently the most sensitive parameter for both species, followed by fecundity (f), standard deviation of survival (s_n) and adult survival (φ_3) (see
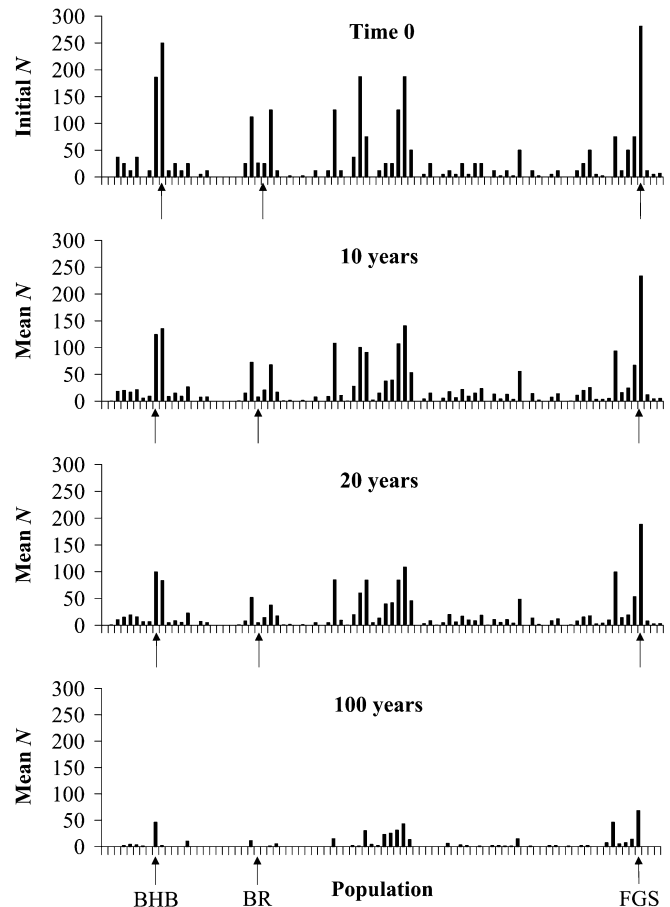

Fig. 1 Predicted metapopulation structure for *Geocrinia alba* at time 0, 10 years, 20 years, and 100 years, based on the best estimate model. Of the 88 known populations of *G. alba*, 65 were extant at time 0. None were successfully recolonised, although some were potentially connected to occupied populations by low-level migration. *BHB* Boathaugh B, *BR* Bruce Road, *FGS* Forest Grove South

mean ranks, Table 5). Further, the deterministic elasticities differed substantially between these parameters.

The Latin Hypercube sensitivity analysis results indicated no strong interactions between parameters. We found 20 years to be the most informative time-frame for analysis of MPO and MFN for both models, and for PE for the *G. vitellina* model. Within 20 years, PE was relatively invariant among simulations (i.e. zero) for the *G. alba* model, so for this model we analysed the results for 100 years. For both models and all state variables we examined plausible interactions among parameters and all were rejected in favour of a more simplified regression model.

The ranking of parameters according to the sensitivity of the models was robust. There was strong concordance among the 18 rankings from the classic sensitivity analyses for both *G. alba* (W = 0.866, df = 10, P < 0.001) and *G. vitellina* (W = 0.866, df = 10, P < 0.001) models over a 100-year projection. There was also considerable concordance in the key parameters identified using the Latin Hypercube sensitivity analysis. The stepwise linear regression analyses
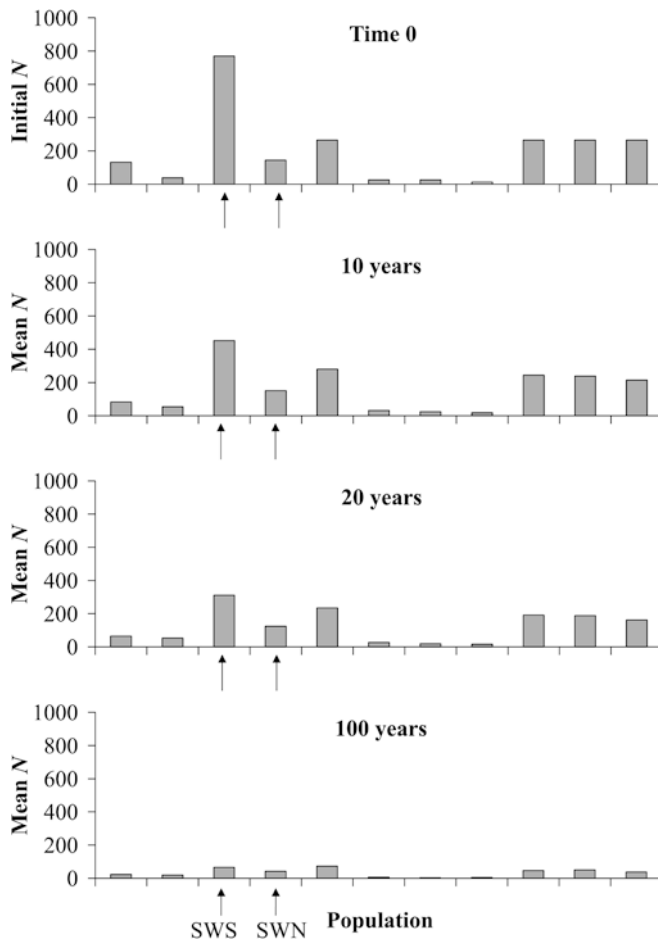
Fig. 2 Predicted metapopulation structure for *G. vitellina* at time 0, 10 years, 20 years, and 100 years, based on the best estimate model. *SWS* Spearwood South, *SWN* Spearwood North

for MPO and MFN and the logistic regression analysis of PE were in broad agreement for both *G. alba* and *G. vitellina* models (Table 6), and similarly agree with the simple sensitivity analysis.

On average, coefficients of sensitivity for juvenile survival were 1.6 times those for fecundity, and coefficients of sensitivity for fecundity were in turn about 1.6 times those for standard deviation of survival and adult survival. These four input parameters had consistently higher coefficients of sensitivity than other parameters (Table 5). Both species' models were also sensitive to increases in fire frequency, although less consistently so. Quasi-extinction risk curves (Ginzburg et al. 1982) for the *G. alba* (Fig. 3) and *G. vitellina* (Fig. 4) best estimate models, as well as models with juvenile survival, fecundity, adult survival, and standard deviation of survival varied to their lower and upper plausible bounds, and fire frequency at its upper bound, indicate the relative importance of these parameters to extinction vulnerability.

Decreases in mean juvenile survival and fecundity to their lower plausible bounds translated to almost 100% risk of extinction for both species within 100 years, while

a decrease in adult survival or an increase in standard deviation of survival translated into probabilities of extinction of 50–70%. Over the shorter projection length of 20 years, decreased juvenile survival translated into a 3.1% probability of extinction for *G. alba* and a 5.2% probability of extinction for *G. vitellina*. For *G. vitellina* a decrease in adult survival or fecundity, or an increase in fire frequency, all also led to low probabilities of extinction within 20 years. For *G. alba* varying other parameters to their plausible bounds did not increase the probability of extinction within 20 years above zero.

Both models were sensitive to the absence of fire, with MPO and MFN at 20 years increasing substantially and PE at 100 years decreasing. When carrying capacity was relaxed, MFN increased dramatically, as expected, but there was little change in PE or MPO, indicating that habitat area may limit the growth of a few large populations, but for the vast majority of populations, demographic processes predominate. A systematic decrease in carrying capacities also had a limited affect on PE, MPO, and MFN, further reinforcing this point. Simulations were insensitive to dispersal or sampling distribution.

Sensitivity of life history attributes

Metapopulation dynamics of the two anuran species were most sensitive to changes in juvenile survival, then to fecundity, and third to both adult survival and standard deviation of survival to about equal extent. In practical terms this indicates that a reduction in juvenile survival is more likely to lead to metapopulation declines than the same magnitude of reduction in fecundity or other less sensitive life history attributes. Large (though conceivable) decreases in mean juvenile survival or fecundity translated into predictions of almost certain extinction of both species within 100 years, compared with low probabilities of extinction for both species when all parameters were held at their best estimates.

The finding that juvenile survival is a key sensitive parameter in the long-term metapopulation dynamics of *G. alba* and *G. vitellina* is consistent with their overall life history pattern. Adults of these species are short-lived, and most mature individuals survive only one breeding season. They also have low fecundity, which precludes "boom" years of massive juvenile production, meaning population persistence depends on consistent and high levels of juvenile recruitment to the adult life stage. In accordance with these findings, the rates of survival recorded for juveniles of *G. alba* and *G. vitellina* in the field are among the highest observed for anuran species (Conroy 2001). However, the juvenile life stage is the longest phase for most individuals of these species (Conroy 2001), and it may also be the most vulnerable to the vagaries of the environment. As such, a decrease in juvenile survival is not only a theoretical threat, but a realistic one.

Table 5 Mean rank of the coefficients of sensitivity for each of the 11 input parameters of interest over 14 comparisons[a], and coefficients of sensitivity of probability of extinction (C_{PE}) within 100 years, mean patch occupancy (C_{MPO}) at 20 years, and mean final N (C_{MFN}) at 20 years. Input parameters were varied from their best estimates to either a higher ($+$) or lower ($-$) plausible bound. Because values of PE, MPO, and MFN from the best estimate model were all close to the lower end of their possible ranges, coefficients of sensitivity are provided for the direction of change which resulted in a movement of the state variables (PE, MPO, MFN) away from zero. This provides an estimate of each sensitivity coefficient that is not limited by zero. The direction of change in the input parameter is provided in parentheses. Ranks and coefficients of sensitivity in bold are those for the most important parameters

Parameter	Mean Rank[a]	C_{PE} (100 years)		C_{MPO} (20 years)		C_{MFN} (20 years)	
G. alba							
Juvenile survival	**1.0**	**(−)**	**54.500**	**(+)**	**4.570**	**(+)**	**12.399**
Adult survival	**3.4**	**(−)**	**27.889**	**(+)**	**1.702**	**(+)**	**3.214**
SD of survival	**3.3**	**(+)**	**27.222**	**(−)**	**1.868**	**(−)**	**3.632**
Fecundity	**1.9**	**(−)**	**51.667**	**(+)**	**2.702**	**(+)**	**6.260**
SD of fecundity	5.7	(+)	8.167	(−)	0.636	(−)	0.973
K multiplier	9.4	(−)	0.722	(+)	0.083	(+)	0.519
Cool fire multiplier	8.4	(+)	2.778	(−)	0.248	(−)	0.453
Hot fire multiplier	7.4	(+)	3.000	(−)	0.347	(−)	0.527
Fire frequency	6.0	(+)	23.778	(−)	0.322	(−)	0.540
Fire mix	9.1	(+)	1.667	(−)	0.248	(−)	0.364
Patch correlation	9.6	(+)	5.889	(−)	0.107	(−)	0.081
G. vitellina							
Juvenile survival	**1.0**	**(−)**	**7.621**	**(+)**	**0.612**	**(+)**	**0.961**
Adult survival	**3.8**	**(−)**	**5.043**	**(+)**	**0.097**	**(+)**	**0.476**
SD of survival	**3.7**	**(+)**	**4.707**	**(−)**	**0.136**	**(−)**	**0.447**
Fecundity	**1.8**	**(−)**	**7.569**	**(+)**	**0.272**	**(+)**	**0.828**
SD of fecundity	5.9	(+)	1.991	(−)	0.039	(−)	0.244
K multiplier	8.5	(−)	0.129	(+)	0.000	(+)	0.128
Cool fire multiplier	8.9	(+)	0.414	(−)	0.019	(−)	0.049
Hot fire multiplier	6.3	(+)	1.974	(−)	0.049	(−)	0.216
Fire frequency	**5.1**	**(+)**	**5.457**	**(−)**	**0.117**	**(−)**	**0.468**
Fire mix	9.3	(+)	0.517	(−)	0.010	(−)	0.006
Patch correlation	9.1	(+)	1.448	(−)	0.019	(−)	0.010

[a] Mean rank calculated without PE at 10 years and 20 years

Drivers of population declines

The population dynamics of amphibians have widely been regarded as being driven by embryonic and larval survival (Duellman 1985; Berven 1995; Alford and Richards 1999). This view of amphibian demographics reflects the dominance in the literature of species that oviposit in ponds and leave unattended eggs to develop into aquatic larvae [despite this being only one of a huge diversity of reproductive modes among the amphibians (Duellman 1985)]. In these fully aquatic breeders, pre-metamorphic vital rates can have a strong effect on population dynamics because they sometimes take on extremely high or low values (Caldwell 1987; Berven 1990; Pechmann et al. 1991): frequent years of low survival or reproductive failure are interspersed with occasional years of high juvenile production, resulting in "boom and bust" dynamics. However, while highly variable embryonic and larval survivorship may drive short-term, natural fluctuations in adult population sizes, there is little evidence that changes to these vital rates are important in determining long-term (meta-) population dynamics (Alford and Richards 1999).

Theoretical predictions suggest that less variable vital rates, like juvenile survival, are also likely to be the key determinants of the long-term population dynamics of species with "fast" (high fecundity, early maturation) life history patterns. Natural selection should act to limit variability in traits that have a large impact on fitness, so changes in highly variable vital rates (e.g., embryonic and larval survival) are less likely to influence long-term population dynamics. Biek et al. (2002) provided evidence for the importance of juvenile survival to the dynamics of highly fecund species that oviposit in ponds and leave unattended eggs to develop into aquatic larvae. Using population models and sensitivity analyses, they found that population growth rate was most highly sensitive to incremental changes in juvenile survival. Their results were consistent with ours, despite the sets of species in question being from the opposite end of the spectrum of amphibian reproductive modes.

The identification of juvenile survival as a key parameter in long-term population dynamics has important implications for our understanding of amphibian autecology. Estimates of survival during the juvenile life stage have been obtained for relatively few anurans—most such studies have focussed on the pre-metamorphic life stages. This has been forced in part by logistic considerations, and in part by the view of amphibian demographics as being driven by embryonic

Table 6 Coefficients for the multiple linear regression equations relating variation in mean patch occupancy (*MPO*) and mean final *N* (*MFN*) at 20 years, and the multiple logistic regression equation relating variation in probability of extinction (*PE*) at 20 years (*G. vitellina*) and at 100 years (*G. alba*), to key parameters in the Latin Hypercube sensitivity analysis for *G. alba* and *G. vitellina* populations. For the multiple linear regressions parameters were eliminated from the regression equation when their *F*-statistic was less than 4. For the multiple logistic regression AIC was used to identify the most parsimonious statistical model, given the log-likelihood and a penalty for the number of parameters used. Parameters are ranked according to their standardised regression coefficients [(Coeff·range)/max(Coeff·range)]

Dependant variable	Coeff	Std. Coeff	SD	Statistic	*P*
Predictor					
G. alba					
MPO at 20 years				*t*	
Juvenile survival	123.53	1.00	12.30	10.04	0.000
Fecundity	33.94	0.92	3.77	9.00	0.000
Adult survival	63.60	0.37	15.77	4.03	0.001
Hot fire frequency	−99.73	0.27	37.29	−2.67	0.019
MFN at 20 years				*t*	
Fecundity	0.70	1.00	0.08	8.34	0.000
Juvenile survival	2.33	0.99	0.28	8.48	0.000
Adult survival	1.35	0.41	0.35	3.82	0.002
Hot Fire frequency	−1.67	0.24	0.83	−2.00	0.067
K multiplier	0.70	1.00	0.08	8.34	0.000
PE at 100 years				*z*	
Fecundity	−14.76	1.00	0.34	−43.50	0.000
Juvenile survival	−47.21	0.96	1.02	−46.32	0.000
Hot fire frequency	61.49	0.42	1.36	45.25	0.000
Adult survival	−25.51	0.37	0.72	−35.67	0.000
SD of survival	28.02	0.21	1.57	17.83	0.000
G. vitellina					
MPO at 20 years				*t*	
Juvenile survival	18.26	1.00	2.78	6.58	0.000
Fecundity	4.47	0.95	0.75	5.99	0.000
Adult survival	16.01	0.63	3.43	4.67	0.000
Hot fire multiplier	5.75	0.41	1.91	3.01	0.010
Cool fire multiplier	−4.65	0.23	2.74	−1.70	0.113
MFN at 20 years				*t*	
Fecundity	1931.20	1.00	493.90	3.91	0.002
Adult survival	4702.00	0.45	2269.00	2.07	0.059
Juvenile survival	2761.00	0.37	1840.00	1.50	0.157
PE at 20 years				*z*	
Fecundity	−5.82	1.00	0.27	−21.59	0.000
Juvenile survival	−21.65	0.96	0.91	−23.77	0.000
Hot fire multiplier	−12.31	0.72	0.92	−13.41	0.000
Adult survival	−21.15	0.67	1.42	−14.89	0.000

and larval survival. However, this focus on pre-metamorphic life stages has almost certainly confounded our current perception of amphibian autecology, as well as our view of which mechanisms of decline represent the greatest threats to the persistence of amphibian species (Biek et al. 2002). Further, the importance of juvenile survival suggests that this vital rate is an important target for management intervention and intensive field studies. The most promising species for such studies are likely to be those displaying high levels of philopatry, because confidence that surviving individuals have some probability of recapture is a precursor to collecting longitudinal demographic data. High levels of genetic differentiation among populations may be a reliable indicator of philopatry.

Robustness of results

The sensitivity analysis suggests our results are likely to be robust to parameter uncertainty, because the most critically sensitive parameters are those for which we have the most detailed field data. For instance, estimates of adult survival rate were obtained from 7-year mark-recapture studies at several populations each of *G. alba* and *G. vitellina*; estimates of juvenile survival rates were obtained from mark recapture studies at six *G. alba* populations and three *G. vitellina* populations; and estimates of the other crucial components of fecundity—survival rates for eggs and tadpoles and clutch size—are based on a large number of nests from several populations over several years. Those parameters for which we had few empirical data (e.g., patch correlation and carrying capacity), were the least critical, since model outputs were shown to be insensitive to potential inaccuracies in these parameter estimates.

The strong concordance in the results of the simple and Latin Hypercube sensitivity analyses in this study provides further confidence in the results. The parameters identified as important were consistent among sensitivity techniques, and consistent with a priori predictions of whether population viability was expected to increase or decrease. Similarly, results from the different output metrics (PE, MPO, MFN) were largely concordant, which gives us confidence that our conclusions are not sensitive to how we describe and gauge metapopulation dynamics.
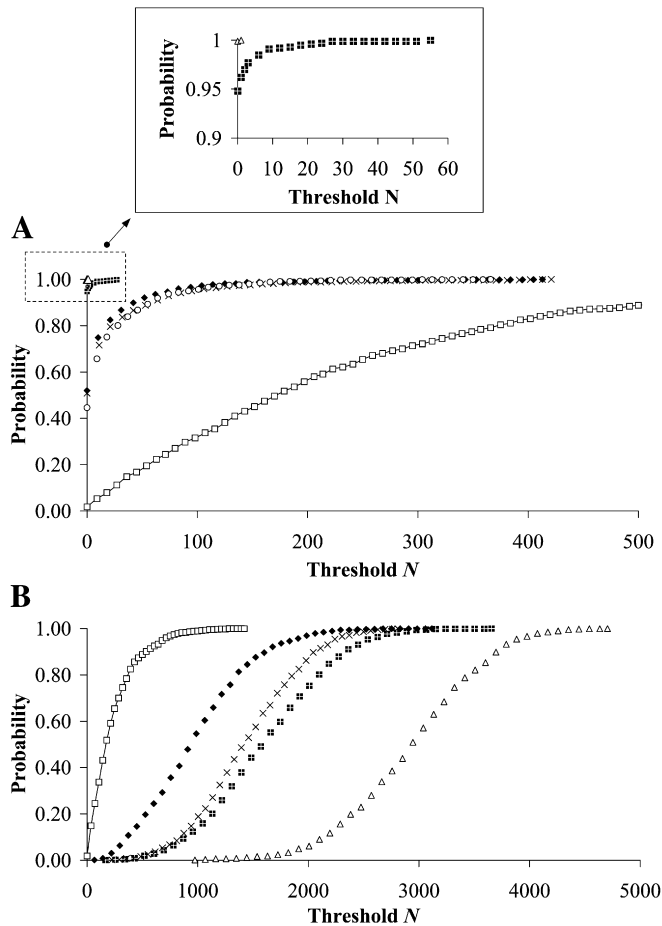
Fig. 3A, B Quasiextinction risk curves for the *G. alba* metapopulation model. The best estimate model is indicated by ——□——. **A** Models with juvenile survival (Δ), fecundity (■), and adult survival (◆) at their lower plausible bounds, and standard deviation of survival (x) and hot fire frequency (o) at their upper plausible bounds. **B** Models with juvenile survival (Δ), fecundity (■), and adult survival (◆) at their upper plausible bounds, and standard deviation of survival (x) at its lower plausible bound

Fig. 4A, B Quasiextinction curves for the *G. vitellina* metapopulation model. The best estimates model is indicated by ——□——. **A** Models with juvenile survival (Δ), fecundity (■), and adult survival (◆) at their lower plausible bounds, and standard deviation of survival (x) and hot fire frequency (o) at their upper plausible bounds. **B** Models with juvenile survival (Δ), fecundity (■), and adult survival (◆) at their upper plausible bounds, and standard deviation of survival (x) at its lower plausible bound

Future of *G. alba* and *G. vitellina*

The metapopulations of *G. alba* and *G. vitellina* are not likely to go extinct within the next century, but will probably undergo substantial range reductions, with local population extinctions and a concomitant loss of genetic variation (Frankham 1996). Driscoll (1998) argued that in the long term, *G. alba* and *G. vitellina* can be considered to have non-equilibrium metapopulations (Harrison 1991), undergoing a series of range expansions and contractions, perhaps driven by climatic fluctuations. It is therefore conceivable that the persistence of relatively few populations in the long term might ensure the survival of the two species, assuming that the next phase is an expansion rather than a contraction phase. However, the extensive historical land clearing in this region effectively precludes range expansion, such that the long-term survival of these anuran species probably depends largely on the persistence of their few remaining strongholds.
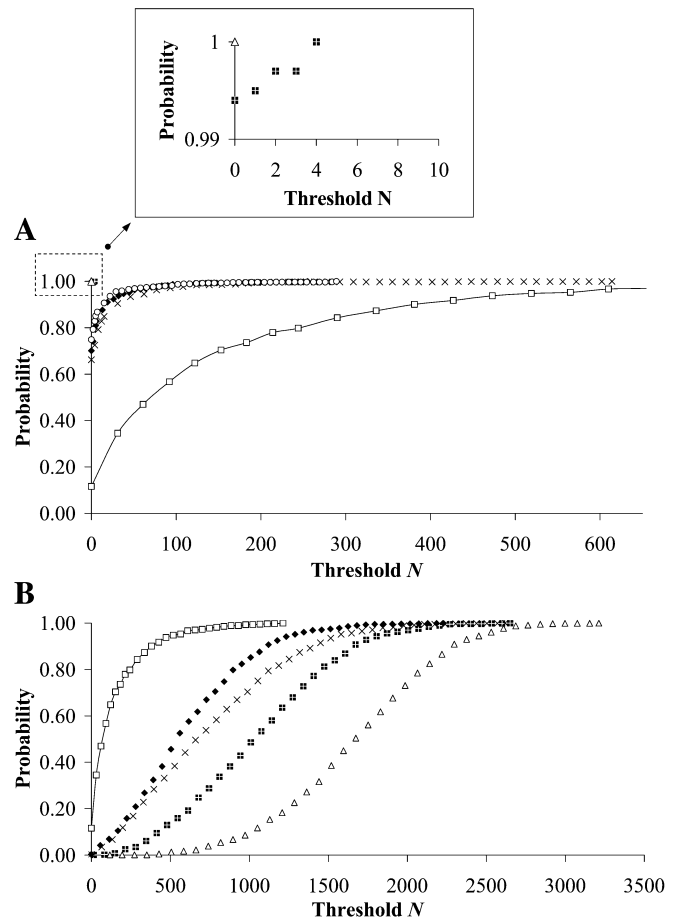
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